



HAL
open science

From Evolutionary Biology to Economics and Back

Jean-Baptiste André, Mikaël Cozic, Silvia de Monte, Jean Gayon, Philippe Huneman, Johannes Martens, Bernard Walliser

► **To cite this version:**

Jean-Baptiste André, Mikaël Cozic, Silvia de Monte, Jean Gayon, Philippe Huneman, et al.. From Evolutionary Biology to Economics and Back. Springer International Publishing, 28, 2023, History, Philosophy and Theory of the Life Sciences, 978-3-031-08790-5. 10.1007/978-3-031-08790-5. hal-03941484

HAL Id: hal-03941484

<https://hal.science/hal-03941484v1>

Submitted on 16 Jan 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

This book is dedicated to *Jean Gayon*,
struck down by illness during its writing

André Jean-Baptiste

Cozic Mikael

De Monte Silvia

Gayon Jean

Huneman Philippe

Martens Johannes

Walliser Bernard

From evolutionary biology to economics and back

Parallels and crossings between economics and evolution

Acknowledgements

This book is the completion of a collective adventure. Based on an initial idea of Silvia De Monte, who thought of writing a short dual lexicon of concepts in evolution and economics, and proposed it to all of us in the context of the ANR Project Evo Eco (Conceptual transfers between evolution and economics) that had just started, it grew up into a real philosophy book, after many sessions of discussion that the authors had undertaken about these concepts. It would not have been possible without the commitment, the energy and the creativity of Jean Gayon, who inspired us to never stop to question philosophically notions that were supposed to be well known. Unfortunately Jean left us in may 2018, and won't be there to see the result of this collaborative work. However, at the time he passed away the book was almost done in the form of a complete first draft and he contributed to the whole content and validated it. The last steps towards completion were technically small steps but, in these conditions, became a hard move to make. This book is dedicated to his enduring memory.

The authors thank : the ANR Evo Eco; the EUR FrontCog grant ANR-17-EURE-0017 and the Labex Who I Am.

Originally written partly in French and partly in English, the book benefitted from a thorough editing and translating job done by Anita Conrade, to whom we are all grateful.

Introduction.

P. Huneman

It has long been acknowledged that economics and evolutionary biology have a lot in common. Ever since Darwin borrowed Malthus's ideas about the scarcity of resources and geometric population growth, economic ways of thinking are known to have influenced biology. In the 1970s, the import of game theory, elaborated by economists, into evolutionary biology via behavioral ecology, by Maynard-Smith and Price, among others (Maynard-Smith and Price, 1973; Maynard-Smith 1982), is another well-known instance of this relationship. And in a canonical text of the Modern Synthesis, Fisher's *Genetical Theory of Natural Selection* (Fisher 1930), the author refers to basic economic notions, i.e. loans and investments, to define the key concept of fitness. Inversely, economists drew on schemes and concepts from evolutionary biology throughout the 20th century. Evolutionary economics, elaborated first by Nelson and Winter (1980), is an obvious example. One could also cite the acclimatation of evolutionary game theory within economics, as well as the various inflexions of the concept of rationality through confrontation with biological parameters, such as the idea of "ecological rationality" (Gigerenzer et al. 1999), an instance of the bounded rationality Herbert Simon described as a more realist alternative to neoclassical notions of rationality.

Transfers of concepts between economics and evolutionary biology are therefore pervasive, and any specialist in either discipline can point out a few. However, this is far from constituting an analysis of the conceptual interplay between the two fields. Granted, there are several historical analyses of the role played by key figures behind such transfers, starting with Darwin, Friedman, Hayek, Maynard-Smith, or others. There are also in-depth analyses of specific correspondences between concepts, such as fitness and utility in economics (Okasha 2007). But no systematic understanding of the economics/ evolutionary biology interplay is currently developed. This is the project of the present book.

This project stems from the realization that, as biologists and economists, and philosophers of biology or economics, we very often use the same words to name key concepts in both disciplines -- think of "strategy," "resources," or "competition." Sometimes, different terms seem to function in a similar way within theories or models. Let's think here of how utility and fitness both play similar or analogous roles in predicting states (choices, phenotypes, gene frequencies) on the basis of some sort of maximization principle (namely, natural selection or rationality).

Hence, as a small group of philosophers, biologists and economists, we began to consider a general investigation of these conceptual similarities. We developed several questions: what are the correspondences or similarities really made of? Is the parallelism between the use of two notions merely formal, in their own formal settings? Are the concepts ever identical? What exactly does it mean when the same word is used in both fields - e.g. "competition," or "market"? Is the concept really the same? Beyond that, if there is a conceptual core of commonality between the two sciences, what is it? Does it bind economics to evolutionary biology, or subsets of one and the other? Or might deeper analysis reveal that identical terms do not indicate completely identical concepts?

One consequence of these questions is that focusing on concepts that appear to be shared by the two fields may highlight differences that have been overlooked, merely because the same words are used. As a result, the nature of the difference between those sciences comes into question.

But what do such commonalities mean, finally? If there are so many possible transfers between evolutionary biology and economics, if indeed those transfers fueled the progress of both sciences, could it be the case that economics and evolutionary biology are the same sciences? Or, more precisely, are they two branches of the same general science, the nature of which should be further defined? Given Darwin's original reference to competition for rare resources, and the pervasiveness of the notions of optimality in both fields, one could for example hypothesize that this broad, general discipline to which biology and economics both belong is a science of the optimal allocation of rare resources. This is wholly hypothetical, and our project ultimately aims at providing elements to formulate this question.

Put in such terms, the project almost prescribes its modus operandi. Because it is a general investigation of a conceptual space, focused on shared terms or concepts, the idea emerged that it should be organized around a detailed analysis of the use of some of those key concepts in both sciences. We therefore assembled a set of 25 concepts that are obviously present in both fields, as attested by textbooks, handbooks, or just major historical works. As a result, the core of this book resembles a sort of lexicon. However, each concept is presented twice, once in its biological context, according to evolutionary biologists' usage, and once in its economic context.

We agreed to keep the presentations short, and to focus on what could be seen as uncontroversial and essential - essential in the sense that, if there are any theoretical controversies involving the concept at stake, the controversies still involve a kernel of accepted truths about it, a kernel we intended to describe. Next, we discuss some of the key debates that have arisen, or that are still going on, in the field, to the extent that these debates play a structuring role.

Keeping the entries short – despite the fact that any of the concepts could justify a whole book (“competition” in evolutionary biology, “market” in various economics theories, etc.), and trying to pry the kernel free of the various philosophical or theoretical choices we might be inclined to make, are in themselves fruitful exercises. Moreover, focusing on a single concept forces us to make our knowledge of the concept as clear as possible, as opposed to simply *using* the concept, which does not require a rigorous definition of what the concept means. For example, fitness can be measured, and the best ways to measure it can be discussed, without any clear statement of what fitness is. Likewise, one can study the impact of innovations in economics without having to state the meaning of “innovation.” This is especially salient with *operational* concepts such as “strategies” or “investments,” in biology. Namely, these concepts that are pervasively used within the model, but whose interpretation doesn’t usually seem to convey major theoretical options. As a result, their proper definition is often omitted. Either researchers are confident that everyone in the field understands the word the same way, or they are relying on a common formalism, the understanding of which is ensured by the fact that researchers share a common training.

Thus, although biologists may not learn much from reading the “biology” entry about a given concept, and inversely, both entries were conceived of as two parts of a single examination. The “biology” entry serves to remind the biologist of a few things when she reads the “economics” entry, so that she can capture what goes on with this concept across the two fields. We hope that this text could also be of use to students in each of these fields. There exist excellent handbooks of philosophy of biology - e.g. Rosenberg and Mc Shea (2007) or Sterelny and Griffiths (1999) -, where one can be introduced to the discipline, and this book doesn’t pursue such an aim: its dual focus is essential to the project. Certain biology students may be intrigued by the economic flavor of some of the concepts they are learning to use (and vice-versa, for students of economics), and eager to know more about the similarities. Likewise, because this book is not a set of monographs on each concept, we don’t give many bibliographical references. The entries are supposed to be read in relation to each other, and secondly in relation to the other concepts in the book.

Finally, each of the concepts gives rise to a “synthesis,” following the entries for each discipline. We kept this synthesis separate; first, because we want to leave the reader free to make her own synthesis after having read the two entries; and second, because we make theoretical choices in analyzing the commonalities between the two versions of a concept. Those choices are additional to the exposition of the concept in the context of each field, and may be in turn discussed.

The book stemmed from seminar sessions devoted to each of the concepts. Regularly, the authors met and discussed a dual entry written by two of them about one concept. It was later revised. Once all of the dual entries had been composed, the authors of each entry wrote the

synthesis together. As a result, this is a collective work, even though each single entry was written by only one of us.

The core of the book, the twenty-five entries, may seem like a lexicon - and to some extent, it is. But there are two major differences. It's a "dual lexicon," so to speak: each entry from either field was conceived in relation to its companion entry, and with the intent to reach a synthesis - the synthesis being, in turn, part of our investigation of the general interplay between the sciences. The book is a study of this interplay, in the form of a list of entries. As a consequence, the relationships between the entries are crucial, since they are precisely what allows us to map the interplay, to guide further inquiry.

Two more words should be said about the *modus operandi*.

First, we decided that this systematic investigation should be, if not ahistorical, at least not in principle historical. We are perfectly conscious that the current state of economics and evolutionary biology, and the many commonalities, similarities, transfers, etc., that we discuss are the result of 150 years of history - with all the consequences regarding contingency, cultural traditions, personalities, etc. Yet, even if the study of a concept, from the dual viewpoint, or of a subfield (for instance "game theory") could legitimately proceed from a historical perspective - and maybe that would be the clearest way to go - , the systematic investigation of the interplay, ranging through many concepts whose meaning and use have different histories, could not usefully proceed that way. Thus, we start from the current state of both fields. We use textbooks and current literature, especially to outline the structure of ongoing controversies. We mention key texts or works that introduced a concept in the field, but there is no requirement that the historical information be exhaustive. Nor is there any obligation to provide a historical understanding of the evolution of all notions, or parallels evolutions of the field. The book is understood rather as a comprehensive survey of the field as it is now practiced by scholars, who often do not investigate a second field, even though their own discipline borrows or mirrors concepts from that other field.

Second, the choice of the concepts constituting the 25 entries obeyed simple principles. Above all, we sought terms that were regularly used in both fields. Some of them, in one field or another or both, undergo a thorough theoretical elaboration or explicit consideration (e.g., "utility" or "cycles" in economics, "fitness" or "altruism" in evolutionary biology). Others do not, because they are mostly operational, and pervasively used in modeling and theorizing (e.g., "resource" or "trade-off" in economics, "optimality" or "investment" in evolutionary biology). Their theoretical weight did not play a role in the choice. The common use of the same word ("competition," "market," "cooperation," "strategy") was, of course, a reason to consider these concepts. However, we required that in each field, the concept be of widespread use, which is often not strongly the case. For instance, although economists

sometimes mention populations, “population” is not as crucial to economics as it is to evolutionary biology, where one of the specificities of the field has even been termed “population thinking” by Ernst Mayr (among others); economists apply the term “population” basically in the vernacular sense. In the end, concepts that are almost never used in a specific way in one field, even if important in the other, were disqualified.

Second, we looked at concepts that may be named by non-overlapping (sets of) words in both fields, but whose definition and role in the sciences clearly match. Often, the correspondence between them has given rise to a subfield that explicitly relies on the analogies between evolution and economics, namely evolutionary economics and evolutionary game theory. Hence, *utility* corresponds obviously to *fitness*, *innovation* and *mutation* correspond, and the notion of *growth* in economics parallels not only *growth* in evolutionary biology, but also *development*. That is why some entries are pairs of words. In the latter case, the text clarifies why the words do not exactly coincide. But sometimes the overlap proves to be partial. For example, *learning* is a crucial concept to both economics and evolution, but *learning* in economics also corresponds to *adaptation* in evolution, whereas *adaptation* evolutionarily speaking differs from biological *learning*, the latter being an individual process, while the former - genetic or evolutionary *adaptation*, as it is sometimes specified - is a population-level concept describing a generations-long process.

It turns out that many of these dualities are related to the correspondence between *selection* in biology and *rationality* in economics, which are key concepts in both fields. In his game theory book, Maynard Smith already identified selection and equilibrium in rational agents playing games (Maynard-Smith 1982). But this parallel, often noticed, commented upon, and analyzed by philosophers (e.g., Sober 1989, Okasha, 2007, 2018, Khalil , Martens, 2014, Huneman and Martens, 2017, Schulz 2020) is not the whole story. In fact, one of the motivations for this book emerged while we were carrying out this investigatory work. We realized that not all the dualities and the conceptual transfers are emanations or consequences of such a parallel. Moreover, we discovered that the precise details of the parallel are not obvious - even though it's quite easy to translate particular rationality models as maximizing models into selection-driven optimality models of behavioral ecology. But conceptual transfers and relations occur at another level than models, and that is precisely what this book intends to highlight and explore.

However, it turns out that there is no entry on *rationality*. While *natural selection* can indeed be a concept used in economics too, rationality itself is mainly a concept intrinsic to economics, and the “selection / rationality” parallel differs in type from the parallels between homonymous concepts (like *competition*) or concepts whose parallelism can be easily inferred from their isomorphic uses (like *innovation* in economics and *mutation* in biology). Rather, the parallel between selection and rationality is only understandable after a thorough

examination of the semantic correspondences between concepts, according to the *modus operandi* in the present work. The parallel is touched upon to some extent in the afterword to this book.

Thus the 25 paired concepts that we present here are those we see as key thematic or operational notions in both fields today, despite the fact that they may have entered the fields at different times. For instance, a concept like *strategy* in evolutionary biology dates from the emergence of evolutionary game theory. Likewise, the concept of “ecological market” in evolutionary biology is quite recent, while the term *market* is contemporary to the earliest studies of economics. Finally, we could have grouped the concepts in the following way:

- concepts that are mainly *individual-centered*: fitness/utility; altruism; constraint/trade-off; resource/ investment; adaptation/ learning; mutation/ innovation;
- concepts that concern *inter-individual actions*: heredity/transmission; strategic interactions; communication/signaling; cooperation; competition; selection;
- concepts operating at the *supra-individual level*: market, equilibrium; development/growth; cycles; crisis; optimality;
- *transversal* concepts: organizational levels; time scales; population; information; chance/uncertainty; diversity; classification;

This classification system is chiefly pragmatic. Other groupings are possible, and we do not endow this specific one with more virtues than it has. Above all, we make no claim that it is the best way to structure the interplay between economics and evolutionary biology. The reader is invited to think of the set of keywords in terms of this grouping; but since we don't see it as mandatory, in the following we used the more neutral alphabetic ranking.

References

- Fisher R.A. (1930): *The Genetical Theory of Natural Selection*, The Clarendon Press, Oxford
- Gigerenzer, G; Todd, PM.; The ABC Research Group (eds.). 1999 *Ecological Rationality: Intelligence in the World*. New York: Oxford University Press.
- Huneman, P., Martens, J. (2017). The behavioural ecology of irrational behaviours. *History and philosophy of the life sciences*, 39(3), 23.
- Kacelnik, A. (2006). Meanings of rationality. In S. L. Hurley & M. Nudds (Eds.), *Rational animals* (pp. 87–106). Oxford: Oxford University Press.
- Khalil E. 2010. "Are Plants Rational?", *Biological Theory*, 5, 1: 53–66
- Martens, J. 2011. “Social evolution and strategic thinking”. *Biology and Philosophy* 26 (5):697-715
- Maynard-Smith, J. (1982) *Evolution and the Theory of Games*, Cambridge University Press.

- Maynard-Smith, J., Price, G. R. (1973). "The logic of animal conflict". *Nature*, 246(5427), 15-18.
- Nelson, R. Winter, S. (1982). *An Evolutionary Theory of Economic Change*. Cambridge (Mass.): Belknap Press of Harvard University Press.
- Okasha, S (2007). Rational Choice, Risk Aversion, And Evolution. *Journal of Philosophy* 104 (5):217-235.
- Okasha, S. (2018). *Agents and Goals in Evolution*. Oxford: Oxford University Press.
- Rosenberg, A, McShea, D W. (2007). *Philosophy of Biology: A Contemporary Introduction*. Routledge.
- Sculz A. (2020) *Structure, Evidence, and Heuristic: Evolutionary Biology, Economics, and the Philosophy of Their Relationship*. New York: Routledge.
- Sober, E (1998). Three differences between deliberation and evolution. in Peter Danielson (ed.), *Modeling Rationality, Morality, and Evolution*. New-York: Oxford University Press.
- Sterelny K, Griffiths P (1999) *Sex and death: an introduction to the philosophy of biology*. Chicago: University of Chicago Press.

Preliminary reflections.

Analogical reasoning between economics and biology

B. Walliser

In the current scientific vocabulary of economics and biology, it is easy to find common concepts which are used with similar interpretations. In both fields, *resources* are consumed, *information* is exchanged, and *externalities* are produced. *Altruism* is shown, *competition* is faced, and *cooperation* may ensue. States of *equilibrium* are reached, *cycles* are described, and *crisis* may occur. Moreover, concepts with different names can be considered as analogous to each other. For example, the selection of biological organisms is governed by *fitness*, while the behavior of economic agents is driven by *utility*. Biological evolution is induced by *mutations*, while economic change is conditioned by *innovations*.

This introduction specifies the nature of such analogies, especially when applied to models. A basic taxonomy distinguishes three types: a given model that can be applied to instances of a same field (integral analogy); two models with same structure and similar interpretations in two different fields (substantial analogy); and two models that are just similar in structure (formal analogy). This chapter discusses the nature of analogies (§1), the depth of analogies (§2) and the use of analogies (§3). After a brief history of popular analogies between economics and biology (§4), some examples of scientific analogies between both disciplines are given (§5 to 7). Finally, the significance of Universal Darwinism is examined (§8) and a conclusion presents the content of the book (§9).

Nature of analogies

An analogy first asserts the similarity of some object with another one, according to selected features (Walliser, Zwirn and Zwirn, 2021). Such an “analogical assessment” has a more or less extended scope depending on the features concerned. A “notional analogy” is restricted to a set of properties between two objects, and states that “a is like b.” A “relational analogy” concerns a relation shared by two objects between corresponding properties and states that “a is to b what a’ is to b’.” A “structural analogy” deals with a more complete structure common to the objects and states that “a model of a is analog to a model of b.” For scientific models, an analogy is “external” when a model is compared to another belonging to the same discipline. An analogy is “internal” when a model is compared to another belonging to a sub-discipline.

Biology and economics have more and more in common a high degree of formalization, which facilitates their comparison. Historically, both disciplines initially considered physics as the most complete science, and mimicked its reasoning by formal models. Any model can be characterized by three essential epistemological features. The “formal structure” concerns the logico-mathematical language in which it is expressed: usually, a system of relations between variables. The “field” defines the material domain to which it applies, each variable being related with some concept, measurable or not. The “interpretation” is a literary sense given to the links between concepts, as enacted by the relations (implicit causality, hidden variables).

An analogical assessment states then that two models present similar features, on the basis of a well-defined notion of similarity. According to the preceding characteristics of a model, three types of analogies, less and less demanding, can be defined. An “integral analogy” is obtained when two models not only have equivalent structure and comparable interpretation, but apply to the same general field. A “substantial analogy” is at work when two models have an equivalent structure, and share close interpretations, even though they apply to different fields. A “formal analogy” occurs when two models have equivalent structures, but differ regarding both their fields and their interpretations.

The three types of analogies can be illustrated within the field of classical physics. The universal attraction observed between sun and planets (planetary motion) is integrally analogous to the attraction between Earth and a body (freefall). The same concepts are used (force, mass, distance), and Newton’s law applies in both cases. A hydraulic circuit is substantially analogous to an electrical circuit. In this case, the concepts are only corresponding (water depth vs voltage, water flow vs electric current) but the relationships between them are identical in structure and interpretation. Thirdly, the probability law of the life span of a radioactive particle is formally analogous to that of an electronic component. In both cases, the law is exponential, but the underlying processes are quite different.

Depth of analogies

Analogies are defined according to both the similarity and the dissimilarity of the properties associated with two models. The nature of the analogies is the first clue as to the depth of an analogical assertion. Deeper analogies concern a greater number of characteristics of the models from among the three basic types. But this notion of depth can be specified even further, by assessing the substantial aspects of the models as well as the formal ones. For each aspect, there is a general hierarchy of models in which they are more and more differentiated by various criteria and sub-criteria. Any two models can then be compared by their “distance” from each other in the hierarchy.

As concerns the semantic aspect, the similarity qualifies the “general ontology of concepts” that models convey when they become more precisely instantiated. They are first distinguished by the type of entities involved, defined by a set of structural properties. They are further distinguished by the type of processes they follow, defined by a set of temporal properties. They are finally distinguished by more accurate modalities of entities and processes, especially their localization or date. In practice, various ontological hierarchies have been built in order to classify either very general systems or more specialized ones (technological systems). Two models are considered to be the same for properties above their level of ontological similarity and to be different beneath this level.

As concerns the formal aspect, the similarity qualifies the logico-mathematical structure that models adopt when they become more and more specific. They are first distinguished by the functional form of their relations (convexity, temporal delays). They are further distinguished by the form they adopt when relations are completely defined but with free parameters. They are finally defined by the value of the parameters which are included in each relation. In practice, a structural hierarchy is easy to build, especially when the overall class of “dynamical systems” (either random or deterministic) is considered. Two models are considered to be the same for features above their level of formal similarity and different beneath this level.

It follows that two models may always be considered as similar, either substantially or formally, at some sufficient degree of generality. Ideally, it is tempting to build a scale expressing a degree of analogy between two models, on a qualitative or even quantitative basis. But a measure of similarity this precise and unequivocal is unattainable. Firstly, although the structure and field of two models can be compared, their literary interpretations are more difficult to assess. Secondly, unlike formal hierarchies, many different ontological hierarchies are available. Thirdly, the different points of view characterizing models are not easy to aggregate into a single index.

Use of analogies

All applications of an analogical assessment, in popular thinking as well as in scientific thought, are based on an “analogical inference.” It assumes that if two phenomena in different fields are similar, other phenomena which are respectively correlated to them should be similar too. However, this mode of reasoning is nothing other than an induction drawn from a single case. Like for any induction, its validity is problematic, because its amplifying character cannot be logically justified. To be sure, such a mode of reasoning is defeated when new (contradictory) information comes in. In practice, analogical reasoning is used either heuristically, especially in science, or rhetorically, especially in common thinking.

In its heuristic use, analogical reasoning aims at transferring some properties from one field to another when other properties remain fixed. Such a reasoning device is useful in the

context of discovery, in that it helps suggest new assumptions. But it is not valid in the context of proof, since the new assumptions still need to be tested, like any assumption obtained by other means. Practically, substantial analogies are the most interesting and fertile, since they suggest new ideas for underlying mechanisms. Formal analogies merely state that some formally identical phenomena may be attributed to identical factors. Integral analogies contribute only to delineating the field of some model.

In its rhetorical use, analogical reasoning advocates for new ideas by presenting already accepted ideas. It seeks a didactic goal when it clarifies and sustains an original idea for an audience unfamiliar with it, especially students. It seeks an argumentative goal when it tries to convince a skeptical audience of the truth of a recently updated unconventional idea. In practice, substantial analogies are again the most efficient through the images they convey. Formal analogies make pedagogical shortcuts possible, since they state that formal consequences of analogous models are also analogous. Integral analogies are able to convince that different phenomena may adopt the same model even in the same field.

Often, when progressively developed, analogies undergo a drastic change in nature. At the start, a formal analogy simply acknowledges that a same logico-mathematical structure may apply to two different fields. However, such an analogy may be the sign of a more substantial analogy which asserts true similarities of mechanisms in the two fields. Conversely, a substantial analogy may be suggested by an apparent similarity between processes assumed in two fields. But a deeper examination may show that this similarity is only superficial, and reduces finally to an abstract link between concepts, namely a formal analogy.

Analogies between biology and economics

Since its origin, economics has considered some rough analogies with biology, with the converse movement being more limited. Mandeville (1714), in his famous "fable of the bees," asserted that "private vices may create public benefits." Malthus (1798) emphasized the constant human struggle for existence. He influenced Darwin, while Marx (1867) rejected Darwin for his gradualist point of view. Marshall (1890), influenced by Spencer, insisted on the division of labor in production, as already noted by Smith (1776). Finally, for his critique of marginalism as too hedonistic and equilibrist, Veblen (1899) drew inspiration from Darwin.

In the 20th century, analogies became deeper, even if they did remain fairly qualitative. Schumpeter (1912) was the first to promote the idea of a cumulative development of industry, attributing a driving role to managers. Alchian (1950) and Friedman (1953) compared the natural selection of the best-adapted organisms to the market selection of optimizing firms. Hayek (1973) insisted on the spontaneous emergence of institutions adapted to economic life, following a group selection process. Nelson and Winter (1982) proposed a more ambitious

theory of the development of firms and industries, directly inspired by Darwinian theory (see §6).

More recently, with the spread of formal models, analogies became more difficult. On the one hand, internal analogies are now common practice. In biology, an analogy soon operated between natural selection and artificial selection of species. In economics, the compelling analogy between learning and evolution was recognized, as concerns the dynamics of agents' behavior. On the other hand, external analogies are proposed in both ways. From biology to economics, Fisher (1922) indicated that evolution of stochastic populations obeys similar phenomena for organisms and for humans (drift). From economics to biology, Nash (1951) observed that an equilibrium state can take place between animals as well as humans.

In fact, game theory constitutes a platform for generating analogies between biology and economics (von Neumann-Morgenstern, 1944). Game theory is the ideal ontological framework applicable to both disciplines. It was created in order to provide economics with a general language for characterizing strategic interactions when they are involved at some generic level. The entities are "agents" endowed with a simple rational behavior which consists in computing actions. Interactions between entities are reduced to mutual (informational and operational) actions, but are more sophisticated. The same framework applies to biology by assuming that organisms act as if they were computing their actions.

Integral analogies

An integral analogy is at work when economic phenomena appear merely to be the extension of a new field of true biological phenomena. Such an analogy is well summarized in its consequences by the "principle of continuity" (Witt, 2008). This principle simply asserts that biology imposes fundamental constraints on the functioning of the socio-economic system. In particular, cultural evolution continues biological evolution and takes place inside the framework imposed by biological evolution. These exogenous and exclusive biological constraints are defined upstream of the development of the economic system, which then appears to be autonomous.

Of course, economic agents are true biological organisms or entities. They are endowed with classical biological properties, which are more or less integrated, individually or on average, in economic analysis. They have a more or less extended life span during which they proceed to changing activities. For instance, the "overlapping generations model" (Samuelson, 1958) considers that each agent lives two periods, one where he learns without producing and one where he produces without learning. Furthermore, agents' varying fertility rates condition their reproduction rate and are influenced by economic conditions.

But the agent's behavior is itself mainly considered with regard to biological evolution. This behavior is indeed assumed to result from a normal process of natural selection. Agents' preferences are at first designed by evolution, aimed at their long-term interest. For instance, altruistic preferences may have been selected gradually (Bergstrom, 2002). Agents' beliefs are further structured by evolution, in order to ensure their survival, as assumed by "evolutionary epistemology" (Popper, 1976). Even more precisely, natural selection may have structured probabilistic beliefs (and the rules for their revision) as well as expected utility preferences (Robson-Samuels, 2011). Finally, global rationality of behavior may itself have appeared by natural selection, due to its efficiency.

Finally, the development of the socio-economic system takes place in complete symbiosis with the biosphere. The biological environment provides many natural resources, devoted to feeding (plants, animals) as well as to energy (biofuel) or construction material (wood). It imposes some drastic conditions which have an impact on our health (unsanitary zones) or our well-being (national parks). Conversely, economic activity contributes to the renewal of the environment in some primordial aspects (reforestation, repopulation). But, at the same time, it is responsible for the degradation of our planet by the growing accumulation of aerial particles and toxic waste.

Substantial analogies

A substantial analogy exists when a biological model and its interpretation are transposed to the field of economics, or vice versa. The concepts from each field are first linked along "bridge principles." They do not refer to the same domain of reality, but have similar interpretations in qualitative terms. The models exhibit analogous concepts that are sufficiently similar in structure. Above all, their interpretation is the same as concerns the underlying mechanisms. In practice, such an analogy may be only partial, because some concepts lack a counterpart and some relations are only vaguely similar.

Some analogies concern the behavior of basic entities (organisms, agents) in relation to their natural or social environment. They refer to decision theory or to game theory, hence proceed from economics to biology. For instance, confronted by a random environment, pigeons and rats seem to adopt the same behavior as humans, based on the model of maximization of expected utility (Battalio et al., 1985). When fighting for a common resource, two different animal profiles (aggressive, passive) induce the same utilities and define the same type of equilibrium as husband and wife choosing to go together or not to some entertainment, caricatured as the "battle of sexes."

Other analogies concern the way by which heterogeneous entities are coordinated into overall organizations (organisms, firms). They refer to the structure of cells or of organisms, hence proceed from biology to economics. For instance, the production system of a firm works by

an information network traveling bottom-up, from the operating organs to the management, and a decision network going top-down, the other way around, according to the same scheme as an animal locomotion system. Bilateral exchanges of services between animals from two different species, considered to be mutually favorable, resemble spontaneous barter exchanges of various products between sellers and buyers.

Finally, some analogies compare the mode of development of different entities. They are suggested in both ways between economics and biology. Nelson and Winter (1982) consider that a firm implements different sorts of "routines" (productive routines, search routines), comparable to genes. These routines are revised either by autonomous research or by imitation of innovations (on products or techniques), comparable to mutations. Likewise, adaptation to pressure from competition governs the firm or industry: its population development, size, specialization in certain products, or orientation towards some regions, just as adaptation to pressure from competition affects the population of a species.

Formal analogies

A formal analogy means that the same mathematical structure is used in economics and in biology to represent specific phenomena. These phenomena produce the same formal consequences, which can be verified by the modeler in order to strengthen the analogy. But no similarity between the underlying processes is assumed in order to justify it, especially as concerns the causality between the respective variables. However, it is clear that similar mechanisms can be formalized by equivalent formal models, even if the formally equivalent models are not necessarily identical. Hence, if few mechanisms are compatible with some models, the formal equivalence of models may reflect similar underlying processes.

In the simplest way, the evolution through time of two variables taken in different fields may be simultaneously linear, exponential, or cyclical, with corresponding properties. In the cyclical case, the same four formal explanations of a cycle are available whatever the domain (temporal delay of order 2, non linearity, cyclical exogenous factor, random external shock). Likewise, the relation between two magnitudes taken respectively from biology and economics may be either linear or nonlinear. In the latter case, the reasons for non-linearity are numerous and heterogeneous, but non-linearity always induces the same consequences, i.e., some instability and unpredictability of the system.

More complex formulations of processes have been transferred from one discipline to the other. For instance, in biology, the "replicator formula" expresses the rate of evolution of the number of entities of some sub-population as a function of its fitness. In economics, it expresses the probability for an agent to use some strategy as a function of its improved utility. Likewise, the predator-prey model represents in biology the evolution of the number of rabbits and foxes in an ecosystem, under the assumption that the second are the predators of

the first, and that they reproduce spontaneously. In form, it is analogous to Goodwin's macroeconomic model, of very different inspiration (see CYCLES).

More generally, driven by game theory, some global models are used in both disciplines. The proportional reinforcement learning model asserts that any player chooses, at each period, some action with a probability which is proportional to the total utility brought by that action in the past. This model is formally equivalent to the replicator model in biology, when fitness is replaced by utility. Likewise, an evolutionary stable equilibrium expresses the stability of a population of biological entities when introducing mutant entities in this population. Such an equilibrium state is just a weakening of a strict Nash equilibrium, a situation where no player has anything to gain by moving, if the others do not move.

Universal Darwinism

The most commonly used model for analogy in economics and more generally in social sciences is the neo-Darwinian model of evolution, based on three principles which operate at three organizational levels, respectively (see Rosenberg, 2000). Variation consists in abrupt changes happening at the infra-individual level of genes. It deals with mutations and recombinations assumed to be random and blind. Transmission consists in the inheritance of traits at the level of organisms. It mainly results from sexual reproduction, which implies a similarity from parents to children. Selection consists in sorting out operations at the supra-individual level of populations. It is determined by the survival conditions of organisms in their natural environment.

A first conception makes use of the Darwinian trilogy as a pure formal analogy that captures some social phenomena. As an intermediary tool, evolutionary game theory adapts some biological models to game theory and transfers them to evolutionary economics. New strategies for the player are comparable to variation. They are randomly generated and used when the traditional ones produce poor results. The fact that each player survives for a long period and keeps in mind all his past experiences, eventually transmitted to others, is comparable to transmission. Lastly, players are selected based closely on the utility derived from their past interactions, without making the underlying process explicit, and this is comparable to Darwinian selection.

A second conception makes use of the Darwinian trilogy as a substantial analogy, with a clear examination of possible distortions in its interpretation. Distortions occur when the analogy is applied to firms and other organizations, and departs significantly from the biological model. Variation is carried out by technological and organizational innovations, which are directed by deliberate research processes, instead of being blind and random. Transmission is not ensured by successive generations, but by simple perpetuation of firms, which are moreover

subject to merger and fission. Selection results from the comparison of short term profits of firms, which differ profoundly from their long term capacity to survive.

However, “Universal Darwinism” (Dawkins, 1983; Dennet, 1995) has even larger ambitions. It involves a unique discipline combining biology and social sciences, elevating neo-Darwinism to the level of an integral analogy. It assumes that the same phenomena apply everywhere, in structure as well as content. Such an assertion can only be sustained by gross generalization which erases all the details of a phenomenon. At this level, an analogical assertion can only concern generic laws such as “innovations appear continuously,” and “individuals survive by their skills.” Analogical reasoning inevitably loses its fruitfulness, since it no longer allows for the transfer of specific and testable properties.

Field origin of studied analogies

This book aims to examine and evaluate the main analogies between biology and economics. As concerns economics, it covers two general levels of the field. One of these is classical economics, and the study of such phenomena as production, distribution and consumption. This field includes microeconomics, for which agents are identified as individuals, and macroeconomics, which works on aggregates. The second subfield, standard game theory, studies strategic interactions between non-specialized players. As concerns biology, it is considered only at the empirical level of cells or organisms. Although classical game theory may also be active in biology, it is essentially for modeling purposes.

However, a lot of analogies we point out belong to the evolutionary branches of each discipline. Evolutionary economics is concerned with the long-term development of industry and trade. Evolutionary game theory is concerned with players with bounded rationality who adapt through time. Evolutionary biology considers the evolution of species according to the neo-Darwinian theory. Some analogies are nevertheless related to the classical branches of the corresponding disciplines. It can be noted that evolutionary biology is more developed than evolutionary economics, unlike their classical counterparts. Hence, classical analogies go mainly from economics to biology while evolutionary analogies go mainly from biology to economics.

Even if the considered analogies become relevant only in broader contexts, they are associated with basic concepts rather than with relations or even models which may follow. Twenty-five concepts have been chosen. At first glance, they may appear to be heterogeneous and non-exhaustive since they concern not only properties of the described entities. They could be classified according to various criteria, but are treated separately in the book. Some arose either from biology (*selection*) or from economics (*market*) while others are common to both disciplines (*learning*), with a possibly specific vocabulary (*fitness/utility*). Some are

completely interdisciplinary either in a technical sense (*stochasticity*) or in a commonly used sense (*crisis*).

Each concept (or pair of concepts) is introduced with a page or two presenting the concept's application in biology, and separately, in economics. In each discipline, the origin and history of the concept, its relation to other concepts, its main interpretations, and some concrete illustrations are considered. Each entry provides an abridged bibliography, referring chiefly to a more complete treatment of the concept. Next, a tentative synthesis is outlined conjointly by the two authors of the disciplinary presentations, for the purpose of evaluating the depth and the relevance of the analogy *ex post*.

References

Alchian, A. (1950): Uncertainty, Evolution and Economic Theory, *Journal of Political Economy*, 58, 211-21.

Battalio, R.C., Kagel, J.H., McDonald, D. (1985): Animals' Choices over Uncertain Outcomes, *American Economic Review*, 75, 597:613.

Buenstorf, G. (2006): How Useful is Generalized Darwinism as a Framework to Study Competition and Industrial Evolution?, *Journal of Evolutionary Economics*, 16(5), 511-27.

Cordes, C. (2006): Darwinism in Economics: from Analogy to Continuity, *Journal of Evolutionary Economics*, 16, 529-41.

Dawkins, R. (1983): Universal Darwinism, in Bendall D.S. ed. *Evolution from molecules to men*, Cambridge University Press

Dennett, D. (1995): *Darwin's Dangerous Idea*, Simon and Schuster.

Fisher, R.A. (1922) : On the Mathematical Foundations of Theoretical Statistics, *Phil. Trans. of the Royal Society*, 222, 309-368.

Friedman, M. (1953): The methodology of Positive Economics, in *Essays in Positive Economics*, 3-43, University of Chicago Press.

Hayek, F. von (1973): *Law, Legislation and Liberty*, University of Chicago Press.

Malthus, T. R. (1798, 1803, 1826): *Essay on the Principle of Population*, J. Johnson.

Mandeville, B. (1714): *The Fable of the Bees*, J. Roberts.

Marshall, A. (1890): *Principles of Economics*, Macmillan.

Marx, K. (1867) : *Das Kapital*, Verlag von Otto Meisner

Nash, J. (1951): Non cooperative games, *Annals of Mathematics*, 54, 286-97.

Nelson, R. R. , Winter, S. (1982): *An Evolutionary Theory of Economic Change*, Harvard University Press.

Rice, C. , Smart J. (2011) : Interdisciplinary modeling : a case study of evolutionary economics, *Biology and Philosophy*, 26(5), 655-75.

Rosenberg, A. (2000): *Darwinism in philosophy, social science and policy*, Cambridge University Press

Samuelson, P. (1958): An exact Consumption-loan Model of Interest with or without the social contrivance of Money, *Journal of Political Economy*, 66, 467:82.

Schumpeter, (1912, 1934): *Theory of economic evolution*, Harvard University Press.

Smith, A. (1776): *An inquiry into the Nature and Causes of the Wealth of Nations*, Strahan and Cadell

Veblen, T. (1898): Why is Economics not an Evolutionary Science?, *Quarterly Journal of Economics*, 12(4), 373-97.

Von Neumann, J., Morgenstern, O. (1944): *Theory of Games and Economic Behavior*, Princeton University Press.

Walliser, B., Zwirn, D., Zwirn, H. (2021): Analogical Reasoning as an Inference Scheme, *Dialog*, to appear.

Whitta-Jacobsen, H.J. (2011): Economic Darwinism, *Theory and Decision*, 70, 385-98.

Witt, U. (2008) : What is specific about Evolutionary Economics, *Journal of Evolutionary Economics*, 18, 547-75.

Witt, U. (2016): *Rethinking Economic Evolution*, Edward Elgar.

KEYWORDS IN ECONOMICS AND EVOLUTIONARY BIOLOGY: twenty five concepts.

Adaptation/ Learning

Evolutionary biology (J. Gayon)

Etymologically, the word “adaptation” means “adjustment,” with an evaluative connotation (harmony, compliance, suitability). In its contemporary biological usage, the term is affected by several ambiguities, some of which are the source of serious theoretical confusions. The first arises from the use of the word in both static and dynamic circumstances. In the *static* sense, “adaptation” designates an adapted condition. For example, large testicle size in chimpanzees, compared to other anthropoid primates, is adapted to an exceptionally high degree of sexual promiscuity, and therefore intense spermatic competition. In the *dynamic* sense, “adaptation” designates the process leading to an adapted state. This usage of the word is common in physiology, where the process is located within the individual (when speaking of thermal adaptation, for example). But it is also used in evolution (where species adapt to environmental changes).

In contemporary evolutionary theory, the distinction between adaptation as a state and adaptation as a process is complicated by the close relationship adaptation maintains with the principle of natural selection, considered to be the only admissible explanation for adaptations (in the static sense). This leads us to differentiate between four concepts of adaptation, which are too often confused with each other.

Adaptation in the sense of the optimal solution to an environmental challenge (1)

An organism that is adapted (or well adapted) for a given trait is one whose structure and behavior enable it to adjust to the environment in which it is found in the optimal way. The concept in this case derives from engineering, and is indifferent to the evolutionary history that produced the trait. Hence, functional morphology shows how such and such a bird wing profile is best adapted to such and such a type of flight. Methodologically, the concept is onerous: one must first demonstrate that a given engineering problem has an optimal solution and then, taking existing limitations into account, examine the degree to which an organism nears the optimal solution, or not, due to other challenges it must overcome. In English, this pre-Darwinian meaning of the term "adaptation" is often expressed as “fitness,” the word itself being used in a pre-Darwinian way; that is, in an absolute, non-relative way.

Adaptation in the sense of the variable, relative efficiency of an organism’s solution to dealing with an environmental challenge (2)

This relative conception of adaptation was introduced by Darwin. It results from observing the ubiquity of the variation: for any trait, individual organisms exhibit an individual variation, and are more or less adapted to such and such an environmental challenge. And this variation, as long as it is heritable, is a necessary condition for the process of natural selection.

Consequently, the concept of adaptation becomes closely tied to that of natural selection. On the one hand, any adaptation is relative, a fact that gives traction to a natural selection process; on the other hand, natural selection opens the prospect of an endless adaptive process, as long as an heritable variation is available in a population. Finally, natural selection provides the major—or even exclusive—explanation of the source of adaptations.

These first two senses (1) and (2) are the ones that interested Darwin, who went from (1) to (2) as he became more aware that variation for all traits of all organisms was ubiquitous.

Observed differential reproductive success (realized fitness) (3)

This is a quantitative concept, related to the treatment of natural selection in population biology. In this case, the terms *fitness* and *selective value* are interchangeable. In a given population, different selective values, or fitness values, are assigned to different entities (see FITNESS/UTILITY). Population genetics almost always reasons in terms of relative fitness values, W_1 , W_2 , etc., assigned to genotypes or, if appropriate statistical processing is available, to genes (Rice 2004). Knowing the frequency of genotypes and their relative fitness to a given generation, the genetic composition of the following generation can easily be predicted, as can the evolution of the population over n generations, assuming that the conditions (environment, genetic context) remain the same. In certain cases, particularly in ecology, researchers reason in terms of absolute fitness values; in other words, net reproductive efficiency. The concept is then applied to organisms (or, to be more precise, classes of organisms) as such. In every case, fitness values are empirical parameters, measuring the reproductive success of one generation over another.

Expected reproductive success (expected fitness) (4)

The only difference between expected fitness and realized fitness is that expected fitness is interpreted as a probabilistic property. In this case, selective or fitness values are computed as expectations. Certain philosophers interpret them as propensities (Mills and Beatty 1979).

These two last concepts are the ones currently used in population biology. They resulted from the equivalence Darwin himself established between “natural selection” and “survival of the fittest.” After Darwin, the expression was reversed, yielding “fitness to survive”. And now we have reached the point where adaptation as an engineering concept is completely divorced from adaptation as the target of competition.

(3) is weaker and more general than (4), because if a propensity exists, we are entitled to ask the reason why. And this refers us back to (2), a much more cumbersome concept than (3). One last difficulty—a sizable one for the field evolutionist—is that, to be complete, the explanation of a trait by natural selection must demonstrate that the trait spread due to its adaptive differences in the sense (3) of the word (Brandon 1990). In practice, explanations of the origin of a trait by natural selection often skip one or several of the steps required for such a demonstration (Parker and Maynard Smith 1990). This failure is what motivated the criticism

of “adaptationism.” Even though the concepts of adaptation and natural selection seem to be intuitive and easy to grasp, they can be awkward and hard to implement in the field.

References

Brandon R. (1990): *Adaptation and Environment*, Princeton, NJ: Princeton University Press.

Mills, S. K., & Beatty, J. H. (1979): The Propensity Interpretation of Fitness, *Philosophy of Science*, 46(2), 263-286.

Parker, G. A., Maynard Smith, J. (1990): Optimality Theory in Evolutionary Biology, *Nature* 348, 27-33.

Rice, S. H. (2004): *Evolutionary Theory*. Sinauer, Sunderland, MA.

Economics (B. Walliser)

The generic notion of adaptation concerns the gradual transformation of the behavior of agents placed in a shared material and social environment. All “adaptive processes” are based on agents with imperfect and incomplete information and various kinds of bounded rationality (Rubinstein, 1997). They take place in a dynamic context in which agents are able to exploit their past observation and experience. These processes depart from the classical “deductive processes,” in which agents endowed with ideal cognitive and instrumental rationality are able to predict their opponents’ behavior perfectly.

Adaptation is usually studied within the framework of a repeated game, in which agents are independent and have prior information on the game structure. At each period, any player chooses an action after carrying out a mental deliberation that can be broken down into three steps. In the information step, the player gathers data on past actions and their consequences. In the evaluation step, he processes that information in order to compute various indices: expectation of the other’s future action, adjustment of an aspiration level. In the decision step, on the basis of what he has learned and calculated, he selects one action from a set of possible actions.

Knowing the players’ behavior and the evolution of their environment, the modeler simulates the functioning of the whole system. He computes the transitory regime in which players sequentially react to the others and to the environment. He studies the asymptotic regime in which the process converges towards given states (or sets of states). He compares these states to the equilibrium states which are formally defined in classical game theory without reference to their origin. If convergence actually occurs, the adaptation process appears as a dynamic justification of such and such notion of equilibrium.

Adaptation processes can be classified in three categories, according to players’ diminishing cognitive abilities (Fudenberg-Levine, 1998). The three types also correlate with longer and longer time scales (see TIME SCALES). These types are not exclusive to more or less sophisticated “imitation” of other’s actions, or achievement of progressively revised

“aspiration levels” (Simon, 1982). Moreover, hybrid models can be designed by combining the types: players jump from one adaptation model to another in case of difficulty; they use one type or another depending on decision and environment; they use a mixed model with characteristics of several types.

In “belief-based learning,” players form a representation of their environment and revise it when new information comes in. In the simplest case, each player observes the frequency of past actions of every other player. Assuming (wrongly) that the process is stationary, he interprets it as a probabilistic expectation of his future actions. He finally relies on this expectation in order to define his optimal action as a best short term response. The process may converge towards one of the pure strategy Nash equilibrium states, if one exists, but it may also not converge and cycle, instead. However, the process becomes more robust and liable to converge when random noise is introduced into the computing of the optimal action.

In “reinforcement learning,” players reinforce (or inhibit) the actions that obtained good (or bad) results in the past. In the simplest case, each player is unaware of his environment and only observes the utility he got in each period. Adding up his observations, he aggregates them in a performance index attached to each action, and considers again the (mean) performance as stationary. He finally chooses an action with a probability proportional to its performance index. The process generally converges towards a pure strategy Nash equilibrium. The reason is that it achieves a good trade-off in the action set between “exploration” (by never abandoning any action) and “exploitation” (by favoring the most efficient actions).

In an “evolution process,” players are endowed with a constant behavior, but mutations can appear, and will be selected by a selection process. In the simplest case, each player has a fixed strategy and belongs to a population whose members have different strategies. He faces random mutations which induce an exogenous change of the composition of the population. He reproduces in proportion to the utility he gets in his interactions (assimilated with fitness), which induces an endogenous change of the population. The process often converges towards an “evolutionary stable equilibrium” (Maynard-Smith, 1982), a stronger notion than Nash equilibrium.

A classic example concerns the emergence of a driving convention on either the left side or the right side of a road. In belief-based learning, each agent observes which side the majority of drivers are using, and drives on the corresponding side. In reinforcement learning, each agent adds up the number of accidents he had when driving on the right or left, and chooses the observed safer side. In an evolution process, agents driving on different sides have an accident and die while agents driving on the same side are overtaken by other cars. In all cases, the agents join the same asymptotic state; i.e., driving on the same side, even if transitory states may be very costly.

References

Fudenberg, D.- Levine, D. (1998): *Theory of Learning in Games*, MIT Press.

Maynard-Smith, J. (1982): *Evolution and the Theory of Games*, Cambridge University Press.

Rubinstein, A. (1997): *Modeling bounded rationality*, MIT Press.

Simon, H.A. (1982): *Models of Bounded Rationality*, MIT Press.

Synthesis

In economics, the notion of adaptation is essentially individual, since each specific agent follows a learning or evolution process when interacting with others. This notion is a more accurate expression of a gradual change in an agent's behavior, or at least of the frequency of each of his actions. In biology, the notion of adaptation is directly collective and concerns a whole population of similar agents situated in a common natural environment. It refers to the overall result of the change operated by nature; i.e., organisms adapted to the environment where they live.

In biology, the driving force of adaptation is fitness, considered as the adaptive value of the traits which can be selected by natural selection. Such a view seems tautological, since the most highly adapted species are those that are the fittest, fitness being precisely measured by the average number of their offspring. In economics, the driving force of adaptation is individual utility, assumed to be maximized by each agent, but at a level depending on the achieved equilibrium state. Here again, some tautological reasoning seems at work, since measured utility is nothing other than the utility revealed from the individual behavior.

In economics, an adaptation process is "ameliorating" insofar as it allows an agent to improve his performance, but without reaching an individual optimum. It is only in specific cases that an eventual asymptotic state is also a Pareto optimum, in which there is no scope for any further improvement. In biology, it is often assumed that natural selection is globally optimizing, in the sense that it leads to a local optimum for lack of a global one. In fact, all individuals are embedded with the same fitness, which increases concomitantly until reaching a peak in the fitness landscape.

In biology, individuals are nevertheless able to learn in the short run, in such a way that the learning and evolution processes overlap, with different time scales. It is even possible to consider that the structure of learning processes is subject to evolution. In economics, it appears that reinforcement and evolutionary processes are formally similar, the frequency with which an action is implemented by some agent being replaced by the percentage of individuals implementing that action. Hence, the learning processes are given more attention in the classical literature, the evolutionary processes being interpreted only as their counterpart in evolutionary economics.

Altruism

Evolutionary biology (*J.-B. André*)

In evolutionary biology, the most common understanding of altruism designates the fact that for an individual (known as an agent), may express a characteristic that is costly to his own reproductive success, but beneficial to the reproductive success of another individual, known as the receiver. Care for offspring; assistance provided to the queen by workers (in social species); dispersal of young far from their parents in order to avoid competing with them: these are all examples of altruistic behavior.

Viewed in terms of natural selection, the existence of altruistic traits in biology is a paradox, since, by definition, these traits decrease the reproductive success of the individuals expressing them. In the 1960s, however, British biologist William Hamilton suggested a solution to this paradox, by postulating the theory of kin selection (Hamilton 1964). Hamilton's theory is often considered to be the most important advancement in evolutionary sciences since Darwin. Hamilton understood that altruism could be favored by natural selection if it tends to benefit individuals who are altruistic themselves. Hence, although altruism reduces the reproductive success of altruistic individuals, all other things being equal, the altruistic trait might become more frequent because it benefits individuals who carry the trait themselves and transmit it to their descendants.

Mathematically, the principle is expressed in the form of an equation called Hamilton's rule. Natural selection favors an altruistic trait expressed between an agent and a receiver if $Rb - c > 0$. In other words, altruism will prevail if the benefit (b) of the trait to the receiver, weighted by the genetic relatedness (R) between agent and receiver, is greater than the cost (c) of the altruism to the agent. Genetic relatedness, R , measures the degree of genetic similarity between agent and receiver, compared to average similarity of individuals in the population; in other words, it measures the statistical correlation between the genes of these two individuals. Typically, relatedness is high between individuals linked by kinship.

The notion of altruism, and the evolutionary explanation of its origin, are the subject of much controversy and often confusion, in the scientific literature. At least three of these issues deserve clarification.

Certain behaviors are altruistic in the psychological sense, but not in the evolutionary sense

The case of altruism is a striking illustration of the classical distinction between ultimate and proximate causes, in the form of a distinction between evolutionary and psychological altruism. Psychologists describe a behavior motivated by the intention of doing good to

another as an altruistic behavior. Altruism is therefore defined on the basis of its underlying mechanisms. The evolutionary definition of altruism, by contrast, is purely consequentialist. The only parameter that counts is the effect of the behavior on the reproductive success of the individuals.

Thus, many behaviors are altruistic in the psychological sense, without being altruistic in the evolutionary sense. This is true of “reciprocal altruism,” in particular (although it should be termed more accurately “reciprocal cooperation”). To help another individual spontaneously proceeds from an altruistic intention, so it is psychological altruism. However, it is altruistic in the evolutionary sense only if the assistance provided makes it possible to reinforce an exchange relationship that ultimately benefits the agent itself. There are thus several psychologically altruistic behaviors that can evolve under the influence of natural selection, simply because they benefit the individuals who express them. Viewed in terms of the theory of kin selection, the expression of such behaviors towards unrelated partners is therefore not paradoxical.

Is the evolutionary definition of altruism too strict?

We have adopted William Hamilton’s definition of altruism, which is a strict one. However, this definition has been and still is the subject of debate. Certain authors advocate a broader use of the term. Sometimes, cooperative behaviors that are temporarily costly to individuals are qualified as altruistic, even if they are beneficial in the long term. Consequently, according to this definition, reciprocal cooperation is truly altruistic, because individuals pay an immediate cost for a future benefit. Other authors argue for the existence of two types of altruism, a strong and a weak (Sober and Willson 1998). Strong altruism corresponds to what we simply call altruism. When an agent pays a cost in selective value only in relation to his social partners, it is a case of weak altruism.

Even though these alternative definitions have merits, they are flawed because they are not based on evolutionary mechanisms. Evolutionist terminology must reflect as clearly as possible the selective mechanisms that cause the evolution of traits (West et al. 2007). As a result, the real question is not whether a behavior is beneficial immediately or later. Instead, the causal path that leads to it being favored by selection should be determined. If it is favored because it benefits individuals who carry it via a positive response from others, then it is not altruistic, because it is individually beneficial. It is reciprocal, because it involves a response from the other. Likewise, weak altruism consists of an individual expressing a trait that is beneficial to him, but also happens to benefit other individuals than himself even more. To describe such a behavior, it is clearer to speak of by-product mutualism than altruism.

Kin selection does not imply recognition of kinship

According to the kin selection theory, an altruistic trait (defined by $b > 0$ and $c > 0$) cannot be favored by natural selection unless it is expressed between related individuals (in other words,

those who tend to share more genes than the average). This point recently sparked lively controversy between evolutionists (Nowak et al. 2010). Some of them asserted that other mechanisms, distinct from kin selection, could lead to the evolution of altruism. The main source of disagreement here arises from the fact that these authors confuse kin selection and kin recognition.

Positive relatedness may exist between social partners for a variety of reasons. It may exist because the individuals explicitly know how to recognize family members, and interact only with them. Otherwise, it may exist because individuals simply tend to move around little in the course of their lives, and thus find themselves engaged in social interaction usually with individuals who are close relatives. Or it may exist because individuals live and reproduce within closed groups that therefore contain a high percentage of relatives. These are only a few examples of the many mechanisms that may lead to the existence of positive relatedness between partners. They could potentially enable altruism to evolve, whether or not they imply recognition of kinship (the same is true in the case of the “green-beard effect”; the general mechanism will operate whether or not there is explicit recognition).

Some authors maintain that the theory of kin selection would only concern situations in which relatedness is caused by an explicit recognition of the relatives. They consider other sources of relatedness – especially spatial proximity and group life – as belonging to competing theories. This leads them to assert that kin selection is not the only explanation at the origin of altruism. However, aside from the fact that this viewpoint fails to do justice to the great generality of Hamilton’s theory, it does not promote a good scientific understanding of altruism. Kin selection theory establishes a general framework that can house all of the mechanisms that make altruism possible by generating genetic relatedness between social partners. A fragmented theory piecing together separate mechanisms loses this conceptual unity.

References

Hamilton, W. (1964). *The Genetical Evolution of Social Behaviour* *Journal of Theoretical Biology*, 7:1–52.

Kerr, B., Godfrey-Smith, P., Feldman, M. W. (2004). What is altruism? 19(3).

Nowak, M.A., Tarnita, C.E., Wilson, E.O. (2010): The evolution of eusociality. *Nature*, 66(7310):1057–1062.

West, S., Griffin, A. and Gardner, (2007): Social semantics: Altruism, cooperation, mutualism, strong reciprocity and group selection, *Journal of Evolutionary Biology*, 20:415–432.

Sober, E. , Wilson, D.S. (1998): *Unto Others: The Evolution and Psychology of Unselfish Behavior*, Harvard University Press.

Economics (M. Cozic)

Rational choice theory assumes that agents have well-structured preferences and follow them when they choose. The theory imposes no specific *content* upon preferences: it is not incompatible with it that an agent prefers to share a sum of money equally with someone else rather than keep all the money for herself. However, when conventional economic theory *applies* rational choice theory, it typically adds assumptions about the content of preferences. A major one is that agents' preferences are aligned with their individual "well-being" (or "interest") or with consensual determinants of well-being like money or goods. In this sense, economic theory (e.g., consumer theory) typically assumes that agents are rational egoists. Casual observation suggests that the assumption of egoism is too restrictive: we often seem to act in an altruistic way (trying to promote others' well-being) and sometimes also in a negatively altruistic way (trying to harm others' well-being). More generally, "social" or "other-regarding" preferences are preferences that are at odds with the egoistic assumption. The conceptual and theoretical investigation of non-egoistic preferences is not recent (Fontaine, 2008). The understanding of altruism underwent important changes about two decades ago, when experimental economics attempted to describe the limits of egoism and to test alternative hypotheses aimed at explaining apparently altruistic behaviors.

The study of some specific games played an instrumental role in this endeavor:

- Ultimatum game: Player 1 has to share Y euros with player 2. In the first stage, she offers X euros to player 2. If player 2 accepts, the game ends with $Y-X$ euros for player 1 and X euros for player 2. If player 2 rejects the offer, the players receive nothing. Assuming egoistic preferences, conventional game theory predicts that player 1 will offer a minimal share to player 2, who will accept this offer. However, experiments show that subjects in player 1's role offer around 40%-50% of Y , and that players 2 reject proposals when X is less than 20% of Y ("negative reciprocity").
- Dictator Game: Player 1 again has to share Y euros with player 2, but player 2 can no longer reject player 1's proposal. The theory predicts that player 1 will propose a minimal share to player 2. Experiments show that subjects in player 1's role offer around 25% of Y .
- Trust Game: Player 1 is endowed with Y euros. In the first stage, she chooses a share X of Y that is invested and becomes $(1+r)X$. In the second (and final) stage, player 2 decides how to share $(1+r)X$. If she keeps Z , player 1 ends the game with $Y-Z+rX$ euros. The theory predicts that player 2 will reciprocate minimally and that player 1 will invest minimally.

In the Dictator Game, one may want to explain the fact that player 1 proposes a non-minimal sum to player 2 by assuming altruistic preferences, whereby the agent is willing to sacrifice

(part of) her own well-being to promote the other's. In the Ultimatum Game, the fact that player 2 rejects the proposal of player 1 when X is too low could be explained by negatively altruistic preferences. However, it is less obvious to frame hypotheses that could explain both phenomena. An important part of contemporary research on social preferences and altruism consists precisely in elaborating and assessing hypotheses on individual preferences. For instance, one of the most popular models postulates that people have inequity aversion: the utility of an allocation increases with one's own share but decreases with the difference between one's own share and the share of others (Fehr et Schmidt, 1999). In "reciprocity" models, the altruism of agents depends on how they view the intentions of other people – an assumption which requires a more substantial revision of conventional models. Discussions remain lively on how to assess these models, how to interpret the experimental results, and whether it is plausible to expect them to hold outside the laboratory. Other, more applied, works study the manifestation of altruistic behaviors in social life – for instance within the family or through philanthropic acts (see Kolm & Ythier 2006).

References

Fehr & Schmidt (1999): "A Theory of Fairness, Competition and Cooperation," *Quarterly Journal of Economics*, 114, 817-868.

Fontaine, P. (2008): "Altruism: History of the Concept," in *The New Palgrave Dictionary*, 2nd. ed., ed. by S. Durlauf and L. Blume. London: Palgrave Macmillan

Kolm, S-C., Ythier, J. (eds.) (2006): *Handbook of the Economics of Giving, Altruism and Reciprocity*, Vol.2, Elsevier

Synthesis

Like cooperation (see this entry below), altruism is an important theme in both contemporary economics and evolution theory. The basic analogy between the two fields is that of individual well-being (in economics) and fitness (in biology). (Let us insist on the fact that in economics, as far as altruism is concerned, the relevant concept is individual well-being, not utility. Yet, even though there is relative consensus on the parameters that determine individual well-being, such as wealth, the notion itself is difficult to define, if one is willing to separate it from utility or individual preferences.) Today, altruism in economics is largely immersed in the more general theme of "social" preferences. As a result, it covers a much vaster field (*modulo* the analogy we have just mentioned) than altruism in biology, which is restricted to the cases in which a behavior benefits the reproductive success of the receiver but harms that of the agent (which corresponds, *mutatis mutandis*, to what we have called "strong altruism" in economics).

There is a sharp contrast between the “challenges” raised by altruism in each discipline. In economics, phenomena that are likely to be explained by social preferences cast doubt upon an assumption that is widespread in its applications, although it is auxiliary to the whole theory of preferences. This assumption is the egoism of preferences, according to which individual preferences are based solely on individual well-being. By contrast, in biology, altruism may seem to threaten the founding principles of the theory of evolution. The explanatory agenda is then much narrower and the debate much hotter, because the point is to determine how to *reconcile* altruistic behaviors with the fundamentals of natural selection. The theory of kin selection aims to accomplish precisely this task. In economics, there is no need to dissolve an apparent paradox, and the scientific agenda is more “routine.” The need is simply to determine which auxiliary hypotheses about the content of individual preferences are adequate explanations for the behaviors in question. Some thinkers try to preserve the assumption of egoistic preferences above all (and therefore to explain apparently altruistic behaviors in terms of enlightened self-interest). In this case, they act more out of concern for explanatory parsimony than to protect their theoretical framework (the central tenets of which are not being challenged).

Beyond the analogy, there is a question that is still poorly understood, although it is relevant to both fields, and often mentioned. That is, what constraints do the hypotheses about preferences and evolutionary theory exert on each other? Does the theory of evolution make certain hypotheses about “social” preferences (and the behaviors that the hypotheses must explain) more likely or unlikely? Inversely, are certain variants of evolutionary theory underpinned by recent contributions to the study of “social” preferences? Roughly stated, the point is to find out how much proximate causes in behaviors (preferences) reflect their alleged ultimate causes (evolutionary mechanisms). On these sensitive questions, see in particular Binmore (2005), Robson & Samuelson (2011), and Bowles & Gintis (2011).

References

- Binmore, K. (2005) *Natural Justice*, Oxford: Oxford University Press
- Bowles, S. & Gintis, H. (2011) *A Cooperative Species*, Princeton: Princeton University Press
- Robson, A & Samuelson, L. (2011) “The Evolutionary Foundations of Preferences,” in Benhabib, J., Bisin, A. & Jackson, M. (eds), *Handbook of Social Economics*, vol. 1A, Amsterdam: Elsevier

Chance/Uncertainty

Evolutionary biology (*P. Huneman*)

Evolution occurs through the different replication rates of alleles, which in turn rely on the different reproductive successes of the organisms that carry these alleles, as well as on the types and rates of mutation and migration. The Modern Synthesis holds that natural selection is the most powerful agent driving these changes, and it is quite predictive: the fittest traits most probably become fixed traits. Yet stochasticity occurs at all levels in this theory (Lenormand et al. 2010): the nucleotidic substrates of the genes; the cell and its physiological functions; the organism and its chances to survive and reproduce; and finally, the species and even the ecosystem itself. At each level, this stochasticity is modeled in a specific manner that relies on specific assumptions, and is also properly correlated to factors that, in contrast, are not stochastic (namely, factors that appear deterministic or directional), such as natural selection.

At the lowest level, genes mutate stochastically, in the sense that during meiosis they undergo random changes in their nucleotidic sequences. In sexually reproducing species, recombination is also a stochastic process. Stochasticity here must be understood as specific to the biological context: mutations may be physically deterministic, but from an evolutionary viewpoint what matters is that they are not correlated to fitness. The claim that mutations are wholly random is controversial (Jablonka and Lamb 2005), since some mutations can be more probable than others, but if they were wholly determined by their adaptive virtue natural selection would not play any explanatory role, since mutations themselves would suffice to adapt organisms to their environment (see MUTATION/INNOVATION). It has also been shown recently that, in various cells, levels of gene expression stochastically differ, whereas the average level of phenotypic expression among many cells is the phenotypic trait whose evolution is represented in population/quantitative genetics models. Such stochasticity may give rise to inter-cell selection (Heams 2014).

Mutations and recombinations are the material upon which natural selection is supposed to “act,” in the sense that organisms have different reproductive chances due to their phenotypic traits, these being a reliable expression of genotypes within a given environment. Organism and trait fitnesses measure these chances. In the long run, these dynamics may lead some alleles to fixation and on this basis explain phenotypic changes. After Sewall Wright, population geneticists call “random genetic drift” those differences in reproductive success that are not correlated to these trait fitnesses. Drift behaves like a sampling error, deviating the traits or alleles from frequencies predicted by fitness values; therefore, drift may prevent adaptation from being produced by natural selection. Deviations due to drift are obviously larger when populations are small. Drift, however, comes in two kinds: a. the allele of lowest fitness goes to fixation, or b. one of two equal-fitness alleles goes to fixation. (b) is the limit of

(a) when fitnesses tend to equalize; in this sense it may be modeled through random walks, or diffusion equations (Blythe and Mc Kane 2012).

Evolutionary change, in this respect, appears as being caused or explained by the combination of natural selection, as a deterministic trend, and drift as a stochastic trend. One empirical question consists in apportioning the respective weights of drift and natural selection in a given evolutionary dynamics and assessing, more generally, their role in evolutionary change, which involves questioning the size of populations. Such apportioning is a recurrent issue in evolutionary biology: famously, Wright and Fisher disagreed on the extent and explanatory strength of drift. Later, Kimura's neutralist theory argued that at the level of nucleotides many substitutions are in fact neutral; therefore, drift as a pure stochastic process would underpin an important amount of the genetic make-up of the species. Another empirical controversy consists in determining what actual amount of the genome of a given species is accounted for by neutral evolution. Recently, Michael Lynch (2010) has argued that drift is indeed responsible for the architecture of the metazoan genome, especially since the large size of these organisms implies that they live in small populations, thereby increasing the impact of drift.

Drift also raises conceptual issues. It measures the gap between the frequencies of alleles (or the phenotypic values) predicted by fitness in a theoretical infinite population and the actual frequencies in a real, finite population. Instead of two forces or two factors acting concomitantly on populations (Sober 1984), selection and drift can therefore be seen as, respectively, a linear regression coefficient and an error term (Brandon and Ramsey 2006). All visions of selection and drift are not compatible, and understanding the connection between the stochastic and the deterministic factors in evolution is an open conceptual question, though its answer does not impact directly on modeling evolution (exactly as discussions on the nature of fitness do not impinge on the measurement of fitness or modeling of evolutionary dynamics). However, empirical science is involved in designing tools aimed at recognizing their respective effects on phenotypic frequency change in populations and adaptation, as well as the signature of selection and drift on genomic sequences and proteins (Voight et al. 2006).

While natural selection is fairly well defined, the nature of drift is controversial. Whereas some authors see it as a set of stochastic processes, including random gamete sampling, and ecological chance events such as founder effect, others see it as deviation from a predicted outcome (Plutynski 2008), the way it was initially presented by Wright. All these difficulties have led some biologists to contest the idea that drift encompasses all types of stochasticity in evolutionary dynamics, and to advocate a pluralist view of stochasticity that would distinguish these types according to their sources and time scales (Gillespie 2004).

Indeed, another source of stochasticity comes from the environment: if it changes rapidly and unpredictably, selective pressures will undergo stochastic variations preventing natural selection from giving rise to fixation of alleles, in which instance evolutionary change appears stochastic. “Draft” (Gillespie 2004) means stochastic evolution of genes linked to loci under selection in randomly changing environments, and this often swamps drift.

However, stochasticity also occurs at other levels and scales than those of population genetics. Along very large time scales, macroevolution may include a stochasticity specific to events that are both hugely consequential, and yet unique, and thus not embedded in selective pressures nor represented in the fitness values we use to model evolution and estimate deviations from expected outcomes of selection. This includes, for instance, the causes of mass extinctions, such as the celestial bodies that account for the extinction of the dinosaurs. Gould (1989) famously argued that such stochastic processes rather make evolution contingent at the macroevolutionary level, even if natural selection is a deterministic trend and yields microevolutionary predictions.

Finally, going from evolution to ecology and investigating the causes of biodiversity, “neutral models” in ecology (Hubbell 2001) parallel Kimura’s neutral nucleotidic evolution and are good predictors of actual biodiversity patterns. “Ecological drift” causing the abundances of species to fluctuate in a metacommunity with no respect for niche differences (i.e., effects of selection) accounts for species abundance patterns in the same way as genetic drift accounts for the genomic make-up of populations. Ecologists strive to determine the respective signatures of neutrality and niche effects (Chase and Myers 2011). If the claims of empirical superiority of neutral ecological models are corroborated, it would mean that, interestingly, stochasticity swamps the determinism of selection at the lowest (nucleotidic) and highest (metacommunity) levels, whereas natural selection seems still to be the main driver of the evolution of a given species’ population.

References

- Brandon R., Ramsey G. (2006) “What's Wrong with the Emergentist Statistical Interpretation of Natural Selection and Random Drift.” In: M. Ruse, D. Hull (eds.) *The Cambridge Companion to Philosophy of Biology*. Cambridge: Cambridge University Press.
- Chase J. Myers J. 2011 “Disentangling the importance of ecological niches from stochastic processes across scales” *Phil. Trans. R. Soc.* B366, 2351–2363.
- Gillespie J. (2004): *Population Genetics. A concise guide*. Baltimore: Johns Hopkins University Press.
- Gould SJ 1989. *Wonderful Life*. Boston: Norton and Schuster.
- Heams, T. (2014). “Randomness in biology”. *Mathematical Structures in Computer Science*, 24(3), 403-08.

Hubbell S. (2001): *The unified neutral theory of ecology and biogeography*. Princeton: Princeton University Press.

Jablonka E, Lamb M. 2004. *Evolution in five dimensions*. Chicago: University of Chicago Press.

Lenormand T, Roze D, Rousset F. 2009 "Stochasticity in evolution". *Trends Ecol Evol*. 24(3):157-65.

Lynch M. 2007. *The Origins of Genome Architecture*. New-York: Oxford University Press.

Plutynski, A (2007). "Drift: A historical and conceptual overview". *Biological Theory* 2 (2):156-167.

Sober E (1984): *The nature of selection*. Cambridge: MIT Press.

Voight B.F., Kudaravalli S., Wen X., Pritchard J.K. (2006) "A map of recent positive selection in the human genome". *PLoS Biol* 4(3): e72.

Economics (*B. Walliser*)

Uncertainty runs through game theory just as it does through economics, and does so under three main forms. Firstly, *ontological uncertainty* reflects the uncertainty of the modeler with respect to some intrinsically random behavior of the actors and their environment. Secondly, *epistemic uncertainty* represents an imperfect and incomplete knowledge of the actors with respect to their natural and social environment. Thirdly, *voluntary uncertainty* reflects the will of actors to make their own actions unpredictable by giving them a random dimension.

Generally, all three forms of uncertainty are quantitatively modeled by objective (von Neuman & Morgenstern, 1944) or subjective (Savage, 1954) probability distributions on the corresponding variables. They are more rarely expressed by subsets of the possible values of these variables. In a more sophisticated way, they may also be represented by probability hierarchies (capacities, Dempster-Shafer belief functions), which express the inherent uncertainty in basic probabilities but at a higher level.

In *classical game theory*, ontological uncertainty may involve the contribution of a player's "free will" to a given decision. But where this happens to be the case, it would be difficult to justify an appeal to probability calculus. In a more technical way, ontological uncertainty considers that a player has a deterministic behavior, but suffers from a "trembling hand" at the moment when the intended action is carried out. A probabilistic view is better justified in this very specific case.

Epistemic uncertainty applies to every player and with respect to all three elements of a game: the other players, the player him- or herself, and the common environment they all share. It involves three different kinds of magnitudes: retrospective variables (past states of nature, past actions of others, one's own past actions), structural variables (state generating laws, mental states of all players), prospective variables (future states, intended actions of all players).

In particular, each player is characterized by his or her “type,” a synthesis of his or her preferences and beliefs (Harsanyi, 1967/68). He/she knows his/her proper type, but is uncertain about the others’, and models them according to a probability distribution (or a probability hierarchy). The players are (commonly) endowed with some publicly known prior information and personally receive some private information as the game is played out (especially by observation of others’ actions). Thus, accordingly, they revise their assessment of the other players’ types.

Voluntary uncertainty affects the players’ strategies which become “mixed strategies.” A mixed strategy is simply a non-degenerate probability distribution on a player’s available pure strategies (or actions). Each player computes the best mixed strategy according to its utility, and is assumed to implement it by drawing a strategy in the probability distribution. As a result, the player becomes more unpredictable in action than would have been the case with a pure strategy, and average performance improves accordingly.

Finally, the uncertainty of a given player is transmitted to his/her decision process and, ultimately, actions. Subsequently, the message transmitted by this player through his/her actions reveals information about him/her to another player and this in turn is transmitted to the reasoning and actions of this second player. It follows that an equilibrium state integrates, in a complex fashion, all the sources of uncertainty of the game. Conversely, any random variable of the game is liable to receive several different interpretations.

In the case of a mixed strategy, this may involve a voluntary uncertainty imposed by a given player, or another player’s random expectation of that strategy, or even the frequency of use of that strategy in a population of players. In the case of a player’s random utility, this may involve alternative “states of mind” of the given player, or a subjective uncertainty about his/her utility as perceived by another player, or even an objective distribution of preferences in a population of players.

In *evolutionary game theory*, other sources of uncertainty are also considered. For instance, encounters between players that are determinant of their interactions are assumed to be random. Likewise, certain observations or computations of a player, especially those involving forecast, may be affected by random errors. Finally, the players may use random decision rules, not for strategic reasons this time, but in order to “explore” the consequences of new strategies (see ADAPTATION/LEARNING).

Every game therefore plays out along random trajectories, which depend on both context and history. Technically speaking, any such stochastic dynamic system will be associated with a deterministic one, which will have the same mean behavior, yet may differ profoundly in various aspects. The trajectories of all such systems may or may not converge towards certain attractors, either pointwise or cyclical. In order to become observable, these attractors are subject to conditions of stochastic stability.

In *economic theory*, only a few of the preceding forms of uncertainty have been imported. For instance, exogenous technological innovations are not perfectly expected nor do asset prices exhibit a typically random volatility (Knight, 1921). Moreover, behavioral uncertainty is considered a collective handicap and some institutions are specially set up to regulate it. However, many factors of uncertainty are assumed to cancel out at a macroeconomic level, in accordance with the law of large numbers.

Finally, chance and uncertainty are not the only forms of stochasticity introduced into economic models. On the one hand, random factors result from statistical biases during the collection of variables, either measurement errors on relevant observations or sampling errors when considering populations. On the other hand, random errors result from specification flaws in the relations between variables, either missing explanatory variables or mistaken analytical forms of functions.

References

Harsanyi, J. (1967/68): Games with Incomplete Information Played by Bayesian Players, *Management Science*, 14, 150-182, 320-334, 486-502.

Knight, F. (1921): Risk, Uncertainty and Profit, Houghton Mifflin.

Savage, L. J. (1954): *The Foundations of Statistics*, John Wiley.

Von Neuman, J. , Morgenstern, O. (1944): *Theory of Games and Economic Behavior*, John Wiley.

Synthesis

When it comes to the causes of uncertainty, ontological uncertainty is found in both biology and economics as a result of the impossibility for the modeler to acquire perfect knowledge of any given system. For instance, it is impossible for him/her to predict either biological mutations (even where these are independent of selection processes) or economic innovations (even where these are independent of competition processes). Conversely, epistemic uncertainty is absent in biology since the relevant entities (the rudimentary ones, at least) do not conceptualize the uncertainty they face. As for voluntary uncertainty, frequent in economics, it appears in biology only as selected uncertainty, in the zig-zag course of a gazelle escaping from a predator, for example.

An important factor of ontological uncertainty stems from reasoning in terms of populations. This is well developed in biology, where populations are often small and heterogeneous. Even the fundamental concept of fitness is analyzed in this way, through consideration of an individual's descent. A population is analyzed in a statistical way, by considering not only the mean of a variable, but also its variance and peaks. In economics, populations are given less

consideration, with the exception of evolutionary game theory where populations of players may indeed be considered. Otherwise, agents are considered for as long as possible as being individuals.

As for the consequences of stochasticity, the “drift” of a given variable during its evolution is a direct effect that was stressed in biology. When associated with non-linearity, a “bifurcation” is another stochastic manifestation of a random system. More generally, biology studies the consequences of various stochastic elements of a model. In particular, it analyzes the robustness of deterministic models to the introduction of random variables. Using the same formal tools, economics is less familiar with such studies, with the important exception of financial analysis.

Finally, economics considers that stochasticity occurs essentially at the microeconomic level of the agents. These random elements are assumed to disappear at the macroeconomic level, due to the law of large numbers applied to homogeneous entities, but new sources of uncertainty stem from the environment at the macroeconomic level. Biology considers that, even though stochasticity exists at each organizational level, so that explaining change always has to combine stochastic with non-stochastic (hence selection-based) change, it is very plausible that its impact increases when climbing up the levels beyond the level of organisms, both concerning the history of biosphere in general (i.e. the role of mass extinctions) and changes in macroecology (at least if one is sympathetic to neutralist theories in ecology). The reason for this is that the microscopic random effects of the lower levels are preserved at the higher levels, where novel sources of uncertainty are also added.

Classification

Evolutionary biology (*P. Huneman*)

Natural history takes on the project of classifying organisms. Charles Darwin inherited sophisticated taxonomies elaborated in previous centuries by Linnaeus and others. Classifications lump organisms in species, genera, families, orders etc. – each grouping being a *taxon*, or unit of taxonomy. One of Darwin's main ideas, the Tree of Life, means that all species descend from preexisting species. It yields a general, historical framework for classification: taxa are interpreted in genealogical terms, as descendants of previous groups. More precisely, the metrics of similarity, on which classification is based and according to which A and B will be in the same taxonomic group in proportion to their resemblances, receives a historical interpretation. Faced with A, B, and C, the systematist decides which is closer to which than to the third one – hence deciding whether one should have ((A,B), C), or (A, (B,C)), etc. Then, if A and B are closer to one another than to C in this similarity metrics, it means that A and B share a common ancestor that is not an ancestor of C. This establishes a hierarchy between A, B, and C. Degrees of resemblances indicate degrees of common ancestry. On this basis, systematists build elementary trees, which implement triplet hierarchies, and integrate them in a more general tree.

The similarities are investigated by considering one character, such as the shape of a lateral tooth, and comparing various species with respect to the *character state* it has (e.g. smooth, flat, sharp, etc.), in order to decide on an elementary tree as defined above (Barriol 2015). By considering several characters, a hierarchy between species can be determined, and a *phylogenetic tree* reconstituted. The goal is to uncover the objective ultimate tree of life, as it has been sketched for instance in Lecointre and Leguyader (2006)

Evolutionary biologists realized early on that similarities can emerge in two ways. A and B - the wing of the bat and the wing of the bird, for example - are similar either because they result from similar selective pressures, or because they have a common ancestor that had the same character (the wing of the bird and the fin of the fish). These cases are called analogy and homology, respectively. Homology alone is relevant for the Tree of Life and the classification. Analogies, by contrast, may lead the systematist mistakenly to lump together species that do not share a close ancestor (like dolphins and sharks). Darwin argued that a fine-grained view of analogical traits points out more differences between them than between homologous traits, because in the latter case selection operated with similar initial materials, and not in the former. Yet discriminating between analogies and homologies is a major requisite for building classifications.

Methodological issues currently divide practicing systematists. Competing methods are actually used to determine trees on the basis of data about similarities regarding several

characters. Parsimony is one key principle. Bayesian methods are now increasingly gaining favor as well (Sober 2015). For a given method, specific algorithms are possible and systematists in each given case evaluate their respective merits.

Ontological or epistemological problems are also raised by the systematists' endeavor. In phylogenetic trees, nodes are generally species, though distances based on similarities are assessed by considering specimens of these species. The ontological status of the groups of species – be they families, lineages, etc. – as they should be seen in the tree is debated across various schools of classifications. Researchers also disagree on other subjects: on the proper definition of a genuine taxonomic group; on the understanding of the nature of the mathematical relation “A is the parent of B” in the graph (often called by the term “descent” and initially considered in terms of genealogy by the Darwinians); and on the relation between classification and phylogeny.

Because the classification units are defined through evolutionary history, they are objective. In the cladistics school of classification initiated by Hennig (1966), which is close to being the dominant paradigm in systematics, the basic components of classification are called “clades.” A clade is a set of descendants of a given node in the tree; a cladogram is an elementary tree. A *monophyletic* clade is a clade that includes all and only all the descendants of a given taxon. Monophyletic groups are the genuine biological groupings, according to cladists. Clades are defined by the unique traits or characters – called apomorphies – that are found in the ancestor and then in all its descendants, to the exclusion of other species.

Cladism challenged the usual classificatory approach championed by the Modern Synthesis, as well as some alternatives like “pheneticism.” It calls for a theory of classification which exclusively relies on similarity distances. Consequently, it excludes the “grades of adaptation,” for instance, that classical biologists still considered, in order to establish parallelism of evolutionary progress between lineages. But controversies still exist between cladists and other classificatory schools – and then between brands of cladism (“structural” vs. “non-structural” cladists, etc.). The evolutionary processes are not relevant for establishing the classification. Challengers of cladism, who would like classification to be more informed by evolution, criticize this flaw.

Following their definition of biological groups as monophyletic clades, cladists insist on the fact that the relation between taxa is mostly one of inclusion, rather than filiation. Hence, it is incorrect to say that dinosaurs are ancestors of birds, but correct to say that current-day birds are actually dinosaurs (in the sense that they are included in the clade of avian dinosaurs) (Lecointre 2015).

In recent decades, two important questions have surfaced. First, with the advent of molecular biology and high-throughput sequencing, we have DNA information about species. Many phylogenies are therefore based on comparing DNA sequences. Characters here are loci or positions on the genome, and character states are nucleotides. Tools from population

genetics, such as the coalescent or the “molecular clock” defined in the neutral theory of evolution, are used to assess the distances between taxa. Molecular phylogenies seem to be more objective than the comparisons of morphological characters biologists had done since Linnaeus. However, because of gene deletions and duplications, not all genomes have the same size, and auxiliary assumptions have to be made in order to make them comparable. The debate between biologists is between reducing phylogeny to molecular phylogenies, using them to control morphologically established classifications – or finally, using both and mutually controlling them, which is the dominant approach.

Among bacteria, the major classificatory tool is molecular, obviously. But the discovery of the pervasiveness of horizontal gene transfer (HGT - individual bacteria exchange genes by contact) among prokaryotes and archae – and possibly in eukaryotes – complicates the task of classification, understood as the establishment of the tree of life. A large amount of HGT causes several branches of the trees to coalesce, and as a result, the tree becomes hugely reticulated. Thus, some authors challenge the idea of Tree of Life, at the level of archae and prokaryotes, saying there is a huge network, but not a tree. Others claim that this is just a minor amendment to Darwin’s idea of a Tree of Life. Finally, others claim that there is no Tree of Life, in general, because we are always forced to make pragmatic simplifications regarding some gene families (with respect to HGT) in order to know some branches of the Tree. According to this latter option alone, classifications, even as an approximate or regulative theoretical ideal, would not be objective groupings.

References

Barriel V. (2015) “Character.” In Heams T., Huneman P., Lecointre G., Silberstein M. (eds.) *Handbook of Evolutionary thinking in the sciences*. Dordrecht: Springer, pp.115-139.

Hennig W. 1966. *Phylogenetic Systematics*, tr. D. Davis, R. Zangerl, Urbana: University of Illinois Press, 1966.

Lecointre G. 2015. “Descent” In Heams T., Huneman P., Lecointre G., Silberstein M. (eds.) *Handbook of Evolutionary thinking in the sciences*. Dordrecht: Springer. pp.159-207.

Lecointre G, Le Guyader H. 2006. *The Tree of Life: A Phylogenetic Classification*. Cambridge : Belknap Press.

Sober, E. 2015. “Parsimony in evolutionary biology – phylogenetic inference”. In *Ockham's Razors: A User's Manual*. Cambridge: Cambridge University Press, pp. 153-206.

Economics (B. Walliser)

Economic nomenclatures concern the two pillars of economic analysis, namely agents and goods, even if the third pillar, institutions, is also concerned. The best known classify

production activities, goods and services, agents' formations and more generally socio-professional categories. As usual, the basic objects are gathered in classes supposed to be individually exclusive and globally exhaustive. Moreover, by ordering the properties, classifications become hierarchical in defining nested classes of objects situated at successive levels. It follows that increasingly generic classifications can be produced by grouping the lower-level categories.

Nomenclatures are built according to various properties of the basic objects or even relations between objects. The properties may stay implicit but are mainly explicit, are defined on a qualitative (technologies) or a quantitative (revenues) scale, and are ordered for hierarchical classifications. Practically, the nomenclatures are obtained by various formal methods of categorization, which rely on a distance between objects defined according to their properties. From that point of view, an object is assigned to a single class, even if many may be relevant (firms with multiple activities).

Nomenclatures have a mainly descriptive role in revealing simple patterns between objects. They provide a general framework for the statistical metrics attached to the objects (production volume, growth rate). Statistical indicators make it possible to analyze and compare economic systems from both geographical and historical standpoints. Further on, nomenclatures are an essential part of national account systems, which are themselves influenced by theoretical considerations about agent networks (Keynesianism). Also, simplified nomenclatures are employed in formal models, but their correspondence with empirical ones is not always clear.

Nomenclatures have a further normative aspect, since they reflect a society's conceptions. When used for country comparisons, they already assume that the same classes are relevant at any place and time. When used by the State, they reveal preoccupations in relation to public policy (customs administration nomenclatures). But nomenclatures are increasingly defined by "conventions" accepted and used at an international level. Because they are based on multiple properties that are increasingly exempt of values, they are becoming less subjective. In that way, they are increasingly detached from the "folk" nomenclatures that emerged spontaneously over the course of time (social classes under the Ancien Régime).

In order to be efficient, nomenclatures must be sufficiently stable in structure and interpretation. They nevertheless have to be revised from time to time, for two reasons. On the one hand, knowledge of the economic system becomes keener the more theories evolve, which may explain why it is difficult to classify objects from the present in categories from the past. Existing classes make rough statistical observation possible, but such observation has a retroactive effect on nomenclatures. On the other hand, the economic system evolves and creates original objects (new products, new jobs). When the new products and occupations emerge, the modeler must consider new properties, and create new classes.

Synthesis

Taxonomy is based on different principles in evolutionary biology and economics. In the former, the classification of species is genealogical, reflecting phylogeny and, more recently, the phylogeny of DNA molecules. In economics, classifications of goods or agents are structural, based on properties objects have in common. Yet the two methods of classification have merged to some degree in our era, because economics has begun to study the genealogy and roots of certain similarities between social groups or the technical origin of some innovations.

Another difference lies in the fact that biology is essentially descriptive while economics has a normative orientation. Biological classification is aimed at finding the main bifurcations between species in order to compare their structural properties more efficiently, and identify genuine biological groups (e.g. monophyletic clades, for cladists). Economics classifications were initially oriented towards the identification and regulation of human relationships. Nevertheless, in recent times, these differences have become less marked. Biology has become a public issue, most profoundly with debates on genetic manipulation and stem-cell therapy, and marginally with the denial of evolution and therefore genetic classification. Conversely, economics has tended to become more scientific, at least in its empirical part, using the same taxonomic methods as all physical sciences.

Biological classification is driven by a concern for objective classes and groupings, a concern that ultimately assumes the existence of only one valid classification, whereas economists may propose various a range of equally valid classification systems. By convention, one system is sorted out and institutionalized all over the world.

Finally, in both disciplines, the emergence of new objects triggers new classifications. In biology, this occurred with the rise of molecular biology, and its ability to change the genomes artificially with genes taken from unrelated species. New molecular phylogenies and classifications impact existing morphological systematics, but in turn, are also controlled by them. In economics, new goods or technologies, as well as new jobs or organization modes, periodically require a revision of related classifications.

Communication / Signalling

Evolutionary biology (*J.-B. André*)

Two radically different definitions of communication can be found in biological literature. The first, known as informational, defines communication as the transfer of information, via a signal, between individuals. The second, called adaptationist, belongs strictly to the field of evolutionary biology. It is a more formal definition (since Maynard-Smith and Harper 2003; see also Scott-Phillips 2008). These authors define adaptationist communication as an interaction between individuals in which an individual expresses a trait called a *signal*:

- which affects the behavior of another individual by eliciting a response from it
- which has evolved due to this effect
- which is effective thanks to a response mechanism that has also evolved to be affected by the signal.

The advantage of the adaptationist definition over the informational one is that it distinguishes signaling from other, weaker forms of information transfer, and this is why it is the prevailing choice among evolutionists.

On the one hand, the adaptationist definition differentiates between signaling as communication and the detection of clues that are produced spontaneously. For example, when a predator secretes a scent that alerts its prey, there is undeniably a transfer of information from predator to prey. But it does not qualify as communication, because the odoriferous molecules produced by the predator did not evolve in order to tip off the prey. In this case, it could be said that the predator's odor is a *clue* detected by the prey, not a *signal*.

On the other hand, the adaptationist definition differentiates between communication and a manipulation of behavior. For example, when a carnivorous plant produces a nectar that attracts its insect prey, there is undeniably a transfer of (false) information from the plant to its victims. But it does not qualify as communication, because the insects' response has not evolved to bring about this effect. It can then be said that the plant *manipulates* the insects' behavior, but not that the plant *communicates* with the insects.

In sum, communication is defined by the fact that it is two-way and *adaptive* in nature, rather than accidental or one-way. When one individual affects another's behavior, and the effect is beneficial to both, and the behavior has evolved on both sides because of its benefits, we can

say we are seeing a case of communication. According to this definition, communication raises two evolutionary questions: (1) How can it *evolve*? (2) How can it be *stable*?

Evolution of communication

Communication implies the existence of two mechanisms, a signal and a response, the benefits of which are interdependent. Its evolution, from an initial situation from which it is absent, therefore raises the problem of *priming* (in other words, of “the chicken and egg”). Expressing the signal benefits the sender, because it elicits a response from the receiver, but the receiver’s ability to respond is beneficial only because the signal exists. It would seem that neither side could evolve in the absence of the other.

This is why evolutionists believe communication can emerge only by recycling functions that evolved in the beginning for other reasons. Two possible paths for this emergence have been suggested.

The first path draws on the prior existence of fortuitous clues. For example, the communicative use of urine as a territorial marker probably began because its odor was used by other individuals as a clue that a congeneric was present. This later led to the evolution in behavior consisting in an individual deliberately urinating on the edge of his territory to *signal* his presence. The accidental presence of a clue triggered the evolution of a response mechanism that can be utilized secondarily for true communication.

The second path draws on the prior existence of a one-way manipulation. For example, females of the water mite *Neumania papillator* detect their prey by sensing the vibrations made by the prey in the water. Males of this species have thus evolved the ability to produce the vibrations themselves in order to attract females, which is a form of manipulation. Since the effect also benefits females it is likely that selection operated subsequently to reinforce their ability to respond, thereby giving rise to a true communication system.

Whether communication evolves through either manipulation or the recycling of clues, it invariably necessitates pre-existing conditions. Due to this restriction, communication may never manage to evolve in certain interactions, even when it would benefit both parties.

Stability of communication

The evolutionary interests of the individual producing the signal are not always aligned with the interests of the receiver, and as a result natural selection may promote a form of deception in the communication. In certain cases, this possibility may undermine the reliability of the signal and make communication evolutionarily unstable. There are essentially three main mechanisms guaranteeing the honesty of a signal and the evolutionary stability of the communication.

Firstly, natural selection favors an honest signal when the evolutionary interests of both parties are aligned. This is what occurs in several social animal species, in particular. Due to genetic relatedness, but also due to the fact that these individuals share a common destiny, several mutually beneficial communicative interactions occur in such groups. Consequently, communication is ubiquitous in colonies of eusocial insects, for example, where these interactions make the regulation of the colony's activities possible (the most famous example of this being the bee dance).

Secondly, natural selection favors an honest signal when physiological reasons make deception impossible. The amount of carotenoid pigments in the plumage of certain male birds is an example of a sexual signal, the reliability of which is guaranteed by this very principle. The male bird cannot produce carotenoids; they must be obtained by feeding upon their plant source. The level of carotenoid in the male's plumage is thus an honest signal of his nutritional condition, a signal that females can use to make an adaptive selection.

Thirdly, natural selection favors an honest signal if deception is too costly. This principle, known as the *handicap*, was first suggested by Zahavi (1975) and then formalized by Grafen (1990). It probably plays a role in several sexual signals. For example, the male peacock's tail and the parade behavior associated with it carry a significant physiological handicap. They are so costly that only males that are *truly* extremely strong can allow themselves to express them. In this case, deception is *possible*, but it is not *adaptive*, which guarantees the honesty of the signal.

References

- Bradbury, J. W., Vehrencamp, S. L. (2011): Principles of animal communication. Sunderland, MA: Sinauer Associates..
- Grafen, A. (1990): Biological signals as handicaps. *J. Theor. Biol.* 144:517–46.
- Hauser, M. D., Harper D.J.(1997): *The Evolution of Communication*. Bradford Book.
- Krebs, J. R., Dawkins, R. (1984): Animal signals: mindreading and manipulation. In J. R. Krebs & N. B. Davies eds : Behavioural ecology: an evolutionary approach, pp. 380 – 402, 2nd ed. Oxford, UK: Blackwell.
- Maynard Smith, J., Harper, D. G. (2003): *Animal signals*. Oxford, UK: Oxford University Press.
- Scott-Phillips, T. C. (2008): Defining biological communication. *J. Evol. Biol.* 21:387–395.
- Scott-Phillips, T. C., R. A. Blythe, A. Gardner, and S. A. West. (2012): How do communication systems emerge?, doi: 10.1098/rspb.2011.2181.
- Zahavi, A. (1975): Mate selection-a selection for a handicap. *J Theor Biol* 53:205–214.

Economics (*M. Cozic*)

An economic agent often possesses information that others lack. He may communicate some pieces of information with signals, through behaviors which may or may not be linguistic. Over the past few decades, economic theory and game theory have devoted considerable attention to communication between agents – notably to how communication depends on the structure of the interaction between agents, and especially on their incentives. Such issues find a broad range of applications, from auctions to labor market or the economics of insurance. In what follows, the focus will be on two theories dealing with these issues at a rather abstract level: signaling theory and the theory of mechanism design.¹

Signalling situations

Signalling situations (*lato sensu*) are situations where there is information asymmetry (with respect to some issue or feature) between “informed” and “uninformed” agents. Informed agents may communicate (fully or not) what they know through actions that have some direct consequences (it is typically assumed that they are “costly”). One may distinguish two main categories of signaling situations :

(a) In situations of signaling *stricto sensu*, informed agents make the first move. They choose a signal, and uninformed agents act in a second stage. For instance, on the labor market, in a model like the one proposed by Spence (1973, 1974), it is assumed that workers know their own productive capabilities (their “type,” assumed to be exogenous). They may choose some education level (the signal), the cost of which depends on their productive capability. In the second stage, firms offer wages on the basis of the education level of workers. Game theory studies this kind of situation on an abstract level with “signaling games.”² In these games, the sender observes his type and sends a signal, and the receiver observes the signal and chooses a response. Two families of equilibria then emerge. In “separating” equilibria, the signal sent varies with the sender’s type, and thus carries information about his type. In “pooling” equilibria, senders belonging to different types send the same signal, which is thus non-informative. The ability of signals to transmit information depends on agents’ incentives. Thus, in the abovementioned labor market model, a separating equilibrium requires education costs to be negatively correlated with exogenous productive capabilities.

The fact that signals are (differentially) costly plays a crucial role in (*stricto sensu*) signaling games. By contrast, communication is costless in so-called “cheap-talk games.” In that case, one of the equilibria is non-informative (“babbling equilibrium”). However, some private information may be transmitted in other equilibria, even when the preferences of the sender

¹ The pioneers in both fields were awarded Nobel Prizes: Akerlof, Spence, and Stiglitz in 2001 for their contributions to the theory of markets with asymmetric information, and Hurwicz, Maskin, and Myerson in 2007 for their contributions to mechanism design theory.

² For a survey, see Kreps & Sobel (1994), p. 852

and receiver are not perfectly aligned, and even if there is some information loss (Crawford & Sobel, 1982).

(b) In so-called “screening” situations, uninformed agents act first (Rothschild & Stiglitz, 1976). For instance, insurance companies propose menus of contracts to customers by varying premiums and deductibles. It is assumed that customers (but not firms) know their type (e.g., the probability they will have an accident). The menus of contracts may or may not provide incentives for customers to reveal their type. In such situations, equilibria, when they exist, are typically separating. For instance, high-risk customers choose contracts with fuller coverage and higher premiums, whereas low-risk customers choose contracts with partial coverage and lower premiums.

Mechanism design

Transmission of private information is also at the core of the theory of “mechanism design.”³ The approach, however, is different: it is more prescriptive, and deals not with communication *between* agents but between N agents who hold private information and a mechanism which regulates their interaction. Agents belong to several types -- a type being generally identified to a preference relation on a set X of social outcomes. (X can be a set of possible allocations of an indivisible good, possible provisions of public good, etc). Each agent i knows her own type t_i , but the mechanism’s designer (also called “social planner ») ignores it. The objectives of the designer are expressed by a social choice function which associates a social outcome to each profile of types $t = (t_1, \dots, t_N)$. In order to implement such a social choice function, a mechanism endows each agent i with a set of actions A_i and associates an outcome (in X) to each profile of actions $a = (a_1, \dots, a_N)$. A mechanism and agents’ types jointly induce a game (of incomplete information). A second-price sealed-bid auction for an indivisible good is an example of mechanism. A mechanism is said to *implement* a social choice function if there exists an equilibrium in the game induced by the mechanism that coincides with the social choice function. The mechanism design problem is the issue of knowing, given a social choice function, whether it is implementable. Whereas in traditional game theory a game is given and one wonders which outcome will follow, in mechanism design the “good” outcomes are given and one wonders which game could lead to them.

A fundamental result known as the “revelation principle” states that without loss of generality, one can focus on “direct-revelation” mechanisms (see Myerson, 2008); i.e., mechanisms where an agent’s available actions are messages reporting their types.⁴ A social choice function is incentive-compatible if there is an equilibrium in the direct-revelation mechanism where agents truthfully communicate their types. Incentive-compatibility depends on the assumptions regarding agents’ preferences and on the targeted equilibrium concept. For

³ Cf., for example, Mas-Colell & al. (1995), chap. 23.

⁴ And where the consequence associated with a message profile $t = (t_1, \dots, t_N)$ is what the social choice function associates with $t = (t_1, \dots, t_N)$.

instance, under some assumptions on preferences, reporting the “true” value one assigns to an indivisible good is a dominant strategy equilibrium in a second-price, sealed-bid auction.

References

Crawford, V. & Sobel, J. (1982) “Strategic information Transmission,” *Econometrica*, 50, pp. 1431-1451

Kreps, D. & Sobel, J. (1994) “Signalling” in Aumann, R. & Hart, S. (eds) *Handbook of Game Theory*, vol. 2, chap. 25, Elsevier, pp. 849-867.

Mas-Colell, A., Whinston, M. & Green, J. (1995) *Microeconomic Theory*, Oxford: Oxford University Press.

Myerson, R. (2008) “Revelation Principle” in *The New Palgrave Dictionary*, 2nd. ed., ed. by S. Durlauf and L. Blume. London: Palgrave Macmillan

Rothschild, M. & Stiglitz, J. (1976) “Equilibrium in Competitive Markets: An Essay on the Economics of Imperfect Information,” *Quarterly Journal of Economics*, 80, pp. 629-649.

Spence, M. (1973) “Job Market Signaling,” *Quarterly Journal of Economics*, 87, pp. 355-374.

Spence, M. (1974) *Market Signaling*, Cambridge: Harvard University Press.

Synthesis

The parallel between biology and economics is quite strong regarding communication and more precisely signalling theory (“costly signalling” in biology). The two versions of the theory are identical, point by point, and were successful in both fields. The notion of “screening,” however, is specific to economics, and almost totally absent from biology (see only Archetti et al. (2011) in an explicit reference to economics). But this difference is undoubtedly due more to a terminological contrast than to a substantial one: evolutionists speak of “signalling” for interactions that economists would describe as “screening.” For example, in many courting behaviors, females incite males to compete with them in order to make them reveal their strength. For an economist, this behavior would be a form of screening, since the uninformed agent (in this case, the female) takes the initiative. For an evolutionist, this behavior is a standard case of signalling, because the male is the one who reveals the information.

A more substantial contrast between the two fields of study involves the importance granted to situations of disequilibrium. Economists are chiefly interested in states of equilibrium (and in the question of whether communication takes place there), while biologists are also interested in whether states of disequilibrium lead to the emergence of communication. Hence biologists attribute considerable importance to the distinction between communication and other, weaker forms of information transfer (manipulation, clue detection), even though these weaker forms are *never* equilibria since they have the

potential to give rise to the evolution of countermeasures coming from the manipulated party (or the party observed without his knowledge). But these weaker forms of information transfer interest biologists due to their functional *parsimony*: they do not require that the two partners in the interaction (sender and receiver) be endowed with a function specifically dedicated to information transfer. As a result, they can evolve without raising the problem of priming, and therefore play an essential role in the emergence of communication systems.

References

Archetti, M., Scheuring, I., Hoffman, M., Frederickson, M.E., Pierce, N.E. and Yu, D.W. (2011), Economic game theory for mutualism and cooperation. *Ecology Letters*, 14: 1300-1312.

Competition

Evolutionary biology (*J. Gayon*)

Darwin saw competition as the principal component of “the struggle for existence,” and recognized three types: competition between individuals in the same species; between individuals from different species; and between living organisms and the external physical conditions of their habitat. Competition involves only the first two instances and essentially refers to the organisms’ degree of success in the matter of survival and reproduction. Although Darwin acknowledged competition phenomena between individuals from the same species and individuals of different species alike, he was convinced that the more closely the competitors were related, the fiercer the competition would be. Consequently, the most severe competition occurs between individuals from the same species (Darwin 1859, 121). Hence, the Darwinian concepts of competition and natural selection are closely related (see SELECTION). Nonetheless, they are not identical: competition, resulting from the Malthusian doctrine (conflict between reproductive rate and available resources) is only one condition needed for natural selection, which additionally requires that traits vary and be heritable.

The modern concept of competition is affected by significant ambiguities. The first arises from the proximity between competition and “struggle for existence.” Does competition between organisms include an element of “struggle,” or, more precisely, interaction, or not? The word actually covers two categories of different phenomena: on the one hand, an “active” competition, where individuals or populations compete for limited resources by interfering with each other; and on the other hand, a “passive” competition, in which competitors do not interact directly and are simply searching for the same resource. This question has sharply divided opinion among ecologists. From an evolutionist perspective, it is moot, because what matters in that case is whether the limitation of resources has a differential effect on survival and reproduction. According to this viewpoint, any increase in a resource for one partner results in a loss for the others, whether or not there is interaction (see RESOURCE).

From an evolutionary viewpoint, one difficulty with the concept of competition is its proximity to the concept of natural selection. The closeness is due to the standard Darwinian definition which sees competition wherever there is a difference between survival and fertility (see SELECTION). Another difficulty with the Darwinian concept of competition arises from its application on several levels: the individual one — that of natural selection in the standard sense, where it is meaningful to speak of “differential survival *and* fertility”; that of the group, where the notions of fertility and reproduction are problematic (Okasha 2006), while other concepts, such as differential persistence and fragmentation, must be employed. At this point, ecology, which has traditionally considered competition as referring specifically to its field, comes in. In ecology, the concept of competition has primarily been applied at the level of species, giving rise to the crucial question of its role within an explanation of the regulation of population size (Kingsland 1995). Competition is then the effect of a demand, by organisms from two or more species, for a finite resource. In the 1920s, Gause, one of the pioneers of interspecies competition studies, formulated a doctrine of competitive exclusion. According

to this principle, two species that are ecologically identical cannot coexist. In other terms, two species cannot coexist unless their ecological niches are different (Hutchinson 1957). In reality, competitive exclusion does not occur unless one species produces enough individuals to keep another population from growing. For example, two moth species, A and B, can each colonize a different type of tree (oak and pine), but each with a preference. Species A, preferring oak, will not eliminate species B, preferring pine, unless enough individuals spread to the pine to eliminate species B (or vice-versa).

Ecologists treat competition phenomena by using growth equations. Considered in isolation, a given species grows according to the logistical equation $dN_1/dt = r_1N_1 (K_1 - N_1/ K_1)$ in which N is the number, r the natural rate of population growth, and K_1 is the carrying capacity of species 1 (that is, the maximum number of individuals the habitat can support). When N_1 reaches K_1 , $dN_1/dt = 0$, and growth stops. If there is a competitor (N_2 being the number), the previous equation can be modified by introducing the term αN_2 , which expresses the reduction of species 1's K_1 due to the presence of species 2: $dN_1/dt = r_1N_1 (K_1 - \alpha N_2 - N_1/ K_1)$. By reasoning in a parallel way about species 2, a system of two competition equations is obtained, and the circumstances whereby the two rates of population growth cease can be determined. This means of operating makes it possible to show that in certain conditions, one species eliminates the other, and in other cases, they coexist.

Thus, the ambiguities of the concept of competition have resulted from: (1) its proximity to the Darwinian notions of struggle for existence and natural selection; (2) the usage of the word in the context of two different fields, ecology and evolutionary theory. An unambiguous operative concept of competition can be found in ecology. The explicitly economical nature of the ecological concept (in terms of active demand for a limited resource) deserves emphasis.

References

- Darwin C. (1859): *The origin of species*. London: John Murray.
- Hutchinson, E. (1957): Concluding Remarks. *Cold Spring Harbor Symposium, Quantitative Biology* 22: 415–427.
- Kingsland, S. (1995): *Modeling Nature: Episodes in the History of Population Ecology*. Chicago, IL: University of Chicago Press.
- Okasha, S. (2006): *Evolution and The Levels of Selection*, Oxford University Press.

Economics (M. Cozic)

Competition has played a central role in economic thought since the beginnings of the discipline in the 18th century (Stigler, 1957; McNulty, 1968). However, the term is not unambiguous – across both periods and contexts (Vickers, 1995). The initial meaning consists in the application to economic contexts of the ordinary concept of competition, that could

roughly be characterized as a situation of *rivalry* between several agents, each of whom wants to obtain something that they cannot all obtain (Stigler, 1987/2008). In trade situations, competition can be viewed as follows: two participants in a trade system are competing if it is possible for them to trade with the same participants, and if the action of one agent is liable to impact the benefits that the other may draw from the trade. Economic theory draws much attention to a polar case called "perfect competition." A market is perfectly competitive if it satisfies a set of conditions, most notably the following ones:

- (1) the goods exchanged on the market are homogeneous and perfectly divisible;
- (2) exchanges are mediated by prices;
- (3) unit prices are uniform;
- (4) consumers and producers consider prices as exogenous (they are "price takers"), and
- (5) all know prices and goods perfectly.

This list of conditions is not completely stable across the literature. Condition (4) is front and center, because it is supposed to express the idea of a maximal level of competition among participants. Intuitively, there are so many competitors that no single one considers himself as able to influence prices through his purchasing or selling decisions (i.e., as having "market power"). Perfectly competitive markets are typically represented by the *Walrasian model* (see Debreu, 1959), which integrates the above mentioned conditions and the assumption that an equilibrium is reached ("Walrasian equilibrium"); i.e., that the prices and choices by economic agents are such that each economic agent acts optimally, given prices, and that supply equals demand for each good ("market clearing"). Microeconomic theory has studied the properties of Walrasian markets, notably their ability to realize efficient (or "Pareto-optimal") allocations of goods ("fundamental welfare theorems"). Note that, by itself, the model remains silent on the issue of how the prices are determined.

"Imperfectly competitive" markets refer mainly to economies where agents (and, especially, firms) are not assumed to be price-takers (i.e., they violate condition (4)). For instance, a pure monopoly is an economy where some good is produced by only one firm. In this case, the firm chooses both its production level and the price of the good. Oligopolies are intermediate cases where a small number of firms are on the market. In order to study them, one needs models of strategic behavior, which belong to game theory. Situations of imperfect competition are not the only violations of the Walrasian model. For instance, there are situations where agents have asymmetric information about the good exchanged (see Akerlof 1970). In cases of so-called "externalities," some agents are impacted "directly" (i.e., without the mediation of prices) by the action of other agents – industrial pollution is a classic example (see Laffont, 1988). Violations like these typically entail *market failures*: it's no longer the case that equilibria are Pareto-optimal. One of the aims of "public economics" is precisely to study how public policy may promote efficiency in such situations.

The technical concept of competition, based on the notion of perfect competition, does not exhaust the use of the term in economic analysis. Economists sometimes rely on the ordinary

concept without attempting to characterize it. Interactions between ordinary and technical concepts are particularly important in the field devoted to the policy and regulation of competition, which lies at the boundary between economics and law. More critically, it is sometimes held that there are dimensions of competition (in particular a *dynamic* dimension) that go beyond the technical concept and are important for the understanding of economic phenomena (see, e.g., Hayek 1948 and Schumpeter 1942). The dynamic dimension of competition is also at the heart of the analysis of markets by evolutionary economics (Lesourne et alii, 2006). It has notably studied the idea made famous by Alchian (1950) and Friedman (1953), according to which competition on markets is analogous to natural selection and only optimizing firms survive in the long run.

References

- Alchian, A. (1950) "Uncertainty, evolution, and economic theory", *Journal of Political Economy*, 58, pp. 211-221.
- Akerlof, G. (1970) "The Market for Lemons: Quality Uncertainty and the Market Mechanism," *Quarterly Journal of Economics*, 89, pp. 488-500
- Debreu, G. (1959) *Theory of Value*, Cowles Foundation Monograph, New Haven: Yale UP
- Friedman, M. (1953) *Essays in Positive Economics*, Chicago: University of Chicago Press
- Hayek, F. (1948) "The Meaning of Competition" in *Individualism and Economic Order* Laffont, J. (1988) *Fundamentals of Public Economics*, Cambridge, Mass: MIT Press.
- Lesourne, J., Orléan, A. and Walliser, B. (2006), *Evolutionary Microeconomics*, Springer-Verlag.
- McNulty, P. (1968) "Economic Theory and the Meaning of Competition," *The Quarterly Journal of Economics*, 82(4), pp. 639-56.
- Schumpeter, J. (1942) *Capitalism, Socialism and Democracy*.
- Stigler, G. (1957): *Economic Theory and the Meaning of Competition*
- Stigler, G. (1987/2008) "Competition" in Durlauf and Blume (eds.), *The New Palgrave Dictionary of Economics*. Second Edition. Palgrave Macmillan.
- Vickers, J.S. (1995) "Concepts of Competition," *Oxford Economic Papers*, 47(1), pp. 1-23

Synthesis

Although the term competition always deals with a type of interaction among different units (i.e., either economic or biological), it appears to have different connotations in economics and evolutionary biology, notably in terms of its consequences. Economists consider competition as an essential component of the process that leads to a balance, where prices equalize supply and demand. This balance thus primarily occurs among producers facing

consumer demand. When the system deviates from this equilibrium, perfect competition ensures that it is again attained by a concomitant adjustment of the quantity of goods produced and of their price. In general, it does not entail a change in the number of entities that interact.

In evolutionary biology and ecology, competition is strictly associated with the struggle for existence and takes place among individuals or species with different abilities in exploiting a limited set of shared resources. The principle of competitive exclusion, whereby only the fittest of these variants will survive in a given ecological niche, is a key concept in linking the ecological and the macroevolutionary processes.

If consumers were interpreted as resources, and producers as species exploiting such resources (with an interesting transposition in connotation), a parallel could be drawn between the principle of competitive exclusion (Hardin, Science 1960) and the fact that when the units in competition share the same objective, only the best performing will be present at equilibrium. A by-product of this is that no more species than resources can coexist, the others being doomed to extinction. In the case of firms competing for consumers, this outcome is partially prevented by the fact that firms, unlike biological organisms, can merge. If on the one hand, the merging process reduces the number of competitors below the threshold implying their mutual exclusion, on the other hand, it paves the way to the pathology of monopolistic regimes. In biology, it is often observed that more species exist than resources, stressing the limits of competition in selecting some of these species to the detriment of others. In classical economics, the accent is on the fact that competition guarantees optimal economic exchanges and thus leads to general benefits.

Constraints/Trade-off

Evolutionary biology (*P. Huneman*)

Through increasing fitness, cumulative natural selection shapes traits towards optimization with regard to environmental demands (see OPTIMALITY). Nevertheless, the fact that an organism has several traits and faces several distinct environmental demands leads to the possibility of trade-offs between them. In behavioral ecology, defined as the study of the (often adaptive) origin and value of phenotypic traits, trade-offs are crucial to explaining the actual value of traits. Therefore, trade-offs must be built into optimality models.

Even though differences are not clear cut, it is useful to distinguish several kinds of trade-offs, according to whether they concern selective pressures, traits, or fitness itself. Trade-offs may indeed occur (a) between two selective pressures that bear upon the same trait (e.g., a selective pressure to display few colors in order to avoid predators, and another selective pressure, e.g., a selective pressure to display bright colors to attract females). Or they may occur (b) between the traits themselves: for instance, if selection optimizes a red deer's speed, regarding predators as a selective pressure, it also raises the overall metabolic costs. These costs concern all other traits and therefore negatively impact the selection on them; the resulting actual speed that evolves under selection will be a fitness maximizing trade-off between selection for speed and the metabolic cost paid by all organs. (This trade-off can ultimately be reduced to the previous kind, though for the sake of simplicity, it's better to differentiate between them here). Finally (c), given that fitness is a compound magnitude, made up of survival and reproduction, there may be some trade-offs between survival and reproductive values (to the extent that survival is seen as a legitimate component of fitness in actual populations, as it is done in some simple population genetics models). For example, cottonwood tree branches are thin and fragile, which seems to decrease the survival chances of the tree itself. Yet they actually improve the number of offspring by enhancing seed dispersal (less fragile branches of variant cottonwood trees break less easily and therefore retain their seeds; Endler 1986). Here, the reproduction component of fitness leads to the reproductive optimality of a trait at the expense of the robustness and plausible survival of the whole organism. Even though many trade-offs can ultimately be seen as concerning fitness, in the literature, most talk is about trade-offs between traits.

Trade-offs can occur at various levels, each conditioning the next one. *Physiological* trade-offs concern the allocation of resources to different traits of a single individual, when these traits directly compete for a finite amount of resources that the organism can gather. These trade-offs are studied by comparing rates (metabolic, growth, reproductive, etc.) measured in energy per unit of time. For instance, lactating female red deer cannot store as much fat reserve for the

winter as non-nursing females: this defines a reproductive cost, which will be crucial for determining the evolution of the average offspring size and litter size of the species, and hence constrains adaptation.

Microevolutionary trade-offs are based on the former as soon as there is genetic variation in these traits: selection will favor the value of paired traits that maximizes fitness in a given environment. Individual plasticity can also evolve from these trade-offs. *Macroevolutionary* trade-offs take place within lineages, when negative correlations between trait values are visible in different species of a lineage.

Trade-offs often appear as correlations between varying phenotypes. They can be attested by manipulating one phenotypic value or selecting artificially for one value of the trait, or by directly looking for genetic correlations.

Many trade-offs have been investigated by behavioral ecologists, in general concerning longevity or growth vs. reproduction (e.g. male fruit flies courting virgin females invest more energy than those living with mated females, and live shorter lives); reproduction vs. condition (in aphids, the more gonads the less fat); offspring size vs. number (e.g. small primates have large litters, while large primates have single offspring). The field of “life history theory” (Stearns 1992) explores trade-offs between investments at various stages of the life cycle in various species, and is essentially determined by the intrinsic nature of fitness as a trade-off. Trade-offs taking place in time are of paramount importance for evolution; especially, different environments will favor different trade-offs between *current vs. future reproduction*, and theories of senescence and lifecycles are elaborated on these grounds (Williams 1957). The curvature of the trade-off functions (between reproduction and survival, or current vs. future reproduction) generally predicts the evolutionary response to selection: whether organisms will invest in current reproduction rather than survival, or postponing some reproduction to the future, will depend on whether the correlation is a concave or convex function.

Trade-offs clearly constrain evolution. However, this is not the only meaning of “constraint.” The so-called “adaptationism controversy” was triggered by Gould and Lewontin (1978), who famously argued that many trade-off optimality models are not falsifiable (that is, they are “just-so stories”) because they can always appeal to postulated environmental demands as hidden variables. They also put forth the idea that some constraints on evolution are different from trade-offs in the previous, strict sense, since they bear on the scope of *variation* rather than on the potential for *selection*.

The issue boils down to the distinction between a trait value that is not reachable by genes or developmental systems (constraint), and a trait value that could be there but is tied to another trait which makes it fitness-hampering (trade-off). This distinction can be empirically made when there is evidence that the impossible trait is physically unavailable, or correlated to an unreachable trait value. But even though it is impossible to determine the issue empirically, , the two states of affairs just mentioned are logically different.

Some constraints are purely physical or *morphological*, while others are due to the *history* of the lineage. Morphological constraints may appear as correlations (the variation of one trait entailing the variation of the other through the laws of physics or chemistry). Historical constraints can be understood as *entrenched* traits – namely, so many other traits have subsequently been built on a given trait that any modification of such a trait will be too costly and then counter-selected – which eventually can also be seen as a sort of trade-off. Finally, *developmental* constraints, the most greatly emphasized category (especially by Evo-Devo researchers), are due to the mechanisms producing genotypic or phenotypic variation, that are such that only a small range of the variation needed for selection to bring about an optimal trait value could actually be reached by the developmental system, whatever the possible mutations. A case can be made that this latter sense of constraint is the most irreducible to adaptationism and then to classical Modern Synthesis methodology in evolutionary biology (Amundson 1994). Such constraints can be experimentally investigated now especially in cases of parallel evolution (Brakefield 2008), bringing a more empirical character to the adaptationism debate.

While trade-offs are modifiable, constraints seem untouchable; though this depends upon the timescale: constraints at a small timescale may be superseded on a very long timescale (Maynard-Smith et al 1985).

References

Amundson, R. (1994): Two Concepts of Constraints: Adaptationism and the Challenge from Developmental Biology, *Philosophy of Science*, 61(4): 556–578.

Brakefield PM. 2006 “Evo-devo and constraints on selection“. *Trends Ecol Evol*. 21(7): 362-8.

Endler J. 1986. *Selection in the Wild*. Princeton: Princeton University Press.

Gould S.J., Lewontin R.L. 1979 “The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme“ *Proc. R. Soc. Lond. B*.205: 581–598

Maynard Smith, J., Burian, R., Kauffman, S., Alberch, P., Campbell, J., Goodwin, B., Lande, R., Raup, D. Wolpert, L. (1985) “Developmental Constraints and Evolution“. *Quarterly Review of Biology*, 60, 265–287.

Stearns S. (1992) *The evolution of life histories*. Princeton University Press.

Williams G. 1957. “Pleiotropy, natural-selection, and the evolution of senescence“. *Evolution*. 11:398–411.

Economics (*M. Cozic*)

The notions of trade-offs and constraints are used mainly to conceptualize economic agents' choices. Constraints play a key role in economic theory, which typically views economic choices as optimizations under constraints (see OPTIMALITY). Trade-offs are often put forward in basic introductions to economic analysis but occupy a more informal role in advanced

presentations of the theories where the concepts of preferences and choices take center stage.

Constraints determine the set of options among which an agent can choose (also called the “feasible set” or the “opportunity set”). Two basic examples come from consumer theory and the theory of the firm (see for instance Mas-Colell & al. 1995). A consumer chooses a bundle of goods from among a feasible set (sometimes called in this context the “budget set”) which is determined by market prices p and by the consumer’s income i : a bundle of good x satisfies the constraint if $p \cdot x \leq i$. Similarly, the technology on which a firm relies circumscribes the goods it can produce (its “outputs”) from factors of production (or “inputs”). Thus, the firm’s feasible set (also called the “production set”) can be modeled as a set of vectors, each vector describing the outputs produced by some inputs. Constraints may be physical or institutional (especially, legal) and thus more or less difficult to circumvent.

The agent’s dispositions to choose are described by a “choice function” which specifies, for each set of possible constraints (e.g., some market prices and some budget), the option(s) that the agent is disposed to choose when he or she faces the choice set induced by the given set of constraints. One basic economic prediction method consists in recording the behavior of agents under some constraints. On this basis, one can infer what they are disposed to choose in new circumstances (i.e., under other sets of constraints). The strength and the quality of the prediction depend on the assumptions made about the choice function.

In general, constraints are supposed to be exogenous to the decision maker. However, when one considers a series of decisions distributed over time (situations of “intertemporal choice”), constraints may be endogenous. Like Ulysses who asked his men to tie him to the mast so that he would not abandon the ship when he heard the sirens singing, an agent may constrain his or her own future behavior in order to resist temptation. One may analyze in this way such savings account mechanisms as the “Christmas Club,” whereby borrowers make weekly deposits without any withdrawal until right before the end of the year and without any substantial interest. In a strategic context, it may also be in an agent’s interest to restrict the options that will be available to him or her in order to influence the behavior of another agent (Dr. Strangelove’s famous *doomsday device* may provide an illustration).

The notion of trade-off is relevant when the options that an agent considers may be evaluated according to several dimensions. For instance, cars may be evaluated according to safety, fuel consumption, speed, etc. Choices are relatively simple when one option is better than the others according to all dimensions. In this case, no trade-off is necessary; i.e., there is no need to find a compromise when the values of the dimensions are integrated. In general, however, the constraints that the agent faces make trade-offs indispensable. For instance, among the job proposals open to a job seeker, there may not be one that maximizes both salary and days off. If, *ceteris paribus*, the job seeker prefers a better salary and more days off, then he or she will have to make a trade-off between these two dimensions.

Conventional economic theory of choice assumes that agent's preferences are complete (for any pair of options (x, y) , x is weakly preferred to y or vice-versa) and transitive (if x is preferred to y and y is preferred to z , then x is preferred to z). One way to interpret these hypotheses is that they assume that the agent is always able to compare different trade-offs and that he or she does it in a coherent way. In addition, the hypothesis according to which the agent chooses an optimal option with respect to his or her preferences can be interpreted as claiming that he or she chooses the option that constitutes the best trade-off from his or her point of view.

The concepts of constraints and trade-offs can be transposed to the macroeconomic level, especially in the context of macroeconomic policy. Feasible sets are typically associated with several macroeconomic "instruments" (i.e., intervening variables; for a seminal introduction to this framework, see Tinbergen 1952). Institutional constraints often forbid the same policy maker from controlling distinct types of instruments. For instance, in many countries, monetary policy is conducted by the central bank (through, e.g., the control of money supply) whereas fiscal policy is conducted by the government (through taxes, public expenditure, and borrowing, etc.). In addition, legal restrictions may limit the actions of each policy maker. The consequences of economic policy depend on the relationships between macroeconomic variables. For instance, macroeconomic policy has been much influenced by the hypothesis according to which inflation and unemployment are inversely related ("Phillips curve"). When a macroeconomic policy tries to influence several target variables simultaneously, trade-offs arise more often than not. For example, when the assumption of a Phillips curve is made, a macroeconomic policy targeting both inflation and unemployment has to look for a good trade-off between these two variables.

References

Mas-Colell, A., Whinston, M. & Green, J. (1995) *Microeconomic Theory*, Oxford: Oxford University Press.

Tinbergen, J. (1952); *On the Theory of Economic Policy*, Amsterdam: North-Holland.

Synthesis

In both economics and evolutionary biology, the optimization carried out by natural selection or rationality operates under certain exogenous constraints. Environment, limits, or bias on variation (particularly on genetic mutation) restrict the area in which natural selection will operate. Rational economic decisions respect physical or institutional constraints. True, the restriction is usually contained within a time frame, and in the long term, may turn out to be avoidable.

In both fields, trade-offs are an intrinsic part of the dynamics / action of natural selection or rational thinking. In nearly every case, there is no single trait that maximizes fitness in relation to every single selection pressure, just as there is no absolute dominant relationship that can

be considered between economic gain options. For this reason, fitness will internalize trade-offs between different phenotypic traits or selection pressures, and the way preferences are defined will operate trade-offs between goods and baskets of goods. In every case, “trade-off” designates both the area of possible combinations and the solution that will be selected by the optimizing procedure within this area; i.e., the optimal compromise.

Although the notion of trade-off itself is not the subject of any thematic elaboration in economics, in evolutionary biology the idea is directly challenged and developed. The reason for this difference is primarily the major epistemological problem that is raised by the distinction between two kinds of constraints, namely on one hand allelic mutations that may be constrained for some biochemical reason and therefore impose a constraint on variation, and on the other hand the existence of a trade-off between selection pressures or phenotypic traits, which means that environmental demands, or the multiplicity of traits on organisms, impose a constraint on the optimization that selection is supposed to carry on. In this latter case, there exists an epistemological alternative opposing explanations resorting to the genesis of possible variations (as defended by evolutionary developmental theorists or Evo-Devo) , and explanations resorting exclusively to natural selection (as supported by orthodox Darwinians since the Modern Synthesis). The next point relevant to constraints and proper to biology while absent from economics consists in the structure of fitness, which is intrinsically a trade-off between survival and reproduction; this trade-off that can be carried out multiple times in various models and then variously modeled: for instance, some basic models of population genetics can be centered on survival whereas others focus on reproduction.

Constraint is the subject of direct thematic reflection in economics, especially when it moves from being exogenous to being endogenous, in the case of intertemporal choice (the constraint on the choice being the result of the agent’s rational decision at an earlier point in time). This thematic insistence contrasts with evolutionary biology, where the term “constraint” is most often applied to a limitation on the classic selectionist paradigm (as the evolutionary developmental theorists argued).

Cooperation

Evolutionary biology (*J.-B. André*)

In evolutionary biology, when an individual, known as the agent, does something that boosts the reproductive success of another individual, known as the receiver, the two are said to engage in cooperation. The term can apply to behavioral traits as well as molecular or morphological ones. For example, the formation of biofilms in certain microorganisms or the exchange of nutrients between plants and fungi are cooperative, even if they are not behavioral.

Often, an individual has positive effects on another quite accidentally. For example, animal excrement benefits the organisms that feed on it; shade cast by plants benefits the animals who shelter beneath it, etc. However, this category of phenomena is too broad to be included in the concept of cooperation. To narrow it down, an extra condition is added to the definition: a cooperative trait has to have evolved specifically in order to produce a social benefit. When the benefit is fortuitous, as it is in the cases above, it is termed a “by-product benefit,” rather than cooperation.

Cooperative phenomena are typically observed in three great functional domains of the living world. (1) The care adults provide for the young. For example, certain birds and insects raise their young collectively (this is called “cooperative breeding”). (2) The acquisition of food. For example, many carnivores hunt as part of a coordinated group (this is called “pack hunting”). (3) Protection from predators. Individuals in a colony rely on the watchfulness of their neighbors to warn them of the danger of a predator (this is called “collective vigilance”).

Perpendicular to these functional domains, based solely on the quantitative effect of the traits on individual reproductive success, two forms of cooperation can be observed (see fig. 1). When a cooperative trait benefits the receiver and *costs* the agent, it is called *altruism* (see ALTRUISM). When a cooperative trait benefits both the receiver and the agent, it is called *mutual benefit* (the term *mutualism* is generally reserved for interactions between different species). Thus, two types of evolutionary mechanisms lie at the source of cooperation. Altruistic traits can evolve if the agent and receiver are genetically related: this is the principle of kinship selection (see ALTRUISM). Mutual benefit traits do not necessitate the existence of kinship, and evolve under the influence of two types of mechanisms.

Reciprocity

By redistributing some of the benefits, an individual’s active, reciprocal response to assistance supplied by another can make this assistance mutually advantageous. This mechanism, initially theorized in economics, has given rise to a large number of theoretical developments

in evolutionary biology. Nevertheless, in species other than *Homo sapiens*, relatively few examples of reciprocal cooperation have been demonstrated. For example, it has been shown that impalas groom each other reciprocally, removing lice, or that certain birds help each other in this way to rid each other of predators. But many biological observations that were initially considered to be cases of reciprocity were subsequently challenged. Reciprocal cooperation remains a fairly marginal phenomenon in biology.

Actually, the most common form of conditional cooperation in biology is probably one that differs slightly from the standard model of direct reciprocity. It is the mechanism known as “partner selection”: individuals respond to a partner’s quality by deciding either to maintain or to cease interaction with him (in some cases, to interact with another partner instead), rather than by reciprocating in the strict sense of the term (see MARKET). This mechanism has been observed in several biological systems, especially in interactions between plants and *Rhizobium*, and in social exchanges between certain non-human primates. However, it is still clear that, in the form of partner choice or strict reciprocity, the intensity and richness of the reciprocal exchanges occurring in biology is incomparable to what is observed in human beings. The great majority of the forms of biological cooperation are the result of a much simpler mechanism: interdependency.

Interdependent cooperation

In the absence of an active reciprocal mechanism, it is sometimes *directly* advantageous to help other individuals. For example, birds called “honeyguides” or “indicator birds” actively show humans where bee colonies are located. They then feed on the larva and wax remaining after the humans have opened the hive. Likewise, for a plant that relies on the presence of a fungus for access to mineral salts, it can be advantageous to provide resources that help the fungus develop. A third example, that of pack hunting, implies a coordinated action that benefits each of the individuals through the positive effect of the group’s success as a whole.

The common point between all these traits is that they are adaptive for the individuals that express them, because these individuals are structurally *dependent* on their beneficiaries, and thus share in their success. The term interdependent cooperation is applied to these interactions, although it should be noted that, in the literature, other terms are also used to describe this type of situation: “coordinated by-products,” “investment in by-products,” and “pseudo reciprocity,” depending on the case. It should also be noted that within the framework of group actions of the “snowdrift game” type, some authors have described this type of situation as “weak altruism” (see ALTRUISM).

As is the case with all types of biological traits, but particularly with cooperation traits, two evolutionary questions must be raised: that of emergence and that of stability. To examine the stability of cooperation is to reflect on the problem of cheaters and, more generally, on the inevitable existence of conflicts of interest between the parties involved. To investigate

the emergence of cooperation is to reflect on the evolutionary transition from a situation in which individuals do not cooperate to one in which they do. The two questions raise distinct problems. For example, in the game known as the Stag Hunt, cooperation consists in pursuing a large prey cooperatively rather than a small prey alone, and it benefits the whole pack of hunters. It therefore does not pose any problems of stability (there is no advantage in cheating). Yet the evolution of cooperative strategy based on social strategy raises the question of priming, because the first cooperative mutant is never favored. Likewise, in the case of reciprocity, even when reciprocal cooperation is evolutionarily stable, its emergence is not guaranteed, due to the same problems of priming.

		<i>Effect on the receiver</i>	
		+	-
<i>Effect on the agent</i>	+	Mutualist cooperation	Egoism
	-	Altruistic cooperation	Malevolence

Figure 1

References

- Trivers, R. L. 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology* 46:35–57.
- Axelrod, R., and W. D. Hamilton. 1981. The evolution of cooperation. *Science* 211:1390–1396.
- Leimar, O., and P. Hammerstein. 2001. Evolution of cooperation through indirect reciprocity. *Proceedings of the Royal Society B: Biological Sciences*.
- West, S. A., A. S. Griffin, and A. Gardner. 2007. Social semantics: Altruism, cooperation, mutualism, strong reciprocity and group selection. *Journal of Evolutionary Biology* 20:415–432.
- Hart, B. L., and L. A. Hart. 1992. Reciprocal allogrooming in impala, *Aepyceros melampus*. *Animal Behaviour* 44:1073–1083.

Economics (*M. Cozic*)

The notion of cooperation belongs primarily to game theory. Its status is quite paradoxical. On the one hand, it has been at the center of a multitude of theoretical and empirical studies. Moreover, the notion of cooperation has often been used to export the insights of game theory to other social sciences. On the other hand, cooperation is not explicitly defined in full

generality.⁵ It is rather applied to some paradigmatic games where it refers to specific behaviors – roughly speaking, behaviors that benefit other people. Consider for instance the Prisoner’s Dilemma, a symmetrical 2-player game where each player can either “confess” (C) or “deny” (D). The payoffs are as follows:

		Player 2	
		Confess (C)	Deny (D)
Player 1	Confess (C)	(3,3)	(0,4)
	Deny (D)	(4,0)	(1,1)

Figure 1: Prisoner’s Dilemma.

Action C is said to be cooperative, ostensibly because it benefits the other player whatever action she chooses. Action D is dominant: whatever action is chosen by the other player, it is in one’s player interest to play D. The profile (D, D) is the only Nash equilibrium of the game. It is, however, *Pareto-dominated* by mutual cooperation (C, C): each player prefers (C, C) to (D, D). In other words, if the players do not cooperate (play D), they will be worse off than they would be if they all were cooperating, but it is in each player’s interest not to deviate from (D). Consider now the *Stag Hunt* game where each player can either hunt a stag jointly with the other player, or hunt a hare alone.

		Player 2	
		Stag	Hare
Player 1	Stag	(4,4)	(0,2)
	Hare	(2,0)	(2,2)

Figure 2 : Stag Hunt game.

The actions profile (stag, stag) is also called cooperative. By contrast with (C, C) in the Prisoner’s Dilemma, (stag, stag) is a Nash equilibrium. There exists a second equilibrium (hare, hare) which is Pareto-dominated by (stag, stag). In both games, one may consider that there is a “cooperation problem” because equilibria *lead or may lead* to Pareto-dominated outcomes (and thus miss mutual benefits).

⁵We will not deal with the distinction between “cooperative” and “noncooperative” game theory. Noncooperative game theory studies the interaction of players who may conclude binding agreements.

In market analysis, cooperation is related to “free-rider problems” raised notably by *public goods*. A good is a (pure) public good when its consumption by one agent neither forbids nor reduces its consumption by other agents (*non-rivalry*) and when every agent can consume it (*non-exclusion*). National defense, air quality, radio signals, or public roads are often cited examples of (not necessarily pure) public goods. Public goods raise an incentive problem: since no one can be excluded from consumption, it is in each agent’s interest to rely on others - i.e., to *free-ride* - to contribute to the public goods. As a consequence, they create *inefficiency* in markets. Similar problems arise with common resources (grazing lands, fisheries, groundwater) which are rivalrous in consumption but not excludable (Hardin, 1968). In this case, individual incentives lead easily to overuse of the resources. The relation between free-rider problems and cooperation problems (as they appear in game theory) is made salient by so-called “public goods games.” In a public goods game, each player $i \in N$ has an initial endowment z_i and chooses a level of contribution c_i to the public good. A quantity $g(\sum_{j \in N} c_j)$ of the public good is then produced ($g(\cdot)$ is supposed to be an increasing function), and each player receives $g(\sum_{j \in N} c_j)$. At the end of the game, the payoff of player i is thus $z_i - c_i + g(\sum_{j \in N} c_j)$. In the simple case where $g(x) = m \cdot x$ with $0 < m < 1$, it is a dominant strategy for each player to provide *no contribution* ($c_i = 0$) to the public good. When $z_i = z$ and $m > 1/N$, *full contribution* ($c_i = z_i$) Pareto-dominates no-contribution. The situation is thus very similar to a Prisoner’s Dilemma.

The generic term “cooperation problems” can be used to cover both free-riding problems and cooperation problems in game theory.⁶ Cooperation problems raise several issues that have been tackled by economists and game theorists for decades. One of them is to determine which changes in the initial situation enable rational choices to be cooperative. Two main factors, time and uncertainty, have been investigated, sometimes jointly.⁷ For instance, game theorists have deepened the intuitive idea according to which it may be in one’s own interest to be cooperative, when one has to interact repeatedly with the same person. Theoretical analysis of the Prisoner’s Dilemma shows that, when the game is repeated infinitely, strategies inducing cooperative behaviors are among equilibria (“*folk theorem*”). However, when the repetition is only finite (and players know it), there is no cooperation in equilibrium. A second issue is to know how people really do behave in cooperation problems. Experimenters have observed the behavior of subjects in a wide range of variations around Prisoner’s Dilemma, Stag Hunt or Public Goods games (see e.g. Ledyard, 1995). In original games, fairly high levels of cooperation are recorded – and they are all the higher when players can communicate beforehand. Cooperation decreases when the game is repeated. But it can again rise to a high level (before decreasing again) when a new series of repetitions is launched (“restart effect”).

⁶ In political science, the phrase “problem of collective action” is often used.

⁷ See the paper by Kreps, Milgrom, Roberts, and Wilson (1982), showing that in the repeated Prisoner’s Dilemma, rational players can cooperate for a while if they consider it possible for the other player to play “tit for tat” (i.e., he or she cooperates when the other cooperates, and defects when the other defects).

Public economics attempts to characterize efficient allocations of public goods and to determine which institutional mechanisms or public policies are able to fix free-riding problems (see e.g., Hindriks & Myles (2006), chap.5). One important difficulty lies in the fact that the values that agents ascribe to public goods are typically unknown to policy makers and that agents need to be incentivized to reveal them. Empirical studies produce comparative analyses of the ability of distinct institutional arrangements to solve or mitigate cooperation problems (see Ostrom 1990 on common resources).

References

- Ledyard, J. (1995) "Public Goods: A Survey of Experimental Research", in Kagel, J. and Roth, A. (eds) *The Handbook of Experimental Economics*, Princeton: Princeton University Press, chap. 2, 111-194
- Hardin, G. (1968) "The Tragedy of the Commons", *Science*, 162, 1243-8
- Hindriks, J. & Myles, G. (2006) *Intermediate Public Economics*, Cambridge: MIT Press
- Kreps, D., Milgrom, P., Roberts, J. & Wilson, R. (1982) "Rational Cooperation in the Finitely Repeated Prisoner's Dilemma", *Journal of Economic Theory*, 27, 245-52
- Ostrom, E. (1990): *Governing the Commons. The Evolution of Institutions for Collective Action*, Cambridge: Cambridge University Press

Synthesis

The word cooperation is widely used in economics and evolutionary biology, yet in neither field is the concept fully formalized.

In economics, cooperation is mainly used in relation to symmetrical games involving the "paradoxical" presence of symmetrical solutions that optimize the individual payoff for two or more players. However, these games are also Pareto-dominated by other profiles which cannot be obtained by individual optimization. Typically, even if everybody potentially got the highest payoff by contributing to a common enterprise, the cooperative solution can be out of reach for rational players. Since cooperation always refers to a game structure, it is defined as the result of a set of actions between players.

In biology, cooperation refers to a (genetically determined) trait. An individual – the agent - carrying such a trait will behave in such a way as to increase the Darwinian fitness of one or more other individuals, known as the receivers. Although the term cooperation is often used as a synonym for altruism, it should also include situations where the cooperative action is associated with a direct fitness benefit to the agent (mutual benefit).

Compared to the definition of cooperation in economics, the definition in evolutionary biology seems to emphasize the effect of an action on the receiver(s), rather than the broad spectrum of possible actions. However, the very fact that cooperation is discussed reflects an implicit

view of at least one other situation; that is, one of non-cooperation, from which the receiver derives no benefit.

Such a difference in focus leads to a second major difference in the way cooperation is addressed in the two disciplines. Most of the ongoing debate in evolutionary biology is centered on the origin and evolutionary stability of altruistic behavior, rather than on cooperation in its wider sense. As a result, some authors consider that cooperation must imply a cost to the individual. Economists, by contrast, are more focused on determining what mechanism may induce players to choose the cooperative solution. They are less interested in explaining how the game involving cooperative solutions was established.

The different approaches to cooperation reflect a more general divide in the processes at the core of the two disciplines. Biological evolution is indeed concerned with explaining how traits such as cooperative behavior, which appears to deviate from the spontaneous flow of natural selection, can emerge. After all, the dynamics of a trait frequency are underpinned by constraints dictated by specific rules, namely Darwinian selection or drift. Economic processes, by contrast, are less constrained, in that their description can be exogenously complexified in order to solve paradoxical situations. For instance, externalities or constraints can force the system to attain the desired solution. Moreover, models can be extended to account for features (e.g., moral norms or irrationality) usually neglected in the framework of game theoretical models. These properties may explain the experimental evidence of apparently paradoxical behavior, such as the human tendency to explore the cooperative solution in the first rounds of a game.

Crisis

Evolutionary biology (*S. De Monte*)

Catastrophes or crisis events refer to the appearance, during the course of macroevolution, of sudden and extensive changes in the phenotype of species (for instance, the body plan) or in the features of an ecosystem (for instance, species diversity). They are typically associated with extinction events that reshape the structure and organization of ecosystems.

The fact that life on Earth has witnessed catastrophic events, whereby old life forms were replaced with new ones, was widely accepted in the natural sciences even before the theory of evolution by natural selection had been formulated. Evidence of such changes, presumed to have occurred due to drastic environmental events, could be seen in the fossil record of organisms with morphological features absent from extant species. In the early 19th century, Georges Cuvier suggested that the diversity of fossil species might be explained by “catastrophism,” whereby life on Earth would have been shaped by a succession of sudden, massive geological events. According to this theory, changes in natural systems are driven by external forces, instead of following the gradual process of transformation put forth in the geological and paleontological studies of Lyell and Lamarck prior to 1850, which was regarded as the way life forms evolve.

The mechanism of evolution by natural selection proposed by Darwin in 1859, which envisaged the conversion of standing phenotypic variation into gradual shifts in population characteristics, did not at first appear to be better suited than catastrophism to explaining sudden and major changes in the structure of animals and plants, such as those observed in fossils. However, as paleontological observations increased in number, and Darwin's ideas spread, belief in the role of environmental catastrophes as the major driver of evolution declined. Gradualism not only agreed with the increasing amount of fossil evidence that resolved the change in morphology through time; it also provided the framework within which the process of evolution could be mathematically described by models linking genetics and population size (Fisher, 1930). The problem of understanding “sudden” changes in the number and characteristics of species was thus reduced to accounting for the diversity of time scales that appeared to characterize different moments along evolutionary trajectories (see TIME SCALES).

Stephen Jay Gould's theory of punctuated equilibria (Gould & Eldredge, 1977) (see EQUILIBRIUM) stressed that the mode and tempo of evolutionary dynamics is not uniform along the tree of life. As a result, rapid evolutionary changes ought to be ubiquitous and might arise from intrinsic properties of evolutionary processes rather than under the influence of externally driven catastrophes. Since the most significant changes in species morphology

would have occurred during such shifts, rather than through gradual adaptation, this point of view centered attention on phenomena of fast evolution.

Paleontological records confirmed that eras of evolutionary stasis (wherein species changed their traits quantitatively but to only a limited extent) alternate with crisis events. At these transitions, the Earth biota underwent rapid radiations that greatly increased the number of species; the beginning of the Cambrian era is one example. Analogously, abrupt extinctions, like the one that brought the age of the dinosaurs to an end, led to major rearrangements in the balance between taxonomic classes. At the species level, conspicuous modifications of the body plan occurred on a much faster time scale than would be expected if the pace of change remained uniform through time.

Several mechanisms, most of which rely on various kinds of environmental perturbations, have been considered as possibilities to account for sudden and sizable changes in species number or characteristics.

In the extrinsic scenario, rapid transitions result from adaptation to a newly arisen environmental feature, either because the niche occupied by a species has changed or because a pre-existing niche has become accessible by dispersal. For instance, extrinsic niche variation can be induced by climate change or by geological events. The ability of a species to adapt to new environmental conditions is limited by the time scale at which the species is able to adjust its traits and depends on the selective pressure the new conditions impose. If such a time scale is too slow with respect to that of the external force, then the population may be driven to extinction. Otherwise, its features will change, as natural selection acts on variation – standing or derived from mutation or immigration – at a rapid pace, when compared to the process of adaptation in a constant environment. The resulting abrupt phenotypic variations reflect the ability of the species to keep track of environmental changes arising independently from itself. Consequently, the time scale of the changes is essentially determined by events that are extrinsic to the physiology and ecology of the species.

Discontinuities in the pace of adaptation can, however, stem from intrinsic properties of the species, be they genetic, physiological, or ecological. In this case, interplay between ecological and evolutionary time scales offers the opportunity for selection to act on phenotypically distinct states of the organisms, among which populations can readily shift without needing to undergo major genetic modifications. External perturbations can again play a major role in allowing the system to shift among different alternative equilibria, but under these circumstances, the changes can occur much faster because they are limited by population size rather than by rate of mutation. As a consequence, these mechanisms offer a sounder solution to the problem of adapting to sudden changes in the environment, and have been related to risk avoidance or bet-hedging. Experiments in directed evolution have shown that microbial populations can readily achieve a polymorphic state which allows them to tackle periodic changes in the selective pressure.

Formally, sudden shifts in equilibrium or regime are described by models of ecological or evolutionary dynamics, whereby populations may undergo discontinuous transitions under the gradual change of an external parameter. The so-called “catastrophe theory” inspired by the work of René Thom on bifurcations of continuous fields (Arnold 1984) was applied to classical models of population dynamics as a mathematical framework for studying the properties of abrupt transitions. The concept of the “tipping point” as a bifurcation has become a central concern to the ecology of conservation. Indeed, tipping points are associated with the fast collapse of a population, typically very difficult – if not impossible – to reverse, because of the hysteretic nature of most systems which exhibit multistability.

References

- Fisher R.A. (1930): *The Genetical Theory of Natural Selection*, The Clarendon Press, Oxford.
- Gould, S. J, & Eldredge, N. (1977): "Punctuated equilibria: The tempo and mode of evolution reconsidered," *Paleobiology* 3 (2): 115-151
- Rankin, D.J. & A. Lopez-Sepulcre (2005): "Can adaptation lead to extinction?" *Oikos* 111: 616–61914.
- Arnold, V. I. (1984) “Catastrophe Theory.” Springer-Verlag

Economics (*B. Walliser*)

The notion of economic crisis is essentially evoked when economists confront their theories with unusual and unfavorable empirical situations. Specific taxonomies have been defined concerning the origins and history of some crises, and their remedies. New economic contexts and the implementation of new policies may lead to profound reforms. Of course, the aftermath of the crisis of 1929, when John Maynard Keynes made an original diagnosis and proposed innovative policies, is a textbook example of this process.

For a country, an economic crisis is generally characterized by a combined disjunction of several macroeconomic indicators from their usual trends. The crisis is defined for a given geographic zone and evaluated with respect to a reference trajectory, generally a phase of growth or a sub-period of a cycle. Possible indicators are a lull in activity, a wave of bankruptcies, unemployment increase, wage decrease, and hyper-inflation (or deflation); i.e., increasingly volatile prices.

Various schools of thought attribute crises to structural causes rather than conjunctural ones. Neo-classical theory holds that a crisis results from transitory perturbations induced by various market imperfections. For the Schumpeterians, crisis manifests the exaggeration of the descending phase of a business cycle. For the Keynesians, it can be attributed to a decorrelation between the financial sphere and the real sphere of the economy. For the Marxians, it reflects a profound change of the regulation regime of capitalism.

More prosaically, the crisis may be domestic or State-induced, monetary or financial, self-produced or imported. It is attributed *in fine* to various kinds of shocks: technical (innovations) or economic (shortage of natural resources), political (wars) or social (riots). These shocks are considered as exogenous in the short term, but result as well from long term evolutions of the economy. More recently, a crisis has been attributed less mechanically to a misunderstanding of the evolution of the economy (subprime crisis).

Shocks are transmitted by contagion along various channels: material (respect for constraints), cognitive (change of expectations), behavioral (mimetism) or social (loss of trust). They induce chain effects, interactions as well as retroactions with amplifying effects (high accumulated debt) as well as stabilizing ones (resolution of overproduction). These effects can be studied by relevant models and profoundly modify formerly established equilibrium states, sometimes irreversibly.

On the whole, although a crisis may appear in a specific period and place, its effects can be felt over very large economic zones, due to the increasing interdependence of economic systems. It affects all economic agents and may even destroy some of them (firm bankruptcies). It provokes some specific effects, either economic (underground economy, new insurances) or financial (financial bubbles, stock exchange crashes, new assets). It is often accompanied by a social crisis manifested by distrust of some agents (banks).

Finally, a crisis is treated by economic tools gathered into doctrines which are again relative to the various schools of thought. These tools differ in nature: they may be material (public infrastructures), fiscal (firm subsidies), financial (loan guarantees) and even psychological (incentives to consume). They are implemented by various actors: basic agents (increase of private capital), State (public spending), international institutions (global rules). But note that the tools available to the State are often imprecise, inaccurate, and rather weak.

References

Kindleberger, C. (1989): *Manias, panics and crashes*, Basic Books

Synthesis

A crisis is generally seen as an abnormality in a system, and is typically endowed with a negative connotation. At a superficial level, it is considered as an illness in need of a cure. At a formal level, “catastrophe theory” proposes a model in which small modifications in one of the system's parameters can provoke drastic effects on its behavior. In ecology, the principles of this theory were used to model fast decline of populations. In economics, catastrophe

theory was used only as a rough analogy, although it does reflect certain aspects of the real phenomenon.

A crisis is always represented by an abrupt uncoupling of a system from its usual path. The deviation is irreversible, and the system veers off towards a different state, never to return to its initial one. In biology, a crisis may lead to the complete disappearance of a population (extinction of species). In economics, this specific outcome is impossible, because the population survives. Nevertheless, some agents may disappear.

A crisis is often attributed to causes external to the system, notably major changes in the environment. But it is amplified by internal causes; i.e., certain characteristics which evolve too slowly. In biology, material causes (external perturbations, climate change, geological events) are often invoked as the motor of the critical change. However, their effect can then be amplified by internal rigidity hampering adaptation. In economics, initial causes are both material (impoverishment of resources) and social (political events) and are amplified by internal behavioral and institutional rigidities.

If a crisis can be predicted by tracking the variation of known external causes, it can be prevented if adequate tools are available to affect those causes. Crises, however, often present novel features in their origin and spread, so that known tools can do nothing more than alleviate their impacts. In economics as well as in biology, advance indicators of employment or climate are systematically measured as a means to foresee world-scale crises. Yet even when the causes are known, the current capability to influence global processes is too limited to enforce systematic changes.

Cycles

Evolutionary biology (*S. De Monte*)

Different kinds of cyclical dynamics are of concern in biological evolution, as all levels of biological organization are associated with processes occurring on characteristic time scales. Evolutionary cycles -- intended as the periodic re-occurrence of species -- is however considered to be scarcely relevant on the macroevolutionary time scales. Indeed, species are usually modified (in a more or less continuous manner) directionally and irreversibly by natural selection, thus hampering populations to come back over and again to the same state. Nonetheless, nonlinear models for biotic evolution provided a theoretical foundation to the possibility that cycles of species or traits might be fueled by the same selective processes that underpin evolutionary equilibria.

In the framework of evolutionary game theory, in particular, it has been shown that even simple models involving a non-transitive (rock-paper-scissors) dominance between traits admit periodic solutions, typically in the form of Lotka-Volterra-like cycles [Hofbauer & Sigmund, 1998]. Such cycles are believed to govern, for example, both the alternation of strains in bacterial communities currently used for evolutionary experiments in controlled conditions and the alternation of morphotypes in a lizard species. However, their relevance to macroevolutionary processes, occurring on much slower time scales than ecological dynamics, is far from clear.

In some cases, evolutionary cycles have been proposed as a possible mechanism underlying the so-called “red queen hypothesis,” according to which species can persist thanks to self-perpetuating fluctuations in fitness [Van Velen, 1973]. This is called upon, for instance, when studying the coevolution of parasites and their hosts, where the development of the host’s defense against a given parasite would pave the way for the evolutionary success of another, more virulent, parasite variant.

The underlying characteristic of such evolutionary cycles is the existence of feedback between the environment and the species living in it: the species affect the features of the niche which, in turn, drives their evolution. These feedbacks have been recently formalized in extensions of evolutionary game theory [Weitz et al., 2016], demonstrating that the coupled eco-evolutionary dynamics can display a much more complex dynamics than what would be possible by taking into account only the variation in frequency of strategies for environment-independent interactions.

Based on these models, one might expect that evolutionary cycles to be a common scenario, however observations are so far scant. Indeed, not all feedback would give rise to oscillations,

and – even where they did occur – cycles might be masked either by other fluctuations or go undetected as a result of inadequate temporal resolution.

Different kinds of cycles play a central role in the theory of evolution and are considered keys to explaining the evolutionary trajectory of species, even if they are not driven by the process of natural selection on the evolutionary time scale. These cycles can affect the system through exogenous forcing, such as the diurnal or climatic cycles, or they can be endogenous to the biological system, such as life cycles and ecological cycles.

Although not in direct control of the organisms themselves, exogenous cycles can play a fundamental role in shaping their evolution, in that they influence their reproductive success, thus their fitness. For instance, the alternation of distinct environmental features prevents the rapid extinction of types which are maladapted to one environment, but not the other. The role of exogenous cycles in selecting optimal strategies for phenotypic switches has been demonstrated both in models and in experiments on bacterial populations [Beaumont et al. 2009]. Endogenous cycles, generated by some trait of the organism or its ecological interactions, can on the other hand undergo changes, the result of selection either acting on specific characteristics of the life history or shaping relationships with other species.

Many studies focused on the effect of evolution on the ecological dynamics of populations. For instance, both theoretical and experimental studies have demonstrated that predator-prey cycles can change over evolutionary time scales, due to the gradual change of traits in the interacting populations, highlighting the potential effects of the interplay of ecology with rapid evolutionary dynamics [Yoshida et al. 2003]. These studies paved the way to explorations on whether the features of the emerging cycles are selected per se -- so that optimality criteria could be applied at the level of the ecosystem -- or they are the consequence of changes in individual traits that affect oscillations.

Similarly, natural selection can operate on traits that define the timing and organization of the life cycle. Because these traits have a direct effect on reproductive success, they can be molded on the evolutionary time scale. The possibility for selection to act on specific determinants of the life cycle (e.g., reproduction time and extent, lifespan) is now widely recognized. However, evolutionary biology is still actively dealing with themes such as the evolution of aging and the emergence of life cycles at different levels of individuality.

References

- Beaumont, H. J. E., Gallie, J., Kost, C., Ferguson, G. C., & Rainey, P. B. (2009): Experimental evolution of bet hedging. *Nature*, 462, 90–93
- Hofbauer, J. & Sigmund, K. (1998): *Evolutionary Games and Population Dynamics*, Cambridge University Press.

Van Valen, L. (1973): A new evolutionary law, *Evolutionary Theory*. 1: 1–30.

Weitz, J. S., Eksin, C., Paarporn, K., Brown, S. P., & Ratcliff, W. C. (2016): An oscillating tragedy of the commons in replicator dynamics with game-environment feedback. *Proceedings of the National Academy of Sciences*, 113(47), E7518–E7525.

Yoshida, T., Jones, L., Ellner, S. *et al.* (2003) Rapid evolution drives ecological dynamics in a predator–prey system. *Nature*, 424, 303–306.

Economics (*B. Walliser*)

In economic life and even in the laboratory, cycles are observed at various organizational levels. On exchange markets, available goods follow a “life cycle” governed by technological progress. In game situations, simple learning rules lead the players to cyclical attractors in “matching pennies.” But cycles appear essentially as regular movements of macroeconomic activity around a trend. They concern variables described in level or variation: production, employment, investment, exportation, price, interest rate. These cycles present a more or less periodic path conventionally broken down into four steps: expansion, crisis, recession, resumption.

In fact, macroeconomic cycles are not directly observable, but result from a breakdown of observed evolution along conventional filters. After the 19th century (Schumpeter), cycles of different lengths of time were distinguished and classified. The “seasonal cycle” occurs yearly, and chiefly concerns agricultural activity. The “Juglar cycle” lasts for a period of 8 to 12 years and primarily concerns production and investment (“business cycle”). The “Kondratieff cycle” follows a period of 40 to 60 years and concerns the whole sphere of economic activity. Some intermediary cycles are sometimes considered (period of 15 to 25 years) such as “Kitchin cycle” or “Kuznets swing.”

Classical explanations of cycles, expressed through models, concern both their factors and their means of action. In fact, certain structural features of a system are well known for causing more or less regular cycles. Exogenous explanations consider the influence of shocks, which are inherently either periodic, like cycles, or random. Shocks exert impact from outside and may be due to natural phenomena, technological innovations, or even social transformations. Endogenous explanations consider the role of system structures, which are either non-linear or present time lags of at least second order. These are due respectively to decreasing returns or price stickiness, to decision retroactions or delayed expectations.

For instance, the Kondratieff cycle is attributed to major technical innovations acting from outside on the economic system. These innovations are responsible for a complete restructuring of the economic framework. They bring about new forms of organization, before reaching diminishing returns. The successive inventions concern the steam engine (1815), the railway associated with coal (1875), electricity and chemistry (1920), the automobile

associated with petrochemistry (1960), computer and information technologies (2000). However, this periodicity is debated. Some economists argue for a more continuous and endogenous view of research and development.

Conversely, the business cycle is attributed to various macroeconomic mechanisms acting inside the economic system. Actions and retroactions between institutions and agents' behaviors explain some cycles, either virtuous or vicious. The last are due to imperfections on some markets (credit), to rigidities of some magnitudes (prices), to expectation failures (myopia) or simply to behavioral habits (mimetism). All these phenomena are first discussed as concerns their existence, but even more as concerns their capacity to produce cycles rather than just erratic perturbations.

As an example, the "Samuelson oscillator" (1939) is grounded on two behavioral relations at a macroeconomic level. The "accelerator" links consumption to past production and the "multiplier" links investment to past variations in production. It follows a second order linear difference equation on production, which may generate a cycle. Likewise, the "Goodwin model" (1951) collates various technical and behavioral relations. The evolution of capital links the variation of capital to investment and the "Phillips relation" links wage evolution to unemployment. The reduced model links the ratio of wages to profits to unemployment and produces cycles. In fact, the last model is formally identical to the "Lotka-Volterra model" which studies the interaction of predators and prey in biology.

Nowadays, the study of cycles is no longer very active, since cycles merely reflect specific patterns of the evolution of some magnitude. In any case, in some of their phases, they may be favorable or not. If they are unfavorable, they are considered to be crises (see CRISIS). Some policy tools are then specifically adapted to counter them.

References

Samuelson, P.A. (1939): Interactions between the Multiplier Analysis and the Principle of Acceleration, *Review of Economics and Statistics*, 21, 75-78.

Goodwin, A. (1951): The Non-Linear Accelerator and the Persistence of Business Cycles, *Econometrica*, 19(1), 1-17.

Synthesis

In economics, cycles were first observed empirically as regular oscillations. It was only later that explanations were proposed to account for the features of such oscillations, particularly their period, in both game theory and system theory. In biology, cycles were first obtained through a few idealized models producing self-sustained, intrinsic oscillations. They are

seldom observed either in field observations or in laboratory studies since they are dampened by dissipation and easily hidden by temporal under-sampling.

In economics, cycles may affect the strategies of some agents, but they essentially concern certain indicators of global activity. In biology, cycles concern genotypic or phenotypic traits of a given population; no macroeconomic variables are considered.

Cycles are always interpreted as out-of-equilibrium or equilibrium attractors of some process. The corresponding equilibrium conditions must hold on the same time scale at which the process is observed.

In both fields, cycles may result from external or internal factors. In economics, many explanations rely on some extrinsic force like population or technological innovation, which disrupts a given state of natural equilibrium. In biology, external pressure, for example through climatic oscillations, is not considered to be a major force in the cyclical dynamics of adaptation. On the other hand, both disciplines consider non-linearities in inside interactions as an important source of cycles.

The same explanations are sometimes applied to phenomena studied in both fields. A first example is the rock-paper-scissors game, where players have three strategies with a non-transitive relation of dominance. The game-theoretical framework is applied in economics to competition between commercial strategies and in biology to selection of subpopulations with different phenotypic traits. A second example concerns the Lotka-Volterra model, which involves two variables influencing one other in such a way that the increase in one causes the decrease of the other. It is applied in biology to describe the population dynamics of a predator-prey system and in macroeconomics, through the Goodwin model, to mutual evolution of employment and wages.

Development/growth

Evolutionary biology (*J. Gayon*)

Like nutrition and reproduction, growth and development are essential properties of life. Although the terms are commonly applied in many other scientific fields, they take on a special meaning in the life sciences. Used alone, growth and development fundamentally refer to individual organisms and their organs. The notion of growth is also of primary importance when applied to population size, but in that case, it is used as part of a compound expression such as “population growth.”

At the level of individual organisms, the distinction between growth and development is fundamental, but in practice, it is delicate. Growth is a quantitative concept, whereas development is qualitative. The term growth is applied to all biological phenomena that result in an irreversible increase in the size of an organism or its parts (organs, cells). Reversible changes in volume – for example, a cell’s dilation or contraction in a fluid environment, or weight gain or loss in an organism, due to a change in diet or any sort of disruption—are not growth phenomena. The term development is applied to the neoformation of organs (or, more generally, living parts) which were not previously there. The difficulty with this distinction is that development is usually accompanied by quantitative growth phenomena. But there are many exceptions to this rule: development phenomena are not invariably accompanied by growth. For example, in certain plants, vernalization is a transformation whereby a seed or plant shifts from the vegetative phase to the reproductive one due to prolonged exposure to cold. This transformation is not accompanied by growth, either in terms of the organs or in terms of the cells. Another exception is that of the programmed destruction of tissue by apoptosis (programmed cell death, Kerr et al. 1972) in many morphogenetic phenomena (for example, the destruction of the webbing between the fingers and toes of mammals, an important phase in the formation of the lower parts of the limbs).

At the most elementary levels of biological organization, growth is never mentioned. This is especially true of molecules, even among the most complex cases. These molecules are never said to develop, either, although when a cell fabricates macromolecules like proteins, DNAs, or RNAs, there are significant aspects of construction, neoformation, and morphogenesis. Nonetheless, the term growth is applied to *populations* of molecules (in a cell or in the blood, for example, see Scott et al. 2011).

There are two elementary phenomena of biological growth: gain in cell volume (*auxesis*) and cell division (*merisis*): an increase in size or an increase in number. The increase of cell volume is extremely important in plant growth; it is less so in animals, since their size varies less. There are growth phenomena that do not involve an increase in size or weight. For example, this is what happens when a mass of cells separates into several cells, a frequent phenomenon in

the first moments of embryogenesis, as well as in several organogenesis phenomena. It can also be noted that at the cellular level, the increase in volume is rarely isodiametric – another factor that complicates the matter of distinguishing between growth and development.

Because the facts of growth are defined quantitatively, biologists have long sought laws that would describe it in as universal a way as possible. The search for absolute laws of growth (i.e., applying to an entire organism) has been disappointing (among others Medawar 1941). Growth curves vary in shape. Logistic curves are often found, S-shapes combining self-acceleration and self-inhibition, but there are many other cases, as well. Moreover, a series of logistic curves is usually observed, instead of a single curve covering all of growth. The study of relative growth (that is, the differential growth of an “organ” or body part, compared to total growth) has turned out to be more productive. Allometry, the dominant form of relative growth, is a growth phenomenon widespread in nature, from cellular organelles (for example, the nucleus compared to the cell) to the organs of the most complex organisms (for example, brain size compared to body size) (Gould 1966). The “allometric law” is a power law expressed in the form $y = b \cdot x^a$. It is often written in logarithmic form: $\log y = \log b + a \log x$, which makes it possible to represent a relative growth phenomenon by a line segment. Organ development often resembles a series of segments at varying angles, reflecting relative growth that fluctuates between isometric and allometric. A curve is the sign of a “critical phase,” in which an important phenomenon of organogenesis begins. One of the best-known cases is that of the development of secondary sexual characteristics.

Biological growth phenomena are not limited to organisms and their parts. At a higher level of integration, it is common to speak of population growth, an extremely important notion in evolution and in ecology. On the evolutionary level, it is problematic to apply the term development, because one can hardly speak of neoformation of parts according to a pre-set plan. It is preferable to speak of the differentiation of local populations, of speciation (the splitting of one species into two), or divergence (the increase in the gap between the traits of two species with a common ancestor). Usually, population growth obeys exponential or logarithmic growth laws (if there is a limiting factor). When one is dealing with several interacting populations (for example, several genotypes in a population, or several populations in interaction, like preys and predators) – the mathematical processing becomes more complex, due to the models used. It is practically only at the level of population growth that parallels can be drawn with economic theory.

For most of the 20th century, contemporary evolutionary theory was marked by its exclusion of development as an evolutionary factor. In the Modern Synthesis, evolution plays out on two levels: genes and populations. The elementary phenomenon of evolution consists in a change in the genetic composition of the population, due to the influence of factors like mutation, selection, random drift, mating system, and migration. From this classical viewpoint, development plays no special role in the basic process of evolution. It emerges only as a phenotypic characteristic, exposed to mutation, natural selection, etc., like any other

characteristic in a population. Today, this understanding is contested by the “Evo-Devo” school, whose leitmotif is that the synthetic theory of evolution lacks something essential. Proponents of this theory point out the importance of developmental pathways (Raff 1996; Nuno de la Rosa & Müller 2021). These pathways intervene either as strong constraints that channel possible evolutions, or as emergent phenotypes which represent dynamic, multi-realizable states that themselves are genuine targets for natural selection. They would allegedly play a key role in macroevolution.

References

Gould SJ (1966) “Allometry and size in ontogeny and phylogeny“. *Biological Reviews Cambridge Philosophical Society* , 41(4):587-640

Kerr JF, Wyllie AH, Currie AR. 1972. “Apoptosis: a basic biological phenomenon with wide-ranging implications in tissue kinetics.” *British Journal Cancer* 26 (4): 239–57

Nuno de la Rosa L., Müller G. (2021) *Evolutionary Developmental Biology. A reference Guide*. Dordrecht : Springer.

Medawar, P. (1941) “The ‘laws’ of biological growth.“. *Nature* 148: 772–774

Raff, R. (1996) *The Shape of Life: Genes, Development, and the Evolution of Animal Form*, Chicago: University of Chicago Press.

Scott M, Hwa T. (2011) “Bacterial growth laws and their applications“. *Current Opinion Biotechnology* 22(4):559-565.

Economics (M. Cozic)

Economic growth (in a national economy, for instance) is defined by the increase in Gross Domestic Product (GDP). Together with unemployment and inflation, GDP is one of the most important macroeconomic variables. GDP and national account systems were developed during the 1930s and the 1940s, notably by S. Kuznets and R. Stone, Nobel laureates in economics. One of the main goals of these systems is to provide policy makers with a global view of the state of the economy, on which they can base their decisions. GDP is a measure of the aggregate output of an economy. More precisely, it measures the value of *final goods* produced in an economy during a period (typically, one year). By contrast with *intermediate goods*, final goods are not used to produce other goods. Equivalently, one may define GDP as the *total added value* (the value of the whole production minus the value of the intermediate goods) in an economy during a period, or as the sum of *incomes* in an economy during a period.

Economists estimate GDP (or GDP per capita) of different economies at different times. Some “stylized facts” about growth (per capita) emerge. For instance, growth was almost null during the 1st millennium, and then very weak until the second half of the 19th century (see Maddison 2001). By contrast, a period of sustained growth was observed in the richest countries after World War II (although it has slowed since the 1970s). For the member states of the Organization for Economic Cooperation and Development (OECD), the growth was all the stronger given that per capita GDP was low at the beginning of the period (the so-called “convergence” phenomenon). These trends are not universal. In the sub-Saharan area, between the 1960s and the 2000s, several countries experienced negative growth.

Theories of growth attempt to account for these phenomena. More generally, they attempt to explain and predict evolution and variations of aggregate production across periods and across economies. This aggregate production function, which associates aggregate output Y with several factors of production, most notably physical capital K and labor L , is a basic concept for dealing with these questions. Economists have used these functions to elaborate and study growth models. The basic one is the Solow (or Solow-Swan) model (see Solow, 1956). This model assumes constant returns to scale and decreasing returns of each factor of production. It also assumes that, at each period t , a proportion $s \times Y(t)$ of product $Y(t)$ is invested. s is an exogenous factor, and is equivalent to the *savings rate* in this simple model. Together with capital’s depreciation δ , investment (or saving) determines the capital stock in the next period: $K(t + 1) = (1 - \delta) \cdot K(t) + s \cdot Y(t)$. One of the lessons drawn from the Solow model is that, whereas capital accumulation (and thus, savings rate) promotes growth in the short run and determines the production level per capita in the long run, only an improvement in the state of technology A (sometimes called “knowledge,” and which may be viewed as another production factor) is a source of long-term growth. It is often postulated that the state of technology can be (multiplicatively) combined with labor L to determine the amount of “effective labor” $A \cdot L$. The production function is then formulated $Y = F(K, A \cdot L)$. Another lesson may be drawn from the Solow model, resulting notably from decreasing returns of capital: the GDP per capita of economies starting from different production levels tends to converge.

In the Solow model, savings rate and technological progress, which are key determinants of production and growth, are treated exogenously. More recently, growth theory has attempted to account for the impact of economic factors on these determinants. Savings rate may be viewed as emerging from household decisions. Ramsey models (or Ramsey-Cass-Koopmans models) assume that households face an intertemporal consumption problem. Their budgets are determined by income from wages and interests on assets. Concerning technological progress, the basic idea of so-called “endogenous” growth theories is to capture how it is impacted by the economy. Technological progress may increase through learning (so that knowledge improves productivity and thus marginal return of capital is non-decreasing); or through investment in “research and development,” the outcome of which may be new products or products of higher quality (Aghion & Howitt 1992).

One of the reasons why GDP (per capita) plays such an important role is that it is supposed to provide indications about the *standard of living*, often viewed as a key determinant of *well-being*. For a long time, the (average) socio-economic progress of a population (what is currently called its *development*) was reduced to the variation of its GDP per capita. However, since the 1970s, economists and decision makers have increasingly considered this indicator to be overly restrictive and unreliable, in the absence of other information (for an extensive discussion, see Stiglitz, Sen & Fitoussi 2009). Firstly, GDP per capita does not take into account the *distribution* of income among members of the population, a factor that could be viewed as an important dimension in the assessment of well-being. To address this gap, economists have developed measures of income inequality like the Gini coefficient (see the seminal papers by Kolm 1969 and Atkinson 1970, and the recent survey Atkinson & Bourguignon 2000, esp. Chapter 2). Another reason to question GDP as a guide to socio-economic well-being is that it does not directly include information relative to poverty, unemployment, access to education, health, security, etc. Hence the elaboration of alternative indicators. For instance, in 1990, the United Nations Development Programme (UNDP) proposed the *Human Development Index (HDI)*, integrating data on health (life expectancy at birth), education (years of schooling) and wealth (gross national income per capita). In order to devise an index of this kind, a set of relevant dimensions with appropriate indicators must be *selected* and then *aggregated*. (One exception is the *Better Life Index* devised by the OECD, where each user may aggregate in his or her own way the selected dimensions.) At each stage, value judgments are directly involved. One of the most influential conceptualizations of development, which has notably inspired the HDI, is found in the work of Amartya Sen. He introduces a distinction between “*functionings*” and “*capabilities*.” Functionings are activities or states that are valued by an individual (for instance, the fact of being well nourished), while capabilities are the combinations of functionings that an individual is free to achieve. According to Sen, development should be viewed as a process of expansion of capabilities (see Sen, 1999, chap.3).

Development economics (see, e.g., Todaro & Smith 2012) is the field of economics which deals with the economies of the so-called “developing” (or “less developed”) countries. Developing countries are commonly defined as low- or middle-income countries. Most of the world’s people live in these countries. Development economics tackles the issues raised by poverty, inequalities, unemployment, etc. It investigates the ways of promoting economic development, and in particular the impact of factors such as education, economic policy, institutions, cultural characteristics or the respective weights of private and public sectors. Many of the issues tackled by development economics are directly related to issues of economic policy.

References

Aghion, Ph. & Howitt, P. (1992) “A Growth Model Through Creative Destruction”, *Econometrica*, 60, 323-351.

Atkinson, B. (1970) "On the Measurement of Inequality", *Journal of Economic Theory*, 2, 244-63.

Atkinson, B. & Bourguignon, F. (2000) *Handbook of Income Distribution*, vol. 1, Elsevier.

Kolm, S-Ch. (1969) "The Optimal Production of Social Justice", in Margolis, J. & Guitton, H. (eds.) *Public Economics*, London: Macmillan, 145-200

Sen, A. (1999) *Development as Freedom*, Knopf

Stiglitz, J., Sen, A. & Fitoussi, J-P. (eds) (2009) *Report by the Commission on the Measurement of Economic Performance and Social Progress*, Paris

Solow, R. (1956) "A Contribution to the Theory of Economic Growth", *Quarterly Journal of Economics*, 70, 65-94.

Todaro, M. & Smith, S. (2012) *Economic development*, Boston: Addison-Wesley

Synthesis

In biology as well as in economics, the notions of growth and development are relevant. In biology, they are primarily applied to a given organism during its lifetime, and additionally to populations of organisms belonging to the same (or different) species. In economics, they always concern a whole economy, rather than specific economic agents like firms. It follows that, when considering traditional organizational levels, the emphasis is reversed from one discipline to the other: i.e., on a micro-level in biology and on a macro-level in economics.

However, in both fields, the main concept concerns growth, which is specifically a descriptive and quantitative one. Growth is easily measurable for any organism in biology, but in economics, it needs to aggregate all transactions between firms. As for the concept of development, it is more qualitative (in both fields) and distinguishes different aspects or phases in the evolution of the entity being studied. Biology insists on the progressive differentiation of some organs while economics stresses different aspects of income, health, education, and welfare, country by country.

Furthermore, with respect to growth, both fields attempt to describe the phenomenon with empirical laws and to explain it by specific factors. In biology, the growth of an organism is yielded by approximate local laws at each step of its development, and attributed to different cell processes and substances which promote or inhibit it. In economics, the same growth model is adapted to each country using specific parameters. The growth rate of production,

however, is explained by increasingly complex macroeconomic variables such as labor, technology, savings rate and, more recently, education.

As concerns development, a link has to be established in each field with the more common notion of evolution. In biology, the development of an organism and, even more, of a population is constrained by the general principles of evolution of species, which involve both a deterministic aspect for selection and a stochastic one for mutations. In economics, the development of a national economy coincides with its evolution, and is usually seen as deterministic, although contingent on agents' decisions.

Diversity

Evolutionary biology (*S. De Monte*)

The diversity of life forms on Earth has always been a primary source of scientific interest. An astonishing variety of shapes, colors, sizes, and behaviors all appear to be amazingly “fit” for the specific ecological niche in which they are embedded. This marvelous perfection and diversity were long cited as proof of creationism, achievable only by a divine power. Darwin's fundamental contribution was to prove that a supernatural intervention was not necessary to explain surprising adaptations: they could merely be the consequence of heritable variation among individuals and natural selection; that is, differential survival of individuals that were more adapted to their environment.

At all levels of organization and biotic structure, diversity is manifested as the coexistence of organisms with contrasting features within a population, within a species, or within a community (composed of a multiplicity of species). The origin of such diversity also involves multiple spatiotemporal scales. Macroevolution studies the establishment of species diversity through generation and loss on the geological time scale, and is thus interested in major events such as sudden radiation events (for instance, the “Cambrian explosion”) or mass extinctions (the latest of which is under way, prompted by anthropogenic environmental change).

To account for diversity, one must understand speciation; that is, the splitting of one population into two populations with distinct features. Speciation is the basic mechanism introducing novelty, innovation, and complexification of life forms.

Although the workings underpinning speciation appear to differ from system to system, two classical explanations rely on the establishment of sub-populations that adapt to different niches. In allopatric speciation, the process is initiated by physical barriers that come to separate an initially single population in two or more subpopulations. Such populations then follow different evolutionary trajectories, each adapting to the specificities of the niche they occupy, and undergoing stochastic changes (see MUTATION /INNOVATION). In the long run, individuals of the two subpopulations become reproductively isolated, and they can no longer be recognized as belonging to a single species even when they encounter again. Darwin's finches are the textbook example. When the birds colonized islands with distinct endogenous flora, natural selection caused their beak shape to become adapted to feeding on seeds specific to their home islands. Because the islands were connected by a limited degree of migration, finches could disperse from the environment where they were selected. As a result, diverse species of finches coexist on every island.

The concept of ecological niche has subsequently expanded beyond that of a specific geographical area to something that encompasses temporal variability and biotic interactions both within and between species. In this perspective, the modifications of the environment caused by the gradual adaptation of one species may occasionally create new niches that can in turn be colonized by variants of the original species itself. This process of niche construction can lead to the divergence of different variants, in a process that is known as sympatric speciation. In this case, the emergence of two new species would be the consequence of the feedback between the ecological and evolutionary processes, as described by the theory of adaptive dynamics [Doebeli & Dieckmann, 2000].

On shorter time scales, ecological “community assembly” studies the processes that support the coexistence of similar species. Observations of natural communities are at odds with the principle of “competitive exclusion” that theoretically predicts that no more types than resources can co-occur in a given ecosystem (see COMPETITION) [Hardin, 1960]. Diversity within a community is typically quantified by counting the number of different types (e.g., genotypes, phenotypes, species, taxa) and their relative abundance. Classical descriptors of diversity are species richness; e.g., the number of bird species present in a given area, or indicators that combine richness and abundance, such as the Shannon index. These indices show that diversity is maintained in most natural ecosystems, where a small number of common species coexists with a large number of rare ones. Moreover, communities display “macroecological” geographical patterns: for instance, a decrease of diversity with latitude.

Alternative theories contest the explanation for observed patterns of biodiversity in natural communities [McGill 2007]. They make drastically different assumptions about the relative importance of different ecological processes, notably competition for different niches (see COMPETITION) and stochastic demography or drift plus mutation/speciation events (see MUTATION /INNOVATION).

The origin and maintenance of species diversity are studied through both correlative studies and mechanistic approaches. Biogeography, an example of the former, looks for connections with environmental parameters. The metabolic theory of biodiversity [Brown et al. 2004], an example of the latter, postulates a physical underpinning to the process of differentiation.

Biodiversity is commonly conceived in its value *per se*. For instance, more diverse ecosystems are shown to possess higher productivity and higher resilience, both features of primary concern in the maintenance of a healthy natural world [Hooper et al., 2000]. For such reasons, biodiversity has become a service of capital importance in conservation ecology, and its preservation is now recognized as one of the main objectives in limiting anthropogenic impact on the planet.

References

Doebeli M. and Dieckmann U. (2000) Evolutionary Branching and Sympatric Speciation Caused by Different Types of Ecological Interactions. *The American Naturalist* 156:S4, S77-S101.

Hardin G. (1960) The Competitive Exclusion Principle: An idea that took a century to be born has implications in ecology, economics, and genetics. *Science* 131(3409): 1292-1297.

Hooper, D.U., Chapin, F.S., III, Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. and Wardle, D.A. (2005), EFFECTS OF BIODIVERSITY ON ECOSYSTEM FUNCTIONING: A CONSENSUS OF CURRENT KNOWLEDGE. *Ecological Monographs*, 75: 3-35.

McGill, B. J. et al. (2007): *Species abundance distributions: Moving beyond single prediction theories to integration within an ecological framework*. *Ecol. Lett.* 10, 995–1015 (2007).

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. & West, G. B. (2004): Toward a metabolic theory of ecology. *Ecology* 85, 1771–1789

Economics (*M. Cozic*)

In and of itself, the concept of diversity does not play a central role in economics theory. However, phenomena related to diversity are noteworthy in several areas. One important topic is the diversity of socio-economic organizations or institutions and their respective impacts on resource allocation and economic indicators, but we will not tackle that here. Instead, we will focus on forms of diversity related either to *goods* or to *agents*.

A first form of diversity deals with the specialization of production and trade of goods at an international level: distinct countries specialize in the production of distinct goods. International trade depends heavily on specialization. The field known as “international economics” attempts to analyze these phenomena and assess their impact. Ricardo (1817) introduced the highly influential ideas of “comparative” and “absolute advantage” early in the 19th century. Country *i* has an *absolute advantage* over country *j* in the production of good *x* if the labor required for country *i* to produce one unit of good *x*, denoted by a_x^i , is less than the labor required for *j* to produce one unit of *x*, denoted a_x^j . Consider now another good *y*. Country *i* has a *comparative advantage* over country *j* in the production of good *x* (with respect to *y*) if $a_x^i / a_y^i < a_x^j / a_y^j$. Some countries may have a comparative but not an absolute advantage in the production of some goods. The theory of comparative advantage explains how a country can benefit from trade with another country if it exports goods for which it has a comparative advantage and imports goods for which the other country has a comparative advantage. Trade may lead to mutual benefits even if one of the countries is less productive than the other one for any good. However, the issue of knowing what recommendations (for economic policy, in particular) should be drawn from the classical analysis of comparative advantage is debated. To mention one important dimension: the putative benefits are global, but predictably, the domestic sector of a newly imported good will be harmed by the opening of trade. In particular, income distribution may seriously be impacted by trade.

In its simplest version, the theory of comparative advantage explains specialization and trade by differences in labor productivity. The relative availability of other factors of production and

the relative intensity with which the technology of production uses these factors can also make differences. Thus, the Heckscher-Ohlin theory states that a country which is (relatively) abundant in one factor of production (e.g., capital) tends to export goods which are (relatively) intensive in that factor. Economies of scale (i.e., the fact that the cost per unit of a good decreases with the amount produced) also affect trade..

International economics compares the predictions made by theories and models to empirical data. Some predictions are hard to reconcile with observations. For instance, Leontief (1953) showed that the Heckscher-Ohlin theory that capital-abundant countries will export capital-intensive goods was contradicted by the realities of post-WW2 U.S. exports, which were labor-intensive.

Finally, on the basis of its models, international economics attempts to assess the global effects of trade: its impact on wealth and welfare, and the way they are both distributed, nationwide. This assessment may yield some recommendations for economic policy (tariffs, subsidies, quotas, sanitary and technical norms, etc.).

A second form of diversity concerns *product differentiation*. Consumers view some *physically comparable* goods as imperfect substitutes (i.e., the goods induce different preferences). Two kinds of differentiation are often distinguished. *Horizontal differentiation* relies on diversity in consumer preferences. It refers to cases where distinct consumers are not indifferent between distinct goods (belonging to the same type) sold at the same prices – for instance, two brands of the same type of beverage. By contrast, *vertical differentiation* refers to cases where consumers have homogeneous preferences but goods (still belonging to the same type) are of higher or lower quality.

Product differentiation may be viewed as a way out of the “Bertrand paradox.” In the Bertrand duopoly model (1883), where two rival firms selling the same good set their prices, equilibrium prices are equal to marginal costs and firms earn no profit. If one firm sets its price above marginal cost, all consumers buy the good from the other one. Firms may escape the paradox by differentiating goods, whereby they acquire some *market power*.

Horizontal differentiation is often studied through Hotelling’s Law (1929). In this model, two firms sell the same good but consumers face transportation costs depending on how far they are located from each firm (e.g., two ice cream vendors on a beach). The location of firms and consumers are represented by points in the $[0, 1]$ -interval. A more abstract interpretation of locations is possible: for instance, as varieties of the same type of good. If the price is set exogenously and firms choose only their locations, it is in the firms’ interest to be located as close to each other as possible (“principle of minimal differentiation”). But when firms are free to set the price, this is no longer the case. Two contradictory tendencies are then at work. Differentiation enables a firm to acquire market power (and thus increase its price), but makes it harder to grab consumers from its rival. Under some assumption about the transportation costs, this may lead to maximum differentiation. More generally, horizontal differentiation

analysis, part of the field of “industrial organization” (see, e.g., Tirole 1988), attempts to understand the impact of differentiation on equilibrium prices, the behavior of firms when they can differentiate their products, and the consequences of differentiation (whether firms differentiate “too much” or “not enough”).

Lastly, it is worth mentioning an issue which is related to *agent* diversity. By tackling what is sometimes known as the “aggregation problem,” one investigates the conditions under which a relationship that is supposed to hold for the behavior of each economic agent continues to hold for groups of agents (and for the determinants of these agents’ behaviors as well). Economic analysis often proceeds at a high level of aggregation, for instance by considering the consumers of a national economy. It typically assumes that these aggregates can be identified to agents (so-called “representative agents”), thereby raising the aggregation problem (see LEVELS). Economists have dealt with the problem in distinct theoretical contexts – notably consumer demand functions and firm supply functions. Classical results show that only very stringent conditions ensure that an aggregate of agents will behave as a single agent. Intuitively, they require agents to be strongly homogeneous (for a recent survey, see Chiappori & Ekeland, 2011).

References

Chiappori, P-A. & Ekeland, I. (2011) “New Developments in Aggregation Economics”, *Annual Review of Economics*, 3, 631-668.

Krugman, P., Obstfeld, M. & Melitz, M. (2012) *International Economics: Theory & Policy*, Addison-Wesley

Tirole, J. (1988) *The Theory of Industrial Organization*, MIT Press

Ricardo, D. (1817) *On the Principles of Political Economy and Taxation*, Murray: London.

Synthesis

In biology, diversity applies to the species and has a natural origin, since it results from the usual processes of mutation and selection in a given environment. This environment is made up of physical conditions as well as other species. Mainly, certain physically isolated environments form niches where the favorable adaptations of a species make it especially fit and it can develop. Moreover, the phenotypes of the organisms may become diversified as well as the genotypes.

In economics, agents are diversified due to biological conditions as well as economic ones. The goods are considered as resulting potentially from artificial innovations, and they spread out according to market conditions. Between countries, goods are exchanged according to the

comparative advantage they carry in terms of production. Inside each country, they are favored by their comparative utility for the consumers.

In both fields, the initial state of each species or the initial form of each good is explained by exogenous stochastic factors. But the proliferation of each species is explained by the ecological conditions in which they grow, whereas the amount of each type of good is explained by the economic market conditions in which the goods are produced and consumed. Note that the notion of niche can commute between economics and biology. It expresses the geographical and population conditions that are specifically favorable to the development of some species or good.

In a positive way, the development mechanisms of such and such types of organisms or of such and such types of goods simply present similarities, except that the first occurs naturally, while the second is under human control. However, contrary to the usual point of view, a normative assessment is made by biologists rather than economists. In biology, the maintenance of a sufficient level of biodiversity is considered to be fundamental to ensuring the ecological future. In economics, the existence of a large spectrum of goods in the world has no special importance for the future development of the economy.

Equilibrium

Evolutionary biology (*S. De Monte*)

By definition, biological evolution is concerned with variability in time rather than with stasis. However, the fact that many aspects of biological evolution (e.g., phenotypic traits, habitat range, structure of ecological communities) vary on slow timescales, together with the ease of modeling equilibrium vs nonequilibrium regimes, place equilibria at the heart of many theoretical investigations of biological evolution.

Sewall Wright (1932) introduced the powerful metaphor of the “adaptive landscape” to describe the tendency of biological populations to increase their fitness until an equilibrium point is reached where the allele frequencies in a population no longer change [Wright, 1932]. According to his “shifting balance theory,” the concomitant effect of genetic drift, natural selection, mutation, and gene flow drive the population through the landscape. Eventually, the population will reach a state of quasi equilibrium, corresponding to peak fitness.

The theory of punctuated equilibria, formulated in 1972 by the paleontologists N. Eldredge and Stephen Jay Gould [Eldredge & Gould, 1972], suggested that fossil records were better explained by periods of stasis (the equilibria) “punctuated” by occasional spurts of rapid evolutionary modifications, rather than by the homogeneous trend of gradual changes described in Wright’s theory. The punctuated equilibria picture later found a mathematical formulation in catastrophe theory [Thom, 1972]. It demonstrated that a nonlinear system may undergo fast and extensive excursions (a change of equilibrium in a multi-stable system) as a consequence of infinitesimal changes in one of its parameters. Since then, the existence of “tipping points” that cause qualitative and catastrophic changes in a system’s properties has been associated with the concept of equilibrium for complex systems and processes, including ecology, evolution, and economics [Sheffer et al., 2009]. How to predict and describe sudden changes from one equilibrium to another is still one of the most debated topics in each of these fields.

Evolutionary game theory predicts the existence of equilibria, called Evolutionary Stable Strategies, which are stable with respect to small perturbations: an individual with a mutant strategy will not be able to invade a population of individuals adopting the ESS. Such strategies include strict Nash equilibria, and are defined, as in classical game theory, independently of the process that may lead the system to that solution. One speaks instead of an evolutionary stable state of a population as a configuration (frequency of strategies, equivalent to mixed or probabilistic strategies) that is re-established by natural selection if a small fraction of mutants is introduced in the population. The two definitions coincide (after identifying a polymorphic state with mixed strategies) if the evolutionary dynamics is ruled by the replicator equation

[Hofbauer & Sigmund, 1998]. In this case, one can also address unstable equilibria that, in spite of the fact that they are never observed, may structure the evolutionary dynamics.

The fact that natural processes are able to maintain biological populations in a state that is unchanging (at least at some level of the biological organization, and for sufficiently fast time scales) has been seen as analogous to homeostasis. This is the capacity of an organism (or of a cell) of regulating its internal environment in order to maintain constant conditions in spite of the variability of the external environment. The faculty of responding to external changes via the modification of the internal variables is rooted in the concept of dynamic equilibrium, whereby an overall steady state is maintained in spite of the fact that some system aspects or components change over time (for instance in the red queen mechanism for evolution, see CYCLES).

The idea that the Earth system, and in particular its biotic component, is kept in a steady state by multiple feedbacks is known in the Gaia hypothesis [Lovelock & Margulis, 1974]. This theory conceives the biota as capable of self-regulating in its interaction with the environment. The concept of an equilibrium (be it ecological, evolutionary or of the whole process occurring on Earth) has then to take into account simultaneously an organism and its environment, both shaped by the feedbacks between biotic and abiotic components.

References

Eldredge, N. and Gould, S.J. (1972) Punctuated Equilibria: An Alternative to Phyletic Gradualism in Thomas J. M. Schopf (ed.), *Models in Paleobiology*. Freeman Cooper. pp. 82-115.

Hofbauer, J. & Sigmund, K. (1998) *Evolutionary Games and Population Dynamics*, Cambridge University Press.

Lovelock, Margulis (1974) Atmospheric homeostasis by and for the biosphere: the gaia hypothesis. *Tellus XXVI*: 1-2

Scheffer, M., Bascompte, J., Brock, W. *et al.* (2009) Early-warning signals for critical transitions. *Nature* 461: 53–59

Thom R. (1975) *Structural Stability and Morphogenesis: An Outline of a General Theory of Models* Addison-Wesley

Wright, S. (1932): The Roles of Mutation, Inbreeding, Crossbreeding, and Selection in Evolution. *Proceedings of the Sixth International Congress of Genetics* 1: 356-366

Economics (B. Walliser)

The notion of equilibrium as used in economics is derived from classical mechanics. An equilibrium state of a system is a state which remains invariant when perturbations of its environment occur. But although an equilibrium of forces exerted on a system of physical particles is causal, an equilibrium of actions decided by a system of economic agents is

intentional. Note that the modeler expresses no direct normative judgment on an equilibrium state, despite its denomination. Such a judgment is captured only by the complementary notion of optimality (see OPTIMALITY), an evaluation of whether an economic situation is favorable to the agents. Finally, economics tends to interpret any observable situation as an equilibrium state – in some cases, a short term one. Hence, the field has developed a whole range of notions of equilibrium.

In game theory, an equilibrium state results from the strategic confrontation of several players (see STRATEGIC INTERACTIONS). The fundamental notion is “Nash equilibrium” defined by two conditions which formally determine a fixed point for players’ actions. On the one hand, each player computes his optimal action as a function of his beliefs about others’ actions. On the other hand, the beliefs of each player are assumed to be realized at the equilibrium state. In such a state, no player will gain an advantage by deviating his action unilaterally. As a result, the state ensured some stability. In a first interpretation, the equilibrium state is assumed to be implemented from outside by a “Nash regulator,” which is only a fictitious entity.

Other equilibrium notions have been put forth, to deal with a variety of game contexts. Players may be facing different forms of uncertainty, which are generally probabilized. When endowed with imperfect and incomplete information about the others’ characteristics, they try to reach a Bayesian equilibrium. Alternatively, they may be satisfied with simplified or random beliefs which are more or less strongly validated at equilibrium. Above all, they are engaged in dynamic games expressed in finite or infinite game trees with corresponding equilibrium notions. For instance, a subgame perfect equilibrium assumes that each player computes his actions sequentially by a backward induction procedure starting at the end of the game. Finally, players may not be able to optimize, but they are nevertheless able to reach a bounded rationality equilibrium.

In market theory (see MARKET), an equilibrium state defines the price of each good as well as the exchanges of goods for all agents at that price. The fundamental equilibrium notion is the “perfect competition equilibrium” or “Walrasian equilibrium.” It assigns a price to each good by a fixed-point procedure. Since prices are assumed to be known by agents and to act exogenously on them, each producer expresses a quantitative supply and each consumer a quantitative demand of goods. Conversely, prices result from the equality of total supply and demand on each market. At the equilibrium state, all exchange opportunities have been considered and exhausted. The equilibrium prices are assumed to be fixed by a “Walrasian auctioneer,” a fictitious entity that actually exists on a few markets (copper, fish).

Other equilibrium notions are proposed, always on markets, when some assumptions about perfect competition are relaxed. An “imperfect competition equilibrium” is defined when producers, in small numbers (monopoly, oligopoly), have market power; i.e., define freely the price of their products (the way they do in game theory). An “imperfect information equilibrium” assumes that agents do not observe perfectly the prices or their environment. A “fixed price equilibrium” is possible when prices are sticky and do not adapt instantaneously

to supplies and demands. Likewise, equilibrium notions are defined for dynamic situations in which markets follow on through time. Finally, some global equilibrium notions can be adapted to a single market as partial equilibrium notions.

Except when an equilibrium state simply does not exist, two major problems appear due to the formal and non-constructive definition of games as well as markets. On the one hand, the process by which the agents concretely coordinate on an equilibrium state is not described. On the other hand, the equilibrium states may be many, without a description of a possible selection procedure. In order to solve these problems, two strategies are considered. The “cognitive” point of view assumes that the equilibrium state results from a complex computation made by perfectly informed and hyper intelligent actors. The “evolutionary” point of view assumes that the equilibrium state results from a learning or evolution process followed by boundedly rational actors.

References

Myerson, R.B. (1999): Nash Equilibrium and the History of Economic Theory, *Journal of Economic Literature*, 37, 1067-85.

Van Damme, E. (1999): *Refinements of the Nash Equilibrium Concept*, Springer

Synthesis

In biology as well as in economics, an equilibrium notion is introduced in order to represent the state of a system formed of several subsystems in a given environment. The system and its environment are characterized by observable variables linked by some stable relations including eventually unobservable variables. An equilibrium state is nothing else than a stationary state, in which the observables are temporarily invariant. The interest of the modeler lies in the existence, multiplicity, and stability of equilibrium states.

Such a notion appears as an intercessor between model and reality from the point of view of the modeler. This means that the modeler considers that the situation he observes is precisely an equilibrium state permitted by the equilibrium notion. Empirical observations are thus interpreted either as an equilibrium state, or as the response to its perturbation by exogenous factors. In order to compare the trajectory of the system when exogenous variables change ("comparative statics"), the modeler assumes that the system does not undergo a shift towards a different equilibrium.

A biological equilibrium is grounded in the balance of interactions of species/individuals with their environment and with each other. Equilibria are thus determined by laws that are constrained by the material nature of such interactions, and that are largely conserved during the lifetime of the biological units. An economic equilibrium is obtained by the coordination of actions rationally chosen by economic actors. At a generic level, it is defined as a function

of the beliefs and preferences of the actors. Beliefs and utilities are usually considered as fixed within the lifetime of an economic agent.

Any equilibrium notion provides an explanation for the origin of an observed state based on variables, which can or cannot be directly quantified. "Dynamic system theory" provides a theoretical framework for identifying which variables are really relevant to describe the system. It involves hierarchical time scales (see TIME SCALES) giving rise to short-term and long-term equilibria. Especially, out-of-equilibrium steady states (see CYCLES) may be viewed as dynamical equilibrium states, where temporal or spatial fluctuations are encompassed in the statistics performed on the observations.

In biology, the instantaneous state of the system is represented by the short-term ecological equilibrium resulting from parameters that vary more slowly and integrate the history of the system. In the long term, such equilibrium converges towards an asymptotic steady state specific to evolutionary theories. Even though this equilibrium has long been considered independently of the ecological and demographic fluctuations that underpin it at faster time scales, the role of eco-evolutionary feedback has recently become a central theme of evolutionary biology, and notably of experimental evolution.

For historical reasons, economics was first interested in short term (or static) equilibrium states in order to describe the instantaneous situation of exchanges and prices on markets. It was not especially interested either by local disequilibrium or even by global instability phenomena induced, for instance, by fluctuating resources or abnormal weather. Nowadays, it not only studies the stability of short term equilibrium states, but is fully involved in long term equilibrium states mainly governed by population or technological innovation.

Some more sophisticated equilibrium notions like a "signalling equilibrium" (see COMMUNICATION/SIGNALLING) or an "evolutionarily stable equilibrium" (see SELECTION) bridge the two fields. But evolutionary models tend to be more constrained in biology than in economics, due to the dissipative nature of biological systems. The formal constraints that act on the dynamical description of natural populations automatically exclude systems with particular symmetries. The last can instead be justified in economics, where postulating prior invariances (e.g., zero-sum repeated games) helps simplify some problems.

Fitness / Utility

Evolutionary biology (*P. Huneman*)

Nowadays, fitness is a crucial technical term in all fields of evolutionary biology, even though a single formal or conceptual characterization is hard to find. The word comes from the phrase “survival of the fittest” (borrowed from Spencer by Darwin in the last edition of the *Origin of Species*), which replaced the words “natural selection,” in order to avoid the connotation that “something” is doing the selection. Most generally therefore, fitness means a measure of the chances of evolutionary success of these entities involved in the process of evolution by natural selection, namely, an estimation of their contribution to the population in the next generation.

Fitness is essentially tied to natural selection, a process whereby some individuals (on the average) reproduce more than others, because of some of their heritable properties. As a result, given some conditions on heritability, these properties are passed on to more individuals of the next generation, and increase in frequency. Individuals more likely to contribute to the new generation are thereby said to be “fitter.” This conception makes it possible to define a measurable property of “fitness” that can be used to represent and predict the evolutionary dynamics of a population.

Fitness has two components, survival and reproduction. The fitness of an organism is intrinsically correlated to its adaptedness: the more adapted are organisms to their environment, the fitter they are. If an organism is very well adapted to its milieu, it survives well, but it may not reproduce. In that case, its adaptiveness has no evolutionary impact. Hence, reproduction is often considered to be essential, and survival considered as a proxy for reproduction (the longer X survives, the greater X’s chances are of having offspring).

Formally, fitness can therefore be defined as the probability distribution of the contribution of an entity to the next generation. Yet often equations consider only the expectancy, fitness meaning the *expected* offspring number of an individual rather than actual offspring. Hence fitness is often metaphysically considered as a “propensity” (sometimes called “expected fitness”) rather than as a categorical property (called “realized fitness”). Once the fitness of an individual is so defined, one can define the fitness of a trait (resp. a genotype, an allele), which is given by averaging the fitnesses of all individuals who share this trait (resp. genotype,

allele) (Orr 2009); trait fitness is often taken as the most relevant to population genetics, though it's a more abstract probabilistic construct than individual fitness.

Sometimes several generations have to be taken into account within the fitness value in order to understand the evolutionary dynamics (for example when explaining the pervasive constancy of unbiased sex ratio, which involves considering the effect on grandchildren). Various concepts of fitness have been proposed, such as the fitness as probability to invade, in adaptive dynamics, or Fisher's concept of fitness as a rate of increase of a class (Fisher 1930). The notion of fitness sketched here is sometimes referred to as "Darwinian fitness."

Often absolute fitness cannot in practice be measured, but only relative fitness is evolutionarily important (since individuals with equal fitness do not undergo natural selection). In this sense, the fitness value that is meaningful to evolution is the individual fitness divided by the mean average reproductive output in the population. Sometimes, the fitness of types of organisms is measured after the fact, by counting the number of offspring. This practice raises many specific methodological problems (e.g., sampling, disentangling selection from drift, mutation, gene flow, etc.). Independently, insisting on the idea that individuals that fit their environment better will survive and reproduce more than others, one can consider fitness as strictly correlated to the individual's answer to environmental demands, and then it can be computed before the fact by estimating the performances of various trait types (race speed, rate of metabolism, visual acuity, etc.) (Bouchard and Rosenberg 2008) However, no uncontroversial way to weight various environmental demands (to escape predators, forage, mate, etc.) is available, making the estimation of such "ecological fitness" problematic. Moreover, actual environments are in fact heterogeneous, and this raises general problems, both for the definition of a fitness function and the measure of fitness - leading some to distinguish between coarse-grained and fine-grained fitness functions (Levins, 1965).

In population genetics, fitness is crucially involved in gene pool dynamics models. Together with population size and population structure, the fitness of the various genotypes or alleles determine the evolution of the population. Theoretical models investigate the conditions under which highest fitness alleles actually take over the population, which assumes specific conditions on population size and structure, and on genetic make-up. Because fitness is a probabilistic magnitude, large populations are at least required in order to be entitled to use the law of large numbers and therefore draw on the basis of fitness functions some lessons about frequencies. Fisher's controversial Fundamental Theorem of Natural Selection (Fisher 1930) shows that the change of population mean fitness due to natural selection is always positive; yet the total change is not a priori constrained and therefore no conclusion can be made about global fitness change in actual populations.

However, the reasons why such genotypes or alleles have their determinate (relative) fitness are external to population genetics. Instead, they pertain to ecological inquiries, which investigate the causes of differential reproduction of various organisms. Hence "ecological fitness" and fitness as offspring expectation may not belong to the same theoretical projects, making it difficult to assimilate them. "Behavioural ecology" (Davies et al. 2012) studies those causes, and often considers a specific property like energy intake as a proxy for fitness when investigating the adaptive character of phenotypic traits and trait values (see OPTIMALITY).

The concept of fitness raises many deep problems.

First, even if often correct, equating fitness with reproductive value may mislead; e.g., when some organisms like quaking aspen grow indefinitely rather than reproduce. In some contexts, one has to model the two components of fitness separately, for instance when the issue is to understand how individual investments are divided between reproduction and survival (“life history theory”, Stearns 1992) (see CONSTRAINTS/TRADE-OFFS).

Second, even if the way to construct fitness in a given problem is often straightforward – mathematically speaking –, it can be difficult to assess the bearer of fitness. Originally, fitness was about organisms; with the Modern Synthesis formulation of evolution in terms of gene frequencies, fitness is also ascribed to alleles and genotypes. Organism and genetic fitness are interdependent because the fitness of a gene can be seen as the contribution it makes to the fitness of the organism. Yet the number of offspring equals the number of copies of a given gene only in the case of asexual organisms. Hence some authors do not agree that overall organismic fitness is generally defined. Moreover, fitness is often seen as lifetime fitness, i.e., computed throughout the lifetime of the organism. In behavioral ecology, however, each act is mainly considered individually, and fitness payoffs ascribed to it.

Often, however, we study the evolution of a trait, such as size, without knowing its genetic underpinning. In quantitative genetics a phenotypic trait, even though it is often supported by a large set of alleles related through various complex epistatic interactions, can be modeled according to the Price equation, which analytically states a covariance between trait value and fitness. Such an equation describes evolution in general but one needs additional information about the causal role of traits onto fitness values in order to capture the dynamics of evolution by natural selection.

Third, often traits and behaviors are social, meaning that their fitness benefit depends on the behavior of others. These traits and behaviors may impinge on the fitness of others. A social interaction showing altruism (see ALTRUISM) i.e., an evolution of behaviors which are costly (in fitness) for the individual and beneficial for some others, such as being sterile – compels biologists to consider selection at the level of genes. According to “Hamilton’s rule,”¹ the relatedness between actor and beneficiary accounts for the selection of the altruistic act because the degree of relatedness mitigates the cost (Hamilton 1964). If: if the act increases the number of altruistic alleles at the next generation (as compared to the selfish alleles), whether they are directly alleles of the individual’s direct offspring, or alleles of the offspring of the beneficiaries of its altruistic acts, then altruism evolves. (see ALTRUISM). One can then define an “inclusive fitness” of the individual, which takes into account within the estimation of fitness all those alleles due to the altruistic behaviour of the focal individual, whether they are her offspring or offspring of individuals genetically related to her. What is therefore increased by selection is rather more inclusive than individual fitness, even though calculating inclusive fitness may be difficult in practice (Grafen 2009).

References

Bouchard F., Rosenberg A. (2008): Fitness, *Stanford Online Encyclopedia of Philosophy*.

Davies, N.B., Krebs, J.R. and West., S.A. 2012. *An Introduction to Behavioural Ecology*. London: John Wiley & Sons

Fisher, R.A. 1930. *The Genetical Theory of Natural Selection*. Oxford, England: Clarendon Press.

Grafen A. 2009. "Formalizing Darwinism and inclusive fitness theory." *Phil. Trans. R. Soc. B.* 364, 1: 3135-3141.

Hamilton, W. D. (1964): The Genetical Evolution of Social Behavior, *Journal of Theoretical Biology* 7 (1): 1–16

Levins, R. 1962. "Theory of Fitness in a Heterogeneous Environment. I. The Fitness Set and Adaptive Function." *The American Naturalist*, 96, 891: 361–373.

Orr H. A. 2009. Fitness and its role in evolutionary genetics". *Nature Reviews Genetics*, 10: 531–539.

Stearns S. (1992): *The Evolution of Life Histories*. Princeton University Press.

Economics (*B. Walliser*)

In decision theory, utility is first understood as "decisional utility" for an individual agent. It reflects the satisfaction he expects from the consequences of the actions available to him. Utility summarizes his preferences in the form of a single indicator that implicitly aggregates his different choice criteria, considered as commensurable. Such a utility is ordinal when it reflects his preference order and cardinal when it reflects his preference intensity. Hence, in case of rational choice, the agent first computes the consequences of each action according to his beliefs. Then he chooses the action which maximizes his utility function (defined directly on consequences and indirectly on action) under physical and social constraints.

A consumer's utility function is personal, and defined by the alternative grocery baskets he can afford. Its arguments are his own consumed goods, but may also include the groceries of another, if he responds to them. But the utility function does not depend on prices, which are only arguments of the budget constraint he faces. Its analytical form reflects the complementary / substitutability character of the goods for him. Due to experience or addiction, it may well evolve through time. A producer's utility function is reduced to his profit; i.e., the difference between the value of products and production factors. Note that profit not only depends on quantities of exchanged goods, but on prices too.

In game theory, the utility function of a player depends on his own action and on his opponent's. The reason is that the consequences of his own action also depend on the action of his opponent. However, a player's internalization of another player's actions may express other motivations. It is so for altruism (sensitivity to other's consequences, see ALTRUISM) or imitation (adoption

of another's action). It is so for moral norms which are assumed to directly influence a player. According to Sen (1977), a player may even have preferences about his own preferences ("I would like not appreciating chocolate") and even on others' ("I would like the other being an altruist").

Classical economic theory considers that the utility function has to be inferred by the method of revealed preferences. This abductive method observes the choices of an agent in a given context and infers his underlying preferences. In practice, one considers that the agent is rational and that his beliefs and constraints are already known. However, even with many observed choices, this method is generally not unequivocal, and only reveals a set of such functions. In consumer theory, this method is applied from the observed baskets of groceries he bought for given prices and revenue. In game theory, the method is even more difficult to apply when the utility function does not satisfy previous constraints.

Under the influence of psychology, an alternative notion of "hedonist utility" was introduced. It concerns the well-being directly felt by the agent in some situation, independently of any decision. It can be measured by the agent's direct declaration to an observer on a scale defined by the observer. However, this evaluation is affected by different biases, because either the agent is unable to express the utility he feels or he will gain by deviating from the honest answer. Such a utility can be considered *ex post* (well-being effectively felt) or *ex ante* (expected well-being). For a consumer, *ex post* utility characterizes the satisfaction derived from consumed goods. *Ex ante* utility corresponds to an expectation of the satisfaction of desired goods, and may coincide with the revealed decisional utility.

In social choice theory, a "collective utility" function is introduced in order to compare alternative social states. It is not attached to any precise economic agent representing the society, even if it may be endorsed by the State. It may depend on all the components of a social state, individual as well as aggregated. However, a "welfarist principle" requires that it depends on them only through the individual utility functions of the members of the society. Aggregation of individual preferences is achieved by intuitive conditions of collective rationality. The most famous is the Pareto condition which states that if all members of the society prefer one state to another, so does the collectivity.

If individual utility functions are ordinal, it is impossible to find a collective one which satisfies rather obvious conditions including the Pareto condition. This theorem, due to Arrow (1951), stresses that the notion of "collective interest" is almost void. But if individual utility functions are cardinal, the aggregation procedure becomes trivially possible. The "no bridge problem" is solved since it is possible to compare the utility of any two members. The most frequent collective utility function is the Bentham function, which just adds the individual ones by giving them equal weights. Another is the Rawls function, which considers as a collective index the utility of the worst-off member.

References

Arrow, K. (1951): *Social choice and individual values*, John Wiley

Sen, A.K. (1977): Rational fools, a critique of the behavioral foundations of economic theory, *Philosophy and Public Affairs*, 6(4), 317:344.

Synthesis

Utility and fitness are two different concepts. However, they share many operational characteristics, and thus a deep affinity.

By nature, fitness is an objective variable and can be measured directly as any physical magnitude (relation to offspring number, sometimes including a reference to lifespan). Utility, in contrast, is a subjective variable. Like any state of mind, it can only be measured by the direct statement of some decision-maker.

In practice, though, both fitness and utility are revealed by behavior. Offspring number and a variety of physical performances (assuming some conversion rate) serve as proxies for fitness. Implemented choices indicate utility. Finally, both could be measured both *ex ante* and *ex post*.

Moreover, utility is likely to be impacted by numerous factors (content of decision, environment), whereas fitness values depend only upon some recurrent factors (selective pressures). In the same vein, utility may change at middle term by agent's experience while fitness appears to be more stable, even if at long term, it may change.

The crucial fact is that while utility is a property of individuals, fitness, when evolutionarily relevant, is by essence the property of a class. Utility is related to an agent, while fitness is ascribed to an allele, a genotype, or a trait by aggregating the distributions of offspring of individuals in the class defined by having them. This procedure averages away singular and idiosyncratic sources of fitness variation.

In economics, individual utility is well defined from preferences under mild conditions; it can only be aggregated in some collective utility under very strong conditions. Biology presents the mirror image: individual fitness is difficult to define and is unlikely to be measured, but trait or gene fitness are well defined, tractable, and scientifically meaningful.

The theoretical roles of fitness and utility and their predictive efficiency are identical. Knowledge of fitness or utility functions makes it possible to predict behavior and system dynamics. Hence, certain phenotypic traits or certain actions can be expected as outcomes in either field, by virtue of a maximizing process that we can legitimately expect under most conditions.

Evidence that such maximization is occurring is provided by natural selection, for fitness, and by rationality for utility. Thus, the fact that fitness and utility share theoretical roles and

predictive efficiency is due to the homology between natural selection and rationality. Both are indeed selective processes governed by instantiating maximizing procedures.

Heredity / Transmission

Evolutionary biology (*S. De Monte*)

The fact that certain properties of living organisms are maintained when parents generate offspring was widely accepted before Charles Darwin formulated his Theory of Evolution by Natural Selection. Its empirical application was breeding lineages endowed with specific characters. Beside the possibility of transmitting characters through a genealogy, however, Darwin's theory relied on another cornerstone: variation among individuals of the same species. Darwin's theory pointed out that as soon as characters display a certain degree of variation, then there is space for selection to favor one variant, therefore driving species-level changes. In this respect, Darwin's theory agreed with Jean-Baptiste Lamarck's argument against viewing species as immutable entities. However, their viewpoints diverged with respect to how variation originated, as well as the time scale over which environmentally-driven (today called "plastic") changes could be maintained in a lineage.

Variability in the characters of an organism is strictly related to inheritance, since it is generated as soon as their transmission is not perfectly faithful. In the view (prevalent at the time) that species were unchanging, however, the implications of possible biases in the distribution of traits in a population were unclear.

Although Mendel discovered in the 1860s that the transmission of characters followed specific laws of inheritance, it was not until the development of the field of genetics, at the beginning of the 20th century, that researchers looked at the mechanistic basis of heredity. Population genetics played a major role in reconciling genetics with evolutionary theory by showing that smooth changes in a species were not at odds with the fact that traits were inherited as discrete units. The "Modern Synthesis" [Huxley 1942] established the basis of today's prevailing view of heredity and variation in biological populations, whereby phenotypic traits are underpinned by discrete alleles and natural selection acts on the natural variation of those alleles in a population.

Throughout the first half of the 20th century, the physical substrate for heredity, i.e., the maintenance of a given trait through generations, was gradually clarified [Gayon, 1998]. Eventually, it was identified in sequences of nucleotides in the DNA molecule, which – were it not for "duplication errors" – are copied and transmitted faithfully from parent to offspring. The gene sequences act as discrete and inseparable units displaying the variability within a population, in the same way as alleles do. The causal chain "gene → protein → character" is the backbone of today's paradigmatic view of how characters are inherited: a given feature of the organism is achieved through a developmental process, which unfolds the 'program' inscribed in the genes and coded in the nucleotide sequence. The transmission of chromosomes therefore entails the maintenance of characters within a lineage.

In the 1970s, the gene became recognized not only as the unit holding the instructions for the characters of the organism, but also as the primary unit of natural selection [Dawkins, 1976]. What made genes so central to evolution was not the fact that they vary (a consequence of imperfect copying processes), but rather their permanence. Indeed, genes last long enough for the environment to be able to select those lineages that express the phenotype for which they code.

Together with the identification of the molecular mechanisms involved in “transcribing” the structure of DNA and “translating” it into a protein, in the 1960s the idea that the information needed to construct a given organism was hard-wired in the structure of the DNA molecule was born. According to this view, the sequence of bases that makes up the DNA molecule affects phenotypic traits and evolution would therefore progressively mold the genotype through successive events of mutation (of the sequence) and substitution (of sequences coding for less well-adapted traits by sequences coding for better adapted ones) within a population.

The identification of the physical basis of heredity with a symbolic sequence paved the way for a number of theoretical and computational developments, from molecular approaches to phylogenesis to the creation of “genetic algorithms” and *in silico* evolutionary experiments. The latter computational methods mimic natural selection in its drive towards adaptive optima, and they are used to observe the “evolution in real time” of virtual organisms. In both metaphorical and operational terms, the conceptual tools developed in information theory have conquered evolutionary biology. In particular, they have allowed concepts that previously lacked a solid theoretical foundation, like optimization, to be formalized (see OPTIMALITY).

However, considering the genotype as the essential determinant of a phenotype, and therefore also of an individual’s degree of adaptation to its environment, also led to several oversimplifications. In recent years, they have been widely questioned. One of the most notable of these oversimplifications is the idea that knowledge of the DNA sequence would suffice to yield knowledge of the phenotype. Since it is the DNA molecule that is replicated and passed on to the descendants, the possibility that information (see INFORMATION) is transmitted through a supports other than the DNA, such as by molecules contained in the cytoplasm, implies that other rules - different from Mendelian inheritance - may hold. In that case, environment-driven phenotypic changes may persist within a lineage even though they do not imply changes in the genetic code (“epigenetic inheritance”).

Similar arguments apply when considering behavioral properties of organisms. Other than the genetic underpinning of cognitive abilities, behavioral patterns are strongly dependent on the environment and developmental history of an organism and therefore manifest a much higher degree of plasticity than most genetically-encoded characters. Moreover, behaviors can be transmitted by non-genetic, cultural interactions among individuals. The extent to which behavior is transmitted genetically vs culturally, and how to describe the latter kind of non-

genetic heredity, are still at the center of current research in the evolution of behavior (which largely draws from methods and concepts borrowed from economics). In particular, there is still much debate over the nature of the entities that are transmitted, and whether these units, such as, for instance, “memes” [Dawkins, 1976], respond to natural selection in an analogous manner to genes.

Even though the physical support carrying the information may differ from the mere sequence of base pairs, and other means and modes of transmission have been considered, the framework that sees selection acting on variation has not been conceptually overturned. Indeed, it has long been known that some characters display non-Mendelian inheritance and that their expression or non-expression in the phenotype depends both on the genes and on other properties of the zygote, such as cytoplasmic state, DNA methylation, extra-chromosomal DNA, etc. Different determinants will be transmitted with differing fidelity and will therefore persist in populations over different time scales. The possibility of evolution occurring in such “conserved units” will however depend on their rate of change with respect to the speed of the ecological dynamics of competition. The relative time scales (see TIME SCALES) will determine whether a character is associated with a given lineage for a sufficient lapse of time, allowing selection to operate in a population of individuals that display variants of this character.

References

Huxley, J. (1942): *Evolution: The Modern Synthesis*

Dawkins, R. (1976) *The selfish gene*. Oxford University Press, Oxford, UK

Dawkins, R. (1982): *The Extended Phenotype*. Oxford University Press, Oxford, UK

Gayon, J. (1998) *Darwinism's Struggle for Survival: Heredity and the Hypothesis of Natural Selection*, Cambridge University Press

Economics (*B. Walliser*)

The concept of transmission is little developed in economic theory, even if it is practically present in a naïve form. A “genetic transmission” is already at work at the individual level, especially as technical or commercial skills are concerned. A “material transmission” deals with assets that are inherited by some individual, or capital passed on by an organization. A “symbolic transmission” takes place between individuals or organizations as an exchange of information, especially by education and training. Only this last one was partly theorized and even less formalized .

Symbolic transmission is conveyed by a language, which itself requires some material medium and must previously be learned (Rubinstein, 2000). In some cases, explicit knowledge is transmitted, orally or in writing, through a communication channel. But in other cases, it may proceed implicitly by observation and imitation of others' behavior, in order to acquire some

know-how. For each agent, it takes place in short sequences but continuously and noisily throughout his life cycle. Its scope changes from structural information on the overall environment to specific information on the local transactions.

For individuals, symbolic transmission takes place from one generation to another as well as between humans having few stable relations. A lot of information is stocked in a short-term memory where it stays in isolation and disappears gradually with time. But an essential part is stocked in a long-term memory where it is progressively structured in order to constitute a personal “experience.” This memory is itself continuously revised when receiving new messages, and it is subject to massive phenomena of deterioration, deformation, and lapses.

For organizations, symbolic transmission takes place between members receiving information from inside as well as from outside. It is preserved in human or artificial memories and achieves an “organization culture” well illustrated by the “corporate culture.” Since all members are continuously renewed during the history of the organization, a memory deficit appears when the ones who are leaving block the transmission. Some well-anchored beliefs, techniques, and rules, poorly kept during a firm crisis or transition, become definitively lost.

Technically, symbolic transmission is treated in game theory by signalling games (see SIGNALLING) which associate a sender and a receiver about a piece of information. It leads to “herd behavior” (Banerjee, 1992) which gives rise to “informational cascades” (Bikhchandani et alii, 1992). A piece of information is sequentially transmitted with some imprecisions and even errors, and induces various interpretation shifts. However, similar messages stemming from the same source or different ones are frequently repeated, and are consequently matched up, leading to robust and stable beliefs.

The transmission of information and knowledge appears to be a highly strategic task (see INFORMATION). It can be blocked by individual agents who possess some private information and have a personal interest in not diffusing it. It can be the object of retention by some organization, since it induces some competitive advantage on a market. Some members of an organization may be forbidden to quit for a given time interval, since their knowledge is too sensitive. Some information can nevertheless be acquired by competitors through industrial espionage.

New techniques are especially protected by long term patents which ensure a monopolistic position to the organizations which bear them (Lerner & Tirole, 2015). These patents are guaranteed by law but may nevertheless be sold to other organizations for some price. Such a limited diffusion defines restricted areas where techniques not available outside are common knowledge inside. Organization members are free to enhance the value of an innovation the organization has produced. However, some shared rules are stated, in order to limit the duration of the validity of the patent.

References

Banerjee, A. (1992): A Simple Model of Herd Behavior, *Quarterly Journal of Economics*, 107(3), 797-817.

Bikhchandani, S., Hirschleifer, D., Welch, I. (1992): A Theory of Fads, Fashion, Custom and Cultural Change as Informational Cascades, *Journal of Political Economy*, 12(3), 151-170.

Lerner, J., Tirole, T. (2015): Standard-Essential Cascades, *Journal of Political Economy*, 123(3), 547-586.

Rubinstein, A. (2000): *Economics and Language*, Cambridge University Press.

Synthesis

Even if biological heredity through reproduction has no specific counterpart in economics, the enlarged concept of transmission is considered for comparison between fields.

Evolutionary biology has a central mode of transmission of traits at different degrees of complexity of its entities, namely the heredity of genetic material at reproduction. Of course, other modes of “cultural” transmission exist, especially for higher animals. Birdsong is one example. Conversely, economics considers genetic transmission, material transmission, and symbolic transmission. The last is essential and is realized by informative messages based on a shared language.

An enduring effort in biological sciences aims at clarifying how information encoded in the genotype and transmitted from generation to generation translates into the phenotype. Such information is physically encoded mainly in the chromosomes, and guides the formation of the building blocks of living organisms. This feature underpins a unidirectional flow of information from the genes to the realized phenotype, so that selection can only affect the transmitted information through differential survival. In economics, by contrast, there is a continuous bidirectional exchange between “genetically-encoded information” and other kinds of transmitted information, allowing acquired novelty, for instance, to become hard-wired in a structure that has not given rise to the innovation.

Another feature of genetic information is that the information medium and the machinery to decode it have to be transmitted concomitantly, so it is impossible to separate content from code during transmission. In economics, symbolic transmission is continuous in time, and far more flexible. Transmission happens spontaneously whenever agents interact and can be voluntarily decided when it is in the agents’ interest. Almost everything can be transmitted, especially code and content, in a language that each agent adapts to its object. For instance, all acquired experience may be memorized and transmitted and can be exploited by the concerned agent or other ones.

Finally, transmission in biology essentially takes place at the moment of reproduction, and takes the form of conservation through generations of multiple features of the living being. As a result, for macro-organisms at least, transmission mainly occurs from the parents to the offspring along a lineage. Conversely, cultural transmission is not restricted to specific lineages, but spreads out, in and between organizations. For instance, unlike biological entities (with the notable exception of gametes in sexual reproduction), firms (airlines, for instance) and even civilizations (for instance Greece and Rome) are subject to mergers. Their cultures are then mixed with or without dominating influence. Within time, a culture results.

Information

Evolutionary biology (*J. Martens*)

Two main uses of the notion of information and its associated terminology (signaling, communication, processing, code, etc.) coexist in evolutionary biology. The first pertains to the domain of *behavioral ecology*, and concerns the ways organisms (animals, plants, bacteria) reduce the uncertainty of their fitness prospects via the use of environmental “cues” and/or “signals.” The second pertains to the field of *molecular genetics*, and is closely associated with the view that genes “carry information” or “instructions” about the development of an organism.

In a quite general sense, one might well say that the external world is “filled with information”, where the latter exists in the form of correlations between objects and/or events. For instance, one might well argue that, because the smoke is correlated with fire, the smoke “carries information” about fire; or that, because the tides are correlated with the position of the moon, the latter carries information about the former (Dretske 1988). Yet, in behavioral ecology, the use of the notion of information turns out to be much more *restrictive* than this general sense, for only those correlations that are meaningful or relevant to an organism’s fitness and that this organism can actually process (in adjusting its behavior accordingly) are properly said to “carry information” about its environment.

In behavioral ecology, more specifically, an object or event *X* will be said to *carry information about Y* whenever an organism *O* has evolved some function *F* for dealing with the information contained in *X* in a way that increases its expected fitness relative to *Y*—e.g., by reducing the uncertainty of a fitness outcome that is obtained in state *Y* (*Y* could denote here the edibility of a prey and *X* its color, or *Y* the probability that a food patch is plentiful and *X* the accumulation of previous foraging experience in this patch). This information is usually obtained at some cost to the organisms—through the means of observation, learning and/or communication. But the adaptive mechanisms whereby information flows from the environment to the organisms (or from some organisms to other organisms) can be highly diverse. Thus, humans and higher animals typically process complex information using their brains or their nervous system, whereas bacteria mostly rely on chemical cues or signals to adjust their behavior to the local conditions of their environment (e.g., through quorum sensing).

In (molecular) genetics, the notion of information—termed *genetical information*—is usually related to the idea that genes “contain information” about an organism’s phenotype (the correlate of this assumption being that such information has been “embedded” in the genome by natural selection over the evolutionary times). By extension, it is often claimed that the genes “code” for traits or proteins, a claim which is usually justified by the fact that the combinatorial properties of DNA appear to have been selected so as to facilitate the packaging and the transmission of genetic information, as well as its translation into the corresponding amino acids (which form the building blocks of functional proteins).

This genetic sense of the notion of information has accompanied two major breakthroughs in molecular biology. The first was the “deciphering” of the genetic code that followed the pioneering work of Watson and Crick (1953)—who identified the molecular mapping of the DNA structure (codons) to the protein structure (amino acids). The second is the “discovery” of genetic regulation processes by Monod and Jacob (1961), who showed that some portions of the DNA (the “operons”) have the capacity to switch “on” or “off” the expression of other genes (called the “promoters”)—thereby regulating the production of some proteins essential to the metabolism of organisms.

These pioneering works—as well as subsequent works in molecular and developmental biology—have largely contributed to popularizing the image of the genome as implementing some kind of “genetic program” for the development of each organism (Maynard Smith 2000). Yet, several biologists and philosophers have criticized this representation of the genome for obscuring the importance played by the epigenetic factors in the development of organism, and for conveying a strong form of genetic determinism (Keller 2002). The idea that genes “code” or “carry information about” the phenotype has also been accused of being over-simplistic with regard to the complexity of the developmental pathways through which the phenotypic characters actually relate to the genome (Godfrey-Smith 2000). Today, there is still no real consensus on the scientific value of the genetic use of the notion of information. But in spite of its critics, this genetic use remains quite popular within the community of biologists, and with the general public.

References

- Dretske, F. I. (1988) : *Explaining Behavior. Reasons in a World of Causes*, MIT press, Cambridge.
- Godfrey-Smith, P. (2000) : On the Theoretical Role of ‘Genetic Coding’, *Philosophy of Science*, 26-44.
- Jacob, F., & Monod, J. (1961) : Genetic Regulatory Mechanisms in the Synthesis of Proteins, *Journal of Molecular Biology*, 3(3), 318-356.
- Keller, E. F. (2002) : *The Century of the Gene*, Harvard: Harvard University Press.
- Smith, J. M. (2000) : The Concept of Information in Biology, *Philosophy of Science*, 177-194.
- Watson, J. D., Crick, F. H. (1953) : Molecular Structure of Nucleic Acids, *Nature*, 171(4356), 737-738.

Economics (B. Walliser)

Each economic agent is immersed in a physical and social environment about which he or she has an imperfect and incomplete belief. In the framework of a game, this belief applies to various entities (nature, other players, himself) and concerns various periods with reference to the current one (past, permanent, future; see CHANCE/UNCERTAINTY). The modeler of the game expresses these private beliefs by variables and relations between variables, thereby introducing parameters. Uncertainty on variables (or parameters) is itself represented in two forms: set-theoretical (subset of possible values of the variable) or probabilistic (probability distribution on the values of the variable).

In addition, voluntarily or not, each agent receives information from various sources: direct observation, revelation through other variables, purchase from specialized firms. It is assumed to be modular (it comes by successive flows), unequivocal (its interpretation is obvious and identical for all), and endowed with a truth value (it is true or false). Its form is that of a “message,” linked to an uncertain variable. This message is itself set-theoretic (in the domain of the variable) or probabilistic (a “signal” correlated to the variable by a known relation). It may be affected by some measure which allows the modeler to compare two messages for their informative content.

An agent uses new information to change his initial belief by applying “change rules.” These rules vary depending on the “change context.” In a “revising context,” the message makes the initial belief in a fixed universe more accurate, or contradicts it. The agent then revises his probabilistic belief by applying the “Bayes rule” (or “conditioning rule”). However, this rule needs to be extended to the case where the message (considered as true) contradicts the initial belief. In an “updating context,” the message indicates the direction in which the fluctuating universe has evolved. The agent then revises his initial belief according to the “Lewis rule” (or “imaging rule”).

All the change rules have been extended to the case of “crossed beliefs” of the type “I know that you know that...” between agents. Any message is then defined by two dimensions. The “content” concerns the piece of information effectively received by an agent. The “diffusion” of the message indicates which agents have received the message and what they know about that diffusion. There are various diffusion categories: public (each agent gets the message and knows that the others have received it), private (one agent received the message and the others know he received it, without knowing its content), secret (one agent received the message and the others learn nothing).

A message received by an agent modifies his belief and acts further on a relevant decision. The (*ex ante*) “information value” is the difference in expected utility the agent gets after receiving the message. For individual decisions, under usual decision rules, the value of true information is always positive. But in a game, the information value may be either positive or negative, depending on the type of game. If it is positive, it is in the agent’s interest to buy it directly at some cost (“informational action”) or to acquire it indirectly by modifying his action for a more informative one (“exploration-exploitation compromise”).

In signaling games, private information may be transmitted from a “sender” to a “receiver” before the operational game is played. Depending on his own interest, the sender may diffuse the information faithfully, blur it, withhold it, or even transmit false information. An equilibrium state is said to be “revealing” when it is in the sender’s interest to reveal the information. When it is to his advantage to withhold the information, the equilibrium state is “mixing.” If the game is repeated, the receiver may exploit his experience and attribute to the sender a degree of reliability as a source of information (“reputation”). More generally, an initial information, given to some players, may or may not be diffused. It either becomes homogeneous or stays segmented (“informational cascades”).

Synthesis

There is a fairly close analogy between the uses of the notion of information in economy and in behavioral ecology. First, in both of these fields, the relevance of any piece of information is determined in relation to an individual's agenda (i.e., maximization of either utility or fitness). Second, the scope of what may count as a piece of information is ultimately bounded by the cognitive abilities/architecture of the individual under study (idealized rational agent, human, bird, bacterium, etc.). Lastly, the uses of the notion of information serve a common purpose in both of these fields, which is to explain how new evidence can affect the observable behaviors of individuals (in relation to their particular agenda). For these reasons, there is no real gap between economics and behavioral ecology concerning the use of this notion.

Despite these similarities, economics and behavioral ecology differ in their assumptions about the cognitive structure of the individuals whose adaptive behavior is to be explained. In economics, for instance, individuals are supposed to be self-conscious and (more or less) rational agents. The information about the world they have at their disposal is supposed to be encompassed in representational states—their beliefs—which are themselves likely to be revised in the light of further evidence (multiple rules of revision can apply here, depending on the cognitive architecture of the agent). In behavioral ecology, on the other hand, individuals are not assumed to be endowed with intentional states like beliefs or desires; rather, their cognitive abilities rely mostly on rules of thumb, and vary from sophisticated (apes, birds) to rudimentary (plants, bacteria).

These cognitive differences, in turn, explain why most of the models that are used in economics to describe the *epistemic* behavior of the agents are not directly used in biology. But, in spite of these differences, some of these models can still predict the optimal behavior of biological individuals in the face of new information. Consider, for instance, an animal confronted with two kinds of predators in its environment, e.g. snakes and hyenas. When a gang of hyenas is present, climbing the nearest tree is the safest option, but when a snake is present, freezing is the best option. Suppose now that the animal receives a signal indicating (with a certain reliability) the presence of either a snake or a hyena. Given the joint prior distribution over the states of the world (presence of absence of a snake or a hyena, reliability of the signals, etc.), one could then use Bayes rule to (a) update those priors depending on which signal is received, and (b) derive the behavior (freeze or climb) that maximizes the expected fitness of the individual. This procedure would actually shed light on the possible adaptive responses of this organism, *even if* the Bayes rule proves totally inadequate as a description of the cognitive mechanisms that may lead the animal to freeze or to climb in the corresponding circumstances (Okasha, 2018).

The notion of information—envisaged in its ecological sense—also raises specific issues when it is used in relation to the notions of communication and signaling. These issues are discussed further in the corresponding entry in this volume.

By contrast with its ecological use, the genetic acceptance of this notion does not have a clear counterpart in economics, and relates more naturally to the terminology used in informatics and in the theory of information (Bergstrom & Rosvall, 2011).

References

Bergstrom, C. T., & Rosvall, M. (2011) : The Transmission Sense of Information, *Biology & Philosophy*, 26(2), 159-176.

Okasha, S. (2018) : *Agents and Goals in Evolution*, Oxford: Oxford University Press.

Market

Evolutionary biology (*J.-B. André*)

The notion of market has been used in behavioral ecology since the 1990s, in an explicit analogy with economic phenomena. The term market is applied whenever individuals have a choice between several sources of similar benefit, sources that may, in any case, be substituted for one another. For example, in a mutualist interaction, the choice concerns several social partners supplying benefits of the same nature but of different quantitative sizes. This leads to competition between individuals to be chosen as partners. Thus, in biology, markets are always “differentiated,” in the sense that the quality of the supply they offer varies.

Historically, the beginnings of the notion of market in biology lie in two areas of behavioral ecology. On the one hand, research into *sexual selection* underscored the consequences of the existence of a *choice* between several partners. On the other hand, the study of the relationships between dominants and subordinates in animal societies illustrated the importance of *external options* open to individuals (the “reproductive skew” theory). Since the 1990s and the work of Ronald Noë and Peter Hammerstein (1991), evolutionists have been using the notion of market explicitly, although the usage has not given rise to any formal unified theorization. The mechanisms brought together by the notion are fairly heterogeneous. It is applied to a greater or lesser degree in three main areas:

Sexual market

In species that reproduce sexually, individuals must both choose and be chosen by sexual partners; this gives rise to the expression “sexual partner market.” Initially, biologists studied the *consequences* of this market. In particular, the asymmetry of the male-female relationship – it being possible for males to produce a greater number of descendants – leads to an asymmetrical market, because females are the limiting resource. This asymmetry leads to an especially emphatic expression, in males, of characteristics intended to attract females. Subsequently, evolutionists investigated how the sexual market *functions*. The evolution of strategies whereby individuals choose a partner has been theorized in a way that is analogous to “search” models in economics. It has been demonstrated that evolutionarily stable

strategies are often based on a “satisficing” criterion: the best strategy consists in simply accepting all partners whose quality level is higher than a given threshold.

Mutualism

Positive interactions between individuals and species, known as mutualisms, usually give rise to conflicts of interest. Evolutionists have suggested that the outcome of these conflicts might be regulated by the nature of external options open to the individuals and, in particular, whether or not partners can be chosen. The notion of market has been applied to systems as varied as the interactions between plants and rhizobium, exchanges related to grooming in primates, and interactions between cleaner fish and their “clients.” This last system gave rise to an especially clear experimental demonstration of the importance of market phenomena in biology. Cleaner fish feed on parasites found on the surface of their clients’ skin. However, certain clients range over broad territories and have a choice between several cleaners, whereas others, whose range is more restricted, are captive clients for the cleaner. It has been shown that when several clients are waiting to be cleaned, cleaners always choose to feed on the least captive clients, making the others wait (since they have no choice, in any case). Cleaner fish therefore behave in agreement with their strategic position on the partner market.

How cooperation evolved

Finally, more recently, the notion of the market was introduced to game theory models aimed at understanding the evolutionary origin of cooperation. In fact, the principle of the market has sometimes even been presented as an alternative to reciprocity, thus opposing “partner control” and “partner choice.” Actually, more generally, it is usually a matter of accounting for the wealth of alternatives open to individuals in their social interactions. The concept of “competitive altruism,” for example, interprets cooperative behaviors as signals intended to attract partners on a social market. More recently, sharing the benefits of cooperative exchanges between partners has also been interpreted as the product of a market mechanism: a compromise between the need to attract partners and the need to extract benefits from each interaction.

References

Janetos AC. (1980): Strategies of female mate choice: a theoretical analysis. *Behav Ecol Sociobiol* 7: 107–112

Noë, C. P., Vanschaik, J.A., Van Hooff, J. (1991): The market effect - an explanation for payoff asymmetries among collaborating animals. *Ethology*, 87(1-2):97–118.

Noë, Van Hooff, J. , Hammerstein, P. (2001): *Economics in nature: social dilemmas, mate choice and biological markets*. Cambridge University Press.

Economics (*M. Cozic*)

One of the basic objectives of economics is to understand how markets work. Markets can be viewed as institutions through which goods (or “commodities”) and services⁸ are allocated to participants. Markets rely on *auxiliary* institutions (like the legal system) and can be contrasted with *alternative* institutions that also allocate goods (see below). Markets are notably differentiated according to the *type* of goods that are exchanged (e.g., the wheat market). Depending on his or her interests and on available empirical data, the economist may focus on distinct aggregation levels (markets for agricultural products, cereals, wheat). Despite its central role in the field, the concept of market is rarely characterized in an explicit way. Two properties are recurrent:

(1) market participants exchange goods on a voluntary basis

(2) market exchanges are mediated by prices

The first property distinguishes market allocations from *constrained* allocations. The second property specifies the form of the goods exchange. These two properties are sometimes made more precise. The first one may be augmented by the idea that

(1a) market participants are the legal owners of the goods they exchange,

which points out the importance of the legal system for the market. But it leaves out *a priori* markets for goods which are not legally owned by participants (e.g., the cocaine market). Property (2) may be augmented by the following statement:

(2a) for homogeneous goods, market prices tend to be uniform

Property (2a) is a classical criterion for individuating a market. For instance, Marshall (1890), after Cournot (1836), calls a market “perfect” when the integration of participants is such that prices are uniform. This tendency to uniformity is explained by the fact that there is some *competition* on the market; i.e., some rivalry between agents to exchange the same type of goods. The basic intuition is as follows: if seller 1 sells good x at unitary price p_1 and seller 2 asks price $p_2 > p_1$, no buyer will buy good x from seller 2, who will have to decrease his or her asking price. Similarly, if buyer 1 bids price p_1 and buyer 2 bids price $p_2 > p_1$, no seller will sell

⁸ From now on, we will simplify and mention only “goods.”

good x to buyer 1, who will have to increase his or her bidding price. One may consider competition as a third central property of markets:⁹

(3) market participants compete against each other

Property (2) (exchanges mediated by prices) calls for clarification. Firstly, barter is not necessarily viewed as incompatible with the market. The price concept involved in (2) does not strictly speaking suppose the existence of money but refers more abstractly to ratios of exchange between goods. However, prices are generally expressed using money, which is a fundamental auxiliary institution for markets. Money makes it possible to overcome the issue of the “double coincidence of wants” (Jevons, 1876) that faces barter: in order for agents 1 and 2 to agree to an in-kind transaction, two goods x_1 and x_2 owned respectively by 1 and 2 need to exist, such that agent 1 is willing to exchange x_1 for x_2 (and vice-versa for agent 2). In addition, not every price system is considered compatible with a market. For instance, a planned economy may use prices. To exclude this case, one may add to (2) the following property:

(2b) market prices are set in a decentralized way, either by sellers’ unilateral decisions or by bargaining between sellers and buyers

By endorsing (2b), however, one leaves out mechanisms where prices are set by equalizing supply and demand in a centralized way. To include them, one should replace (2b) with something like:

(2c) markets prices are set in a way that reflects the relationships between participants’ supply and demand for goods

Even if typical markets rely on prices, economists also subsume under the market concept institutions like marriage (Becker, 1973). These institutions do not usually feature prices, but they do match participants to each other (hence the name “matching markets,” see Roth & Sotomayor, 1990). Classical examples are matching between students and schools, medical interns and hospitals or kidney donors and recipients. In these cases, property (2) is not satisfied – at most (1) and (3) are. We have thus a broad concept of market, to be contrasted with a narrow, more traditional one, which satisfies properties (1), (2), and (3).

Economics coincides largely with the study of markets. It elaborates a taxonomy of market forms by taking as a reference the so-called “perfectly competitive” market (see COMPETITION). Other forms of markets are characterized by introducing deviations from the

⁹ See, for instance, the reasons put forward by Becker (1973) to qualify marriage as a “market”: “Two simple principles form the heart of the analysis. The first is that, since marriage is practically always voluntary, either by the persons marrying or their parents, the theory of preferences can be readily applied, and persons marrying (or their parents) can be assumed to expect to raise their utility level above what it would be were they to remain single. The second is that, *since many men and women compete as they seek mates*, a market in marriages can be presumed to exist. Each person tries to find the best mate, subject to the restrictions imposed by market conditions.” (p. 300)

perfectly competitive case: imperfect information, market power, externalities, etc. As for market power, pure competition is typically distinguished from monopoly (only one supplier) and oligopoly (a few suppliers). Notwithstanding some exceptions (e.g., auction theory), economic analysis does not focus much on the details of market organization (e.g., on the price-setting process). The development of experimental economics, however, requires a more fine-grained description, since in an experiment, subjects have to evolve in some specific environment.¹⁰ Economic analysis investigates the properties of these distinct forms of market. It places special emphasis on their ability to achieve appropriate allocations of goods between participants.

Distinct branches of economics specialize in distinct markets: agricultural products markets, real estate markets, insurance markets, etc. By contrast, general equilibrium theory considers a whole economy, with several interdependent markets. Notably, it studies the conditions under which a price system enabling the economy to be in a state of equilibrium, and thus coordinating simultaneously supplies and demands on all the markets, exists; and the properties of such market equilibria (especially (Pareto)-efficiency, see OPTIMALITY). See Debreu (1959).

Economic analysis also attempts to understand the existence and properties of non-market institutions that, like markets, distribute goods. For instance, “new institutionalist economics” (see Coase 1937, Williamson 1975) views firms as non-market institutions whose existence can be explained by the fact that market transactions are costly and that firms alleviate these “transaction costs.”

References

Becker, G. (1973) “A Theory of Marriage” *The Journal of Political Economy*, Vol. 81(4), pp. 813-846

Coase, R. (1937) “The Nature of the Firm” *Economica*, 16(4), pp. 386-405.

Debreu, G. (1959) *Theory of Value*, Cowles Foundation Monograph, New Haven: Yale UP

Jevons, S. (1876) *Money and the Mechanism of Exchange*. New York: D. Appleton & Co.

Marshall, A. (1890/1920) *Principles of Economics*, London: MacMillan & Co.

Roth, A. & Sotomayor, M. (1990) *Two-Sided Matching*, Cambridge: Cambridge University Press

Williamson, O. (1975) *Markets and Hierarchies*, New York: Free Press

Synthesis

Here, biology has clearly borrowed from economics. The notion of market is not among the fundamental concepts of evolutionary biology. These concepts date from the 1960s and

¹⁰ See Smith (1982) who proposes a general framework to describe a « microeconomic system ».

70s, and include kinship selection, the theory of costly signals, reciprocity, etc. The mate-selection market and other concepts came into general usage in evolutionary biology in French in the 1990s. The terms make explicit reference to economics, and the concept plays a much more marginal role than in the field of economics.

This said, the notion is only partially borrowed from economics. Biologists use the concept of the market chiefly in its broader meaning, limiting themselves to conditions (1) and (3) set forth in the economics entry. Individuals on a market proceed with voluntary exchanges of goods or services and as a result are in competition with each other, at least to some degree. Three remarks can be made. First, condition (1) obviously cannot transfer to biology intact, since it is based on the highly anthropocentric notion of *voluntary* trade. In the case of biology, the point instead is the selection of a behavior or a trait (grooming, cleaning, accepting as a mate, etc.) from among several possible others. Second, the notion of price as an exchange coordination tool is absent from biology. At most, price is present in an abstract sense, as the rate of exchange between two goods in a given interaction. Third, in biology, the concept of market is actually used synonymously with the principle of “partner choice.” There is a market when there is partner choice, and vice-versa. As a result, market models in biology are conceptually close to matching market models in economics.

For biologists, the most relevant aspects of the notion of the market are the phenomena and mechanisms generally included within “the law of supply and demand.” Typically, biologists try to show that there is “market activity” in a biological system by testing the predictions of “comparative statics,” (as economists say) associated with the “law.” For example, in a study characteristic of this approach (Fruteau et al. 2009), the authors examine the exchange of grooming services for being tolerated on feeding grounds in vervet monkeys (if A grooms B, then it will be easier for B to tolerate A’s presence on a food site). By using an automatic opening device, they allowed a low-ranking female to control access to a large quantity of food. This female then received much more grooming services than she had earlier. Next, they allowed another female to control access to another food source. The grooming services the first female received dropped sharply. In this way, exchange ratios (prices, in an abstract sense) responded to the supply shock (in this case, an abrupt increase in supply) in the direction predicted by the law of supply and demand.

References

Fruteau, C., Voelkl, B., van Damme, E., & Noë, R. (2009). Supply and demand determine the market value of food providers in wild vervet monkeys. *Proceedings of the National Academy of Sciences of the United States of America*, 106(29), 12007–12.

Mutation /Innovation

Evolutionary biology (*J. Gayon*)

In the life sciences, the term “mutation” was long used as an abbreviation for “species transmutation.” Today, it is used only in the technical sense given to it by genetics. To designate the process whereby a new species is formed, we speak of “speciation.” “Evolutionary innovation” is a vague term applied to any acquisition of a new structure or capability, at any scale of observation. It is especially apt to be used to describe changes observed on a grand scale (for example, the acquisition of mammary glands in vertebrates).

Genetics differentiates between three categories of mutations. (1) Gene mutations consist in the alteration of a gene, when one (or several) nucleotides are replaced, deleted, or added. (2) Chromosomal mutations are rearrangements of the chromosomes in which certain segments are lost or moved, implying breaks and splices. The main chromosomal alterations are: deletions (loss of a fragment of the chromosome), inversions (change in the orientation of a fragment), translocations (relocation of a fragment to another site on the chromosome, or to another chromosome), duplications (an extra copy of a fragment, with or without relocation), fissions, and fusions. The last two processes may result in a change in the number of chromosomes. (3) Genomic mutations, in which no genes or chromosomes undergo alteration; instead, the set of chromosomes is what changes. Polyploidy is the acquisition of an additional set of chromosomes, either endogenously (autopolyploidy), or when two sets merge, following hybridization. The number of chromosomes may also vary if an extra copy of one or several chromosomes is made; this is the case with trisomy.

The causes of mutation are varied. Gene mutations result chiefly from chemical or physical factors, such as radiation, that break the strand of DNA during the delicate process of replication. Chromosomal mutations are the result of morphological errors that occur when the cell divides. Chromosomes may be broken, or spliced, or two identical chromosomes may migrate to the same progeny cell. Genome mutations are morphological errors on a grander scale. For example, the toxic alkaloid colchicine is commonly used in plant breeding to induce polyploidy, an extra set of chromosomes.

In the immense majority of cases, the effects of mutations, especially gene mutations, are harmful (Orr 2005). They are nevertheless of crucial importance to contemporary evolutionary theory, which views the change in gene frequencies within populations as the basic process of evolutionary change. In the neo-Darwinian vision, mutation is the prerequisite for evolutionary change (.

It is often said that mutations occur “by chance.” This expression covers two different cases. At a molecular level of description, gene mutations happen “by chance” in the sense that they

may occur in an equally probable way anywhere in the nucleotide sequence. This description is purely related to the phenomenon itself. The processes that cause the phenomenon are deterministic, like those governing a roll of the dice; they are the result of a causal chain of events to which the molecular biologist usually does not have direct access. In an evolutionary perspective, a mutation is said to be “by chance” in the sense that the probability it will occur in an individual organism is not affected by the advantage or disadvantage it confers on the organism (Carlin 2011). Were this not the case, we would be dealing with a Lamarckian type of evolution, in which populations and species would evolve as the result of a guided process, so that an individual adaptation process anticipates the evolution of the species. However, even if such a process existed (which remains to be proved) it would in no way oppose an evolution channeled by natural selection. To put selection into play, a variation in the population suffices. A wholly Lamarckian evolution would be one in which the mutation pressure resulting from an individual physiological adaptation would be so intense that it would counteract any selection process.

The notion of evolutionary innovation lacks the operative rigor possessed by the notion of mutation. A significant innovation may be produced by a simple genetic mutation, consolidated by selection. This phenomenon is frequently observed in bacteria. For example, in a bacterial culture, it is common to see a unique mutant appear among the billions, a single cell capable of synthesizing an amino acid or an antibiotic-resistant factor the others do not know how to make. In that case, the term innovation is justifiable. Nevertheless, evolutionists prefer to reserve the notion for the acquisition of morpho-functional characters that are complex from the viewpoint of their genetic determinism (for example, the acquisition of fur by mammals, or bipedal locomotion in certain primates) (Wagner 2014). Innovation is a flexible term. The greater the evolutionary change, the more the evolutionist is inclined to speak of innovation. This is the case of the major evolutionary transitions classified by Maynard Smith & Szathmáry (1995): the passage from replicative molecules to colonies of compartmented molecules; the emergence of the eukaryotic cell, of sexual reproduction, multicellularity, and human language are all major innovations that relied on the preceding ones. In any case, the one trait all these evolutionary innovations, large and small, have in common is to enable species to colonize new ecological niches.

References

- Carlin, J. L. (2011) “Mutations Are the Raw Materials of Evolution”. *Nature Education Knowledge* 3(10):10
- Maynard Smith, J. and Szathmáry, E. (1995). *The Major Transitions in Evolution*. Oxford: Oxford University Press.
- Orr, A. (2005). "The genetic theory of adaptation: a brief history" *Nature Reviews Genetics*. 6 (2): 119–127

Wagner G. (2014) *Homology, Genes, and Evolutionary Innovation*. Princeton: Princeton University Press.

Economics (*B. Walliser*)

The sub-field called “economics of innovation” chiefly studies the technological innovations that make it possible to manufacture original products and implement new production processes. But the field could also cover organizational changes like novel management processes, or commercial ones, such as a different sort of retail outlet. Innovations may be classified according to their degree of departure from older processes. Some are radical; others are incremental. The most outstanding innovations have happened in sequential waves, well noted by the historians of techniques.

For Schumpeter, an innovation is driven by an innovative manager, who takes advantage of the inertia and failures of his competitors. This manager inherits a temporary monopoly power, until some copycat managers catch up. The innovator stirs up the dynamics of the economy, which otherwise would be stagnant. Today, it is agreed that innovations need an organized network of firms, small or big, public or private, but specialized and complementary. They are propelled forward by the push of technology and the pull of demand.

Two models for the spread of innovation have been suggested. A first, called the “linear model,” describes the sequential move from fundamental to applied research, then from applied research to development of a new process (or product), if it is commercially viable. It states a clear division of labor between fundamental research and applied research and a free circulation of knowledge acquired by firms at each step. Moreover, due to the weak incentive for firms to innovate spontaneously, public intervention is necessary. The intellectual property rights are protected by patents. Firms are encouraged to pool their investments in by vast research programs.

A second model was proposed more recently by the evolutionary school (Nelson, 1988; Dosi, 1988). Known as the “interactionist model,” it explains an innovation by a learning process initiated by various factors and subject to numerous retroactions. Even if the process is well localized, it is grounded in and structured by R&D “technological paradigms” that are common to several firms. It navigates “technological paths” subject to much irreversibility and leads to results which are path-dependent. Moreover, this process needs a suitable institutional framework and a favorable educational system.

After a first adjustment, an innovation spreads through the industrial fabric despite patent restrictions, if a patent does apply. However, the spread is slowed by the difficulty in sharing the implicit knowledge (know-how) needed for industrial implementation. Likewise, the spread is subject to a technological lockdown, due to coordination costs limiting positive externalities. In fact, technologies that are developed first supplant other potential ones, even

if the latter would have been more efficient (David, 1985). The usual example is that of the typewriter, due to the keyboard layout that remains the same, even if it is not optimal.

As for the microeconomic effects of innovation, competition by innovation is as strong as competition by price. Firms have disparate capacities of adaptation to the change in the market, and the innovating technologies have varied rates of return. At the macroscopic level, innovations induce an increase in the total factor productivity, the main driving force behind growth (see DEVELOPMENT/GROWTH) and cycles (see CYCLES). Considered initially as exogenous, technological innovation is more and more endogenized through its links with complementary factors (education).

Obviously, in evolutionary economics (Nelson & Winter, 1982), innovations are interpreted as mutations acting inside the economic system. These mutations intervene on “routines”; that is, on elementary production and organization processes taking place in the firm. Mutations may mimic biological processes, when they appear as a recombination of some elements (new molecules in pharmacology). They are naturally directed, in the sense that they are conditioned by the firm’s goals. But even when they result from deterministic physical transformations, they maintain a random dimension, because they are partially unpredictable.

In evolutionary game theory, mutations that are introduced act on the strategies implemented by the players. They are often treated as random processes similar to those considered in biology (exogenous modifications, recombinations). In a population-based view, they correspond to the emergence of new strategies, a unique strategy being attached to each player. In an agent-based view, they correspond to a deliberate behavior aimed at the exploration of untested strategies. By a voluntary trade-off, this behavior tends to balance the exploitation of strategies that have achieved good results in the past (see LEARNING).

References

David, P.A. (1985): Clio and the economics of QWERTY, *American Economic Review*, 75, 332:37.

Dosi, G. (1988): Sources, procedures and microeconomic effects of innovation, *Journal of Economic Literature*, 26, 332:37.

Nelson, R. (1988): Recent evolutionary theorizing about economic change, *Journal of Economic Literature*, 33(1), 48:90.

Nelson, R.R.- Winter, S. (1982): *An evolutionary theory of economic change*, The Belknap Press/ Harvard University Press.

Synthesis

The concept of innovation presents obvious similarities in evolutionary biology and economics. For both, it represents the idea of a qualitative factor that changes the monotonic course of evolution. Likewise, both economists and biologists consider a wide spectrum of phenomena to be innovations. In economics, innovations may be products, production processes, labor organization, to name just a few. In biology, a novel structure (the cell nucleus

or the eye) or a new functional capacity (walking, language), anywhere in all possible levels of organization, from molecules to social entities, is considered an innovation. In both areas, the importance and influence of an innovation varies on a large scale.

An important difference between economics and biology lies in the origin of innovations. Economics has a lot to say about the processes producing the technological or organizational innovations. It builds models that may refer either to intentional acts or to groping progress – the latter inspired in part by evolutionary biology. Biology, on the contrary, has no unified theory explaining innovations by specific exogenous or endogenous factors. It only builds some scenarios which are historically contingent, and describes some possible diffusion processes, in terms of proliferation in new ecological niches.

Conversely, economists and biologists agree that innovation chains which present many bifurcations are probably irreversible. The notion of “lock in” in economics is similar to the notion of “entrenchment” in biology. In the same way that in the economics of a human technological world, it becomes too costly to change the keyboard of a typewriter, even if the keyboard is not optimal, many biological innovations travel along developmental paths about which it can be observed that the earliest are the most stable. However, in biology, this differentiation process gives way to the diversified structure of organisms into species, contrary to what is observed in economics.

Comparison between innovation in economics and mutation in evolutionary biology is more hazardous. If biology is latitudinarian when speaking of innovation, it is precise about the causes and effects of genetic mutations. The physical processes leading to mutations at a molecular level have been observed and described, even if only in statistical terms. Likewise, the statistical effects of recurrent mutations in populations as well as the interaction between mutation pressure and other pressures (selection, random drift, migration) are synthesized in accurate formal models. The case is quite the contrary with economics. Models of the origin and consequences of innovations are not only contextual, but express different points of view.

Whether innovations or mutations are emphasized, the direction of the transfer between the fields is reversed. When speaking of innovation, evolutionary biologists draw inspiration, more or less consciously, from technological and economic thought. Conversely, when economists develop “evolutionary” models of economic change, they refer explicitly to evolutionary biologists. In both directions, the analogies are severely limited by the intentional character of agents’ behavior, a dimension which is absent from biological evolution, except perhaps for human cultural evolution.

Optimality

Evolutionary biology (*P. Huneman*)

Optimization, in various ways, is pervasive in evolutionary biology, because evolution by natural selection is generally supposed to support an optimizing trend. However none of the formal attempts to rigorously ground this supposition are uncontroversially successful (Birch 2016), be they Fisher's Fundamental Theorem of Natural Selection or Grafen's Formal Darwinism (Grafen 2002). This doesn't ruin the optimality methods but limits its purported universal applicability. Optimality reasoning goes as follows: If heritable trait x contributes to making the organisms fitter for their environments than organisms lacking trait x , an organism carrying x is likely to have more offspring and pass on this heritable trait. As a result, the frequency of x increases in the population. By the same reasoning, if there is a heritable variation σ on trait x , and if there is an optimal value X_0 of x in the environment, natural selection is expected to lead the population to such value. Optimization consists in either

- determining the optimal value of the trait, by considering some hypothesized environmental demands, and inferring that the trait is selected to meet such demands when it has this expected value: classical examples are the determination of clutch size in bird species (Lack 1954), and foraging time (Charnov 1976).
- inferring the value of the trait given knowledge of the environmental demands - e.g. the number of worms per outing a bird brings back to the nest will change according to the distance from the nest of the locations where the bird finds the worms (see Davies et al. 2012).
- or inferring the environmental demands (and therefore, the reason for selection) from the assumption that the trait was under selection ("reverse engineering," usual in paleontology).

Since optimization chiefly concerns phenotypic traits, it is a concept often encountered in behavioral ecology (Davis et al., 2012). It is less frequent in population or quantitative genetics. In those subfields, "fitness landscape" models define local and global optima as global or local fitness peaks (Wright 1932), and deal with the issue of understanding the shift from local to global fitness peaks, for which some controversial models have been proposed (e.g., Wright's "shifting balance theory").

Optimization of a trait for selection corresponds to the maximization of fitness, a magnitude somehow correlated to the expected number of offspring. It may not be possible to measure fitness directly by counting offspring (and even if it were, fitness concerns probability rather than frequency of offspring; see FITNESS). As a result, many optimality models actually focus on a proxy for fitness: energy intake, predation capacity, metabolism rate, etc. If an organism has to find resources in an environment, and pays a metabolic cost for its foraging effort, there is an optimum value of the foraging time which maximizes the amount of food retrieved given

the metabolic cost of exploring – namely, the overall energy intake (see fig. 1). Note that each behavioral ecology study focuses on a specific trait, and considers the proper proxy for fitness in this case; yet various traits may elicit a variety of proxies for fitness. An investigation of the global organism should therefore assess and match all the proxies for fitness. Since this is plausibly intractable, optimization thinking in behavioral ecology usually considers specific traits rather than whole organisms.

In many cases, however, the benefits of a trait depend upon its frequency in the population. If all individuals tended to fight in encounters, it would be advantageous to be aggressive (because others do not fight back when attacked). When a majority is aggressive, however, it again becomes advantageous to be peaceful (leaving all the aggressive individuals to destroy each other), and so on. With such cases, called “frequency-dependent selection cases,” the proxy for the optimum is the Evolutionarily Stable Strategy (ESS). The ESS is defined as the strategy that is such that a mutant strategy cannot invade (Maynard-Smith 1982) (see STRATEGY). Modeling ESS is a way to understand which phenotypic traits are maintained in the population because of natural selection, even if the origin of these traits is unknown. When traits detrimental to the individual organism (e.g., altruism) are studied, inclusive fitness, i.e. a magnitude defined by considering all fitness benefits caused by the trait (of the focal organism) in all organisms, weighted by a *relatedness* coefficient (Hamilton, 1964; West et al. 2007) (see ALTRUISM).

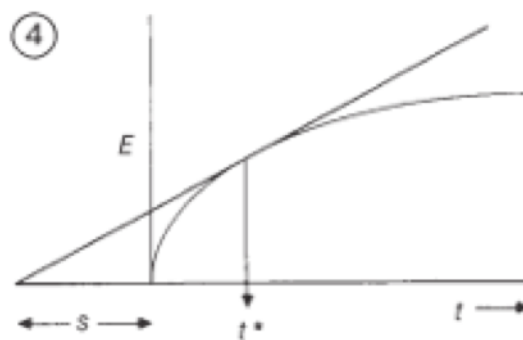


Figure 1. Determining optimal foraging time. (After Charnov, 1976)

Whereas in economics, the choice of a rational action by an agent corresponds to maximized utility, in biology the fixation of an optimal trait through natural selection corresponds to maximized fitness. In addition to this parallel between microeconomics and behavioral ecology, in population genetics one may also talk of optimal distributions in populations. The duality behavioural ecology/ population genetics could parallel the

distinction between individual decision theory -- where actions are explained by their maximizing utility -- and social optima.

Testing optimality models raises specific issues. If the trait does not have the value expected in a given model, one must determine why it was not optimized by selection. There are two possibilities: (a) a lack of genetic variation, a specific constraint on the possible available variation (Amundson, 1994), and (b) an unseen correlation with a trait under antagonist selective pressures; faulty characterization of environmental demands; or even a bad choice of fitness proxy (cases where energy intake, e.g., will not covary with fitness). There is no principled way to choose whether (a) one should reject the optimality assumption (in favor of acknowledging some constraints), or (b) one should change the coordinates of the optimality model while still considering that traits are optimized, but realize an optimal trade-off between environmental demands (see CONSTRAINTS/TRADE-OFF). This validation problem raises non-falsifiability issues about optimization. Criticism of the non-falsifiability of optimality assumptions therefore parallels that of the non-falsifiability of the transitivity of preferences as a methodological assumption in microeconomics, to the extent that *ad hoc* redescription of environmental demands can always support an optimality model. Even so, in specific cases there are methods for dismissing the optimality model and selection claims. In particular, considerations about convergent evolution, that is, similar traits in distinct species facing similar environments, can be applied to this effect.

Given that optimization concerns phenotypes, we should be able to use it when the genetic make-up is unknown. However, mathematical modeling of population genetics has shown that even despite any constraint on genetic variation, in the long run gene frequencies driven by natural selection will not necessarily reflect the phenotypic trend to optimality (Moran 1964; Grafen, 2002). Mainly, complex interactions between loci (sophisticated cases of dominance, epistasis, etc., or the simplest case of heterozygote superiority) constrain natural selection in a way that trumps optimization. Rather than wholly dismissing any assumption of optimization, however, this finding specifies some conditions under which it can be valid. Therefore, optimization is a powerful tool for determining what natural selection should be expected to do under such conditions. The evolutionary biologist can identify cases where either the genetic make-up, developmental systems, or the population structure and size, played an important role in the evolution of traits and the shaping of the gene pool.

References.

- Amundson 1994. "Two concepts of constraint: Adaptationism and the challenge from developmental biology". *Philosophy of Science* 61, 556-578.
- Birch, J. 2016 "Natural selection and the maximization of fitness". *Biological Reviews*, 91: 712-727.
- Charnov E. 1976 "Optimal foraging, the marginal value theorem". *Theoretical Population Biology*. 9(2):129-136.
- Davies, N.B., Krebs, J.R. and West., S.A. 2012. *An Introduction to Behavioural Ecology*. London: John Wiley & Sons

Gould S.J., Lewontin R. (1978) The spandrels of San Marco and the panglossian paradigm: A critique of the adaptationist programme. *Proc. Roy. Soc. Lond.* B205: 581-598.

Grafen, A. (2002) A first formal link between the Price equation and an optimisation program. *J. Theor. Biol.* 217: 75–91.

Hamilton, W. D. (1964). The Genetical Evolution of Social Behavior. *Journal of Theoretical Biology* 7 (1): 1–16

Lack, D. (1954): *The Natural Regulation of Animal Numbers*, Oxford University Press
Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Oxford: Oxford University Press.

Moran, P. A. P. 1964 On the nonexistence of adaptive topographies. *Ann. Hum. Genet.* 27, 383–393.

West, S.A., Griffin, A.S. & Gardner, A. (2007) “Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection“. *Journal of Evolutionary Biology* 20, 415-432.

Economics (*M. Cozic*)

One of the main assumptions of contemporary microeconomics is the hypothesis according to which the behavior of economic agents is optimizing (or complies with an “optimization model” of choices). These agents are assumed to have preferences over options which are transitive (if x is preferred to y and y is preferred to z , then x is preferred to z) and complete (for any pair of options (x, y) , either x is weakly preferred to y or y is weakly preferred to x). In addition, it is assumed that they choose the best option with respect to their preferences. Under some conditions, the choice of a best option can be represented as the choice of an option which maximizes a (real-valued) “utility function” (Debreu, 1954). The chosen option is thus an *optimal* option.

In consumer theory, a consumer is supposed to choose the best bundle of goods among those that he or she can buy, given his or her budget and given market prices. In the theory of the firm, a firm is supposed to choose a goods-production process that maximizes its profit, given the technology at its disposal and given market prices. In theory of choice under risk, further assumptions are made about the form of the utility function that the agent maximizes. Each option induces a probability distribution over consequences. According to expected utility theory (von Neumann & Morgenstern, 1944/1947), the utility of an option is the sum of the values of the consequences weighted by their respective probabilities. In game theory, the consequences of one’s choice depend on the choices made by others. It is still assumed that each agent acts optimally but, in addition, that his or her beliefs about the behaviors of others are correct. This is the basic intuition that underlies the concepts of *equilibrium* (especially “Nash equilibrium”) elaborated by game theory: each agent chooses a best response to the choices of others.

Among the social sciences, economics is alone in using so massively such optimizing models. It has been often criticized for this reason. A first criticism focuses on the optimality assumption itself rather than the assumptions made on the structure of preferences. H. Simon was one of the first to object to the implausibility of these models, from a cognitive point of view. As illustrated by the game of chess, where the discovery of optimal strategies is beyond our cognitive capacities, optimizing models are at odds with our ability to gather and process information. Simon proposed as a substitute a “*satisficing*” model where the agent sequentially considers options and selects the first one to meet some value *threshold* -- sometimes also referred to as an “aspiration level” (see Simon, 1955). This is not the only proposal made. Another class of models is constituted by so-called “stochastic” choice models, whose output is not a set of options (the options that the agent is willing to choose) but a probability distribution over the set of options. Typically, it is assumed that the greater the utility of an option, the greater the probability it will be chosen (see, e.g., Luce 1959). Evolutionary economics often relies on such stochastic models in dynamic contexts where some learning rules must also be assumed. One simple model postulates, for instance, that the utility of an option is the sum of the utility that the agent experienced when he or she chose that option in the past, and that he or she chooses an option with a probability proportional to its utility. The optimizing model has also been challenged from the standpoint of psychology and “behavioral economics.” These critiques question the assumptions, both explicit (like the transitivity property) and implicit (for instance, the assumption that preferences are stable or invariant from one context to another), made about preferences.

Economics, notably in the branch called “normative” or “welfare economics,” is interested not only in agent’s optimum but also in *social* optimum; i.e., what is best for a group of agents. The characterization of social optimality is a perennial issue. It is often assumed that social preferences over possible social states depend only on the preferences of the agents belonging to the group – an assumption that is often called “welfarism.” A weak but consensual criterion is Pareto-optimality (also referred to as (Pareto-)efficiency): a social state x is Pareto-optimal if it is not Pareto-dominated; i.e., if there is no other state y such that everybody weakly prefers y to x and at least one agent who strongly prefers y to x . When economic theory studies a given type of market, one of the basic issues it deals with is knowing whether this market leads to Pareto-optimal outcomes. For instance, a famous result states that perfectly competitive markets do lead to such outcomes (see COMPETITION). Game theory provides well-known cases of interaction where individually optimal choices lead to Pareto-dominated outcomes (see COOPERATION).

References

- Debreu, G. (1954) “Representation of a Preference Ordering by a Numerical Function,” in Thrall, R.M. & al. (eds.) *Decision Processes*, New York: Wiley, pp. 159-165.
- Luce, D. (1959) *Individual Choice Behavior. A Theoretical Analysis*, New York: Dover.
- Nash, J. (1951) “Non-Cooperative Games,” *The Annals of Mathematics*, 54(2), pp. 286-295.

von Neumann, J. & Morgenstern, O. (1944/1947), *Theory of Games and Economic Behavior*, Princeton: Princeton UP.

Simon, H. (1955) "A Behavioral Model of Rational Choice," *Quarterly Journal of Economics*, 69, pp. 99-118.

Synthesis

The central tenet of the analogy between economics and evolutionary biology is the assumption that agents or species tend towards optimization through maximisation: of utility in economics, and of fitness, by the organisms of a species that has had "time to evolve" in biology. It engenders many local parallels. For example, one of the basic uses of economic models is "comparative statics." The evolution of a certain variable is observed following an assumed change in another variable. In this way, one can analyze how trends in demand for a good change when its price increases. Similar applications exist in behavioral ecology, where an organism's behavior is assumed to optimize its fitness. When a certain variable is changed, one investigates what is predicted.

The nature of the maximand and of the process leading to optimization nevertheless differ significantly. (As for the maximand, see UTILITY/FITNESS.) Preferences are subjective; they are mental states. What is more, traditionally, economists have restricted themselves more or less to *behaviors* as a means of evaluating preferences (rather than agent statements). They *use* the optimization hypothesis to do so. This hypothesis does not readily lend itself to direct testing (which would consist in wondering whether, in a given situation, an agent has selected the best option). Conversely, testable implications of optimization can be obtained if the behavior of the agent is compared in different situations, or if auxiliary hypotheses about the content of preferences are accepted (for example, monotony in relation to profit, for a firm).

Since *fitness* is much less subjective, one would expect the epistemic situation to be radically different in evolutionary biology. In fact, it is much less different than one might think. The question of whether a given trait is optimal may be hard to answer, because it requires an ability to measure *fitness* and knowledge of the trade-offs weighing on the evolutionary process. In practice, *proxies* for fitness play an important role (a bit like *proxies* for preferences, in economics). Actually, the hypotheses about proxies and trade-offs are what is usually tested.

Like economics, evolutionary biology (behavioral ecology) subscribes to predictive optimization principles - "agents choose what they prefer," and "the fittest dominate the population by number." These assumptions raise the same testability problems, which are resolved by a similar process of resorting to additional data and information (comparisons, ecological or phylogenetic context, etc.).

In economics, a psychological process (or the coordination of a set of psychological processes, if the agent is an organization, like a firm) is supposed to drive towards optimization, whereas in evolutionary biology, a population process leads to the optimal trait. In behavioral ecology, the process may be complicated slightly by the fact that the trait in question can be a behavioral capability, like the weight of the worms the bird brings back to the nest – a capability that may itself shape the course to the optimal behavior. In this case, the population process causes the selection of the capability itself, while the capability causes the selection of a certain behavior in a given situation.

The justifications for the optimization hypothesis, and its place within the theoretical framework of the field, differ significantly from economics to biology. In biology, the optimization hypothesis is not primitive: it is derived *under certain conditions* from population genetics models, which raises the problems mentioned here. Optimization may follow a simple mechanism of differential reproduction, in which case the dominant force governing the evolutionary dynamics of gene frequencies and trait values is natural selection (and not mutation, or genetic drift). In economics, optimization of well-structured preferences is a more primitive principle. It was long considered to be an acceptable approximation, based on its intuitive plausibility. The hypothesis is sometimes justified on the basis of normative arguments. “Evolutionary” arguments have also been invoked, notably in firm theory, where it has been asserted that firms that do not maximize their profits will disappear (Friedman). Today, economists generally turn to experimental testing to determine the boundaries for the valid application of the hypothesis. In any case, these specialists have traditionally been more interested in applications of the optimization hypothesis (the “downstream” side) rather than in its justification (the “upstream” side). In this respect, the theorist acknowledges that the commonalities of the optimization concept chiefly concern the relationship between economics and behavioral ecology (the “downstream” side) rather than population genetics. Conversely, since Fisher, conditions and limits on optimization via natural selection in evolutionary dynamics of populations are the subject of a foundational debate in evolutionary biology. (See also CONSTRAINT/TRADE-OFF.)

Organizational levels

Evolutionary biology (*J.-B. André*)

The concept of *level* plays a central role in biology. The living world appears to be structured as a stack of nesting levels of organization, with an entity on the upper level being formed by an assembly of several lower entities. Genomes are sets of genes; multicellular organisms are sets of cells; animal societies are sets of individuals, etc.

The relationships between a biological system and the elements that make it up are not all inter-level relationships in the same sense of the term. As a result, the term *level* can be used in several ways. Here, we will limit ourselves to speaking of biological level in the sense of a “level of organization.” To do so, several restrictions are added to the concept.

First, a biological system is considered a level of organization only if it is identical to a system capable of living independently, existing in the present or having existed in the past. For example, the cells of multicellular organisms can be defined as a biological level of organization because they are identical to independent one-celled organisms. The organs of the body (heart, liver, etc.), by contrast, cannot be defined as a level in the same sense, because they have no independent counterpart.

Even with this first restriction, the concept of *level* is still too broad. At least one additional restriction must be placed on it. A system is considered a level of biological organization if the entities that make it up *interact* with each other. Hence a genome is a level of organization made of up interacting genes; an insect society is a level made up of social individuals, etc. Conversely, if the relationships between entities are purely genealogical, the entities do not qualify as a level of organization. A genus is not defined as a level of organization made up of species, and an order is not a level made up of families.

However, these two restrictions still do not suffice to make the concept of level of organization meaningful. For example, individuals of one species often interact with each other, and with individuals from other species. Is that a reason to define a species, or even an ecosystem, as a level of biological organization? To avoid this error, one last restriction is applied: the entities that make up a level of organization must interact *functionally* and not only competitively. At that point, the concept of level becomes *one of degree*, because the interactions between entities are never exclusively cooperative or exclusively competitive. For example, most eukaryotic genes interact functionally and cooperatively for the benefit of the organism as a whole. Yet when meiosis is taking place, certain genes compete with others (meiotic drive genes, for example). Therefore, a eukaryotic genome is a level of biological organization *only to a certain degree*.

This brings us to an evolutionary or adaptationist viewpoint on levels of organization in biology. The mechanism of evolution by natural selection is an abstract principle that could be applied to any entities with heritable properties. Generation after generation, it would tend to confer functional properties on these entities. It must therefore be acknowledged that natural selection can act on several levels in the living world and especially that it can act *at the same time* on several levels, more or less effectively. The term for this is “multi-level selection.” Natural selection acting on a given level tends to produce adaptations and functional systems at that level, thereby accounting for the quantitative character of biological hierarchies. A given hierarchical level is *more or less* a level of organization, depending on the degree to which natural selection has acted effectively on the level, compared to other levels.

The question of the *transition* between levels of organization is therefore a central one, in evolutionary biology. How does natural selection make a new level of organization emerge, formed by assembling several entities from a lower level? In particular, a transition implies a *cooperation* between the lower-level entities, which sacrifice some of their individual success to that of the larger, collective entity. Many of the mechanisms involved in transitions between levels of organization resemble cooperation mechanisms.

Transitions between levels of organization can therefore occur in two different ways. Certain transitions involve interaction between entities who share a recent common ancestor. In other words, they are related, and thus kinship selection can promote cooperative traits. This is the case with a transition to multicellularity, for example. It involves interaction between cells produced by a single ancestral cell (the egg cell). Other transitions involve interaction between entities who do not share a recent common ancestor. They nevertheless share an evolutionary interest with each other, being “in the same boat.” This is the case, for example, with genes located on the same genome. They are transmitted together, and as a result, are shaped by natural selection to cooperate with each other.

Nevertheless, this way of accounting for evolutionary transitions hides the fact that the factors permitting these transitions (kinship and common interest) are not *exogenous* parameters. Actually, they themselves are products of evolution, and are affected by evolutionary transitions. In other words, they are *endogenous*. For example, as a result of natural selection acting on their level, multicellular organisms are equipped with mechanisms making it possible to reduce the rate of mutation during cell replication. This is a means of limiting the appearance of cancers, and results in an increase in the degree of kinship between cells. Likewise, eukaryotic genomes code for meiosis mechanisms that make it difficult for a gene to bias its own transmission. As a result, these mechanisms align the interests of all the genes on the genome. Lastly, workers in several eusocial species express “policing” mechanisms that reduce the intensity of competition between workers, limiting the effects of natural selection within the colony.

In reality, there is a give-and-take between factors controlling the activity of natural selection and the effects of natural selection itself. Organization at a given level is a consequence of the

activity of natural selection on that level. But this organization (for example, anti-cancer or meiosis mechanisms) later affects the activity of natural selection, reinforcing its effectiveness on that level. It is the reciprocal interaction between natural selection and mechanisms that *modify* natural selection that leads to the most radical transitions of level observed in the living world, and to the emergence of the most complex living organizations.

References

- Michod, R. E., and D. Roze. 1997. Transitions in individuality. *Proc R Soc Lond B Biol Sci* 264:853–857.
- Michod, R. E. 2000. *Darwinian Dynamics: Evolutionary Transitions in Fitness and Individuality*. BioScience. Princeton University Press, Princeton.
- Okasha, S. 2005. Multilevel Selection and the Major Transitions in Evolution. *Philosophy of Science* 72:1013–1025.
- Michod, R. E. 2007. Evolution of individuality during the transition from unicellular to multicellular life *104:8613–8618*.
- Lehmann, L., L. Keller, S. West, and D. Roze. 2007. Group selection and kin selection : Two concepts but one process.

Economics (*M. Cozic*)

It is common to distinguish levels in economics, but the notion is not unambiguous. Three distinctions may actually be identified, between: (1) agents and institutions, (2) organizations and their members, and (3) aggregation levels.

In a first view, agents and institutions intervene in representations and explanations of economic phenomena, along with the natural environment where they take place. The following view of agents emerges from economic theory: they have the ability to select options on the basis of their preferences (or “objectives”) and beliefs. The notion of institution is less elaborated. Perhaps one reason for this lack of definition is that economics focuses mostly on one family of institutions; i.e., markets. There have nevertheless been some attempts to characterize institutions. Notably, North’s influential proposal (1990) according to which “institutions are the rules of the game in a society or, more formally, the humanly devised constraints that shape human interactions” (see also Aoki, 2001). Conventional economic theory typically focuses on how agents behave given a natural and institutional environment. A salient feature of institutions is that they influence agents’ choices, notably by sending signals and by constraining choices. For instance, market prices may be seen both as signals emitted by the market and as determinants of agent’s feasible set of options. Less frequently, economics (notably game theory and evolutionary economics) studies the emergence and persistence of institutions (e.g., money, sharing norms, technological standards, etc.).

Secondly, one may distinguish levels of agency in a compositional hierarchy,¹¹ where entities at one level are composed of entities at lower levels. In basic microeconomic theory, the two main types of agents are households and firms. These entities are considered as agents to the extent that choice determinants are ascribed to them and that there are “centers of decision.” On the other hand, they are composed of agents; e.g., household members. Groups of agents who share some common objectives and who act in a coordinated way are sometimes referred to as “organizations” (see Elster, 2007). Basic examples are firms, unions, political parliaments, scientific societies, schools, recreational clubs, etc.¹² Levels may be nested: some workers may belong to a local union, which belongs to a national union, which belongs to a confederation of national unions, etc. In traditional economic theory, organizations are often considered as “black boxes.” However, in recent decades, more attention has been devoted to the nature, structure (information flows, hierarchy and authority relationships, decision making processes), and performances of economic organizations; i.e., organizations involved in production, exchange, and consumption of goods (see Gibbons & Roberts, 2013). Special emphasis is put on the *firm* (why does it exist? What determines its size? what is the relationship between employer and employee?). Households are also studied (by “family economics,” see POPULATION). Two important remarks must be made. Firstly, in general and as far as economics is concerned, the lowest level of this hierarchy is composed of individuals. However, some choice models coming from “behavioral economics” assume infra-individual agents (“multiple self” models). Secondly, at the conceptual level, the relationship between institutions and organizations is largely an open question.

A third distinction is related to *aggregation* levels. For instance, any of the following may be considered: the disposable income of a single household located in Paris; the aggregate disposable income of Parisian households; of French households; of European households; etc. There are different ways of aggregating a variable (e.g., sum, averages, etc.) When economics models a population of agents (e.g., consumers), it often uses a “representative individual” whose properties (e.g., disposable income) are aggregates of the properties of the population’s agents (see below). Aggregation levels are related to the distinction between macro- and microeconomics: macroeconomics is concerned with upper-level aggregates (typically, nationwide aggregates) and states relationships between these variables (accounting identities or other relationships).

The three distinctions above may be merged simply by distinguishing two levels of phenomena: the *individual* level, related to individuals’ behaviors and their proximate determinants; and the *social* or *collective* one, related to institutional, organizational, or aggregate properties, events, and entities. As for the individual level, economics’ conceptual

¹¹ The term comes not from economic theory, but from contemporary philosophy of science. Ecology provides the paradigm of a compositional hierarchy : cell, organism, population, community, etc. See Potochnik & McGill (2012).

¹² The terminology is far from stable: the term “institutions” is sometimes used for what we just called “organizations.”

framework is mainly structured by the distinction between behaviors (or choices) and their mental determinants (beliefs, preferences). This framework has recently been enriched by neuroeconomics, which introduces neurally described determinants of choices. Both mental and neural properties are assumed to cause choices. A common assumption is that mental phenomena supervene on neural ones.

The relationship between the individual and social levels is a perennial ontological and methodological issue in economics and other social sciences. From the ontological point of view, individualism claims (and holism denies) that there is nothing but individual phenomena in social phenomena. From the methodological point of view, individualism claims that any explanation of a social phenomenon has to be based on individual phenomena (or that any nomological relationship couched at the social level must be derivable from nomological relationships couched at the individual level). Economics is often considered as the paradigmatic individualistic social science. However economic explanations typically involve social concepts (e.g., collective agents, institutional constraints) or concepts which are not straightforwardly related to individualistic ones (e.g., equilibrium concepts). Inside economics, individualism is related to the debate on the “microfoundations of macroeconomics.” The controversy was sparked by the fact that, in macroeconomics, some putative nomological relationships between aggregate variables were postulated without any insight about how they could emerge from received assumptions about the behavior of economic agents. A typical theoretical answer to this perceived weakness consists in proposing models built around (optimizing) representative agents, so that micro- and macroeconomics are today largely integrated. However, the meaning of such theoretical move is still discussed (see, e.g., Kirman (1992) and Hoover (2001)).

References

- Aoki, M. (2001) *Toward a Comparative Institutional Analysis*, Cambridge, Mass.: MIT Press
- Elster, J. (2007) *Explaining Social Behavior*, Cambridge: Cambridge University Press
- Gibbons, R. & Roberts, J. (eds) (2013) *Handbook of Organizational Economics*, Princeton: Princeton University Press
- Hoover, K. (2001) *The Methodology of Empirical Macroeconomics*, Cambridge: Cambridge University Press
- Kirman, A. (1992) “Whom or What Does the Representative Individual Represent?,” *Journal of Economic Perspectives*, 6(2), pp. 117-136
- Potochnik, A. & McGill, B. (2012), “The Limitations of Hierarchical Organizations,” *Philosophy of Science*, 79(1), pp. 120-140.

Synthesis

The most significant parallel is the one between levels of social organization and levels of biological organization (definition 2, above). Both fields are dealing with tangible entities made of smaller tangible entities. The definitions are not totally analogous, however. The economist emphasizes the fact that from the outside, an organization behaves like an individual. The biologist, on the other hand, defines a biological level of organization according to the degree of cooperation between the entities that make it up. Yet the difference between the two fields should not be exaggerated. There is some similarity between cooperating and pursuing a common goal. The study of organizations occupies a smaller and more uncertain niche in economics (where it is often sidelined by more central questions). In biology, it is at the heart of the question of *transition* from one level to another.

The biological counterparts of definitions (1) and (3) of “levels” in economics (institutional vs. individual level and levels of aggregation) are much less relevant.

Concerning (3): like any science, evolutionary biology can operate at different levels of aggregation. But there is no parallel to the distinction between micro- and macro-economics, and the questions it raises. One structural reason for this may be that evolutionary theory adopts a viewpoint that is intrinsically population-based.

Concerning (1), the absence of a direct biological counterpart is not especially surprising, insofar as institutions are often considered to be specific to the human race. But the strong affinity between the notions of institution and organization has already been pointed out. In the organization of a biological level, there are *de facto* elements related to the supervision or coordination of behaviors of the level’s members, constraints that appear to be exogenous for these entities. Thus, these organizations are akin to institutions, particularly those that arise spontaneously, without being deliberately created by agents.

To these “analogical” considerations [*sic*], it must be added that by contrast, institutions occupy an important place in the area where social sciences and evolutionary biology meet. For example, certain researchers assert that in our ancestral environment, institutions *co-evolved* with our genetically inherited characteristics (see Bowles & Gintis, 2011). This phenomenon is said to be a particular case of what is called gene-culture co-evolution.

References

Bowles, S. & Gintis, H. (2011) *A Cooperative Species*, Princeton: Princeton University Press.

Population

Evolutionary biology (*P. Huneman*)

Evolutionary biology by essence deals with populations. Darwin himself was famously impressed by Malthus's *Essay on the Principle and Population*, and understood competition most generally by the gap between the growth rate of a population and the scarcity of resources. While individuals *develop* (from the zygote to the adult and reproductive stage), a species *evolves*, and it evolves because evolutionary change takes place in a population of this given species, along the lines Darwin theorized. As indicated by Lewontin (1971), who intended to make clear and general the concept of natural selection that Darwin used, evolution by natural selection occurs in a population of individuals featuring *variable heritable* properties that have *a causal effect* on the reproductive chances of the individuals. This entails that evolution supposes a population of varying individuals.

Mayr famously contrasted the Darwinian reasoning, which he called "population thinking," to the traditional, pre-Darwinian approach in natural history and morphology, labeled typological or essentialist (these notions differ, but here, this difference doesn't matter) (Mayr 1963). While the typologist sees all members of a species as more or less complete copies of a type, the "population thinker" considers the species as a set of varying individuals. To the Darwinian, interindividual differences are not a kind of noise to be ignored or averaged away (for example, by considering the mean values of all traits). Instead, they are of the essence: epistemologically, they are necessary to understand how evolution is possible; ontologically, they are required for selection to operate.

Population thinking in the end calls for statistical tools and probabilistic concepts. Mendel's views on genes (namely, the statistical laws of segregation), as well as statistical mechanics, both elaborated at the same time as Darwin's views, also instantiate population thinking. Although Darwin did not himself work with those mathematical tools, population geneticists of the 1920s and 30s, like J.B.S. Haldane, R. Fisher, and S. Wright, essentially elaborated them in order to deal with populations and population processes relevant to biological evolution. But populations of organisms of one species, in this perspective, came to be seen through the notion of a "gene pool," since according to the classical Modern Synthesis view, evolution is constituted by, caused by, or at least related to, a change in allele frequencies.

Minimally, a population is made up of distinct, variable individuals likely to reproduce; those individuals are supposed to interact, for instance to compete for resources (see COMPETITION), and to mate together. Thus, not all living things in an ecosystem - for instance all trees in a rainforest - make up a population *sensu* evolutionary biology.

For evolutionists, a population is generally of one species. The question of the emergence of a species, a process called "speciation" by Modern Synthesis biologists, focuses on a single population. It may involve spatial separation, migrations, or disruption of gene flow. Studies of mutualism (pollination, symbiosis, etc.) or parasitism, however, will consider populations made up of two species.

Population ecologists, on the other hand, consider populations of organisms, possibly of two species or more. They study the variations of abundances of one or two species, given one particular interaction, for instance competition or predation. Lotka-Volterra equations (see GROWTH/DEVELOPMENT) make it possible to model these variations, and predict either cycles, or equilibria (for instance extinction of one species). The relative constancy of population abundances (which fluctuate, but usually around a given value) is a major question for population ecology, under the names of “population regulation” or “population control.” A major controversy, foundational for theoretical ecology, concerned whether this regulation is mostly due to density-dependent factors (such as competition) or density-independent ones (such as climate) (Lack 1954 vs. Anderwartha and Birch 1954). Current population ecologists acknowledge that ecological dynamics involves connected and interacting populations (for instance, populations exchanging individuals). They have forged the concept of metapopulation (Hanski 1991).

In evolutionary biology, several properties of a population are of key theoretical importance. Population *size* matters, since the predictions based on fitness values assume that the population is very large. As a consequence, the weak law of large numbers can be applied, in order to consider that the fittest traits – namely, the ones with the highest chances of being reproduced - are the traits that have reproduced the most, and now prevail. Sampling error due to small population size is a major stochastic cause of deviations from fitness-based predictions. This is called “drift,” and population geneticists classically view it as one of the forces that shapes the frequencies of various alleles in gene pools at equilibrium (see CHANCE/UNCERTAINTY). Whether or not natural selection is the major force shaping traits in all species relies on the empirical question of the size of most species populations in the field. Through drift, small population sizes may have a large impact on important phenotypes of organisms.

Population *structure* is also, arguably, a major factor of evolutionary dynamics. First, if mating is not random -- if the population allows for assortative mating (e.g., individuals living in close proximity and hence mating together are more likely to be similar), this will impinge on genetic recombination through the generations, and thus bias evolution. Second, all known processes that yield altruism (see ALTRUISM) rely on the idea that altruists should be more likely to interact with altruists, where altruism evolves. Population structures that cluster likes with likes tend to realize such situations and therefore to promote altruism.

While population has been a pervasive and essential concept for evolutionary biologists since Darwin, it differs from key concepts such as fitness, adaptation or inheritance in that the latter have been the subjects of attempts to elaborate theories about them. As a result, often there are major theoretical disputes regarding their meaning (see FITNESS and ADAPTATION). By contrast, theoretical elaboration has rarely focused directly on the notion of population. Like the pervasive and indispensable notion of “environment,” it remains very weakly defined, and is mostly an operational concept (even though some philosophers recently sought to account for it in theoretical terms, e.g. Godfrey-Smith 2009).

References

Andrewartha, H. G., Birch, L. C. (1954) *The Distribution and Abundance of Animals*. University of Chicago Press.

Godfrey-Smith, P. (2009) *Natural Selection and Darwinian Populations*. Oxford University Press

Hanski, I. (1986) *Metapopulation Ecology*, Princeton University Press.

Lack, D. (1954) *The Natural Regulation of Animal Numbers*. Oxford University Press.

Lewontin, R.C. (1970) "Units of selection". *Ann Rev Eco Syst* 1:1-18

Mayr, E. (1970) *Population, Species, and Evolution*. Harvard University Press, Cambridge, MA

Economics (*M. Cozic*)

Since its beginnings in the 18th century, economics has devoted attention to the interaction between economics variables and demographic variables like population size, mortality, fertility, and migration. Studies dealing with the relationships between these two sets of variables are often called "population economics" or "economic demography" (see Kelley & Schmidt (2008)). We will focus on two topics. Firstly, on the relationship between demographic and macroeconomic variables, especially the impact of population size variation on the aggregate product per capita (see GROWTH). Secondly, we will deal with family, one of the major determinants of demographic phenomena. In fact, the study of "family economics" is often integrated with population economics.

In his *Essay on the Principle of Population* (1798), Thomas Malthus made resounding claims. He pointed out, for example, the tension between the *natural* growth of the population (which is exponential) and the growth of the food supply (which is at best linear). According to Malthus, this difference causes a decline in living standards. This, in turn, impacts population size, either by way of a reduction in fertility (a "preventive check"; e.g., sexual abstinence, delayed marriage) or by way of an increase in mortality (a "positive check"; e.g., disease, war, famine). From this point of view, technological progress can be expected to lead only to a temporary improvement in standards of living: in the long run, the improvement will be annihilated by population growth. Such a process is typically called a "Malthusian trap." It is often asserted that up to the Industrial Revolution in the 19th century, economic history matched the implications of Malthusian assumptions reasonably well – notably the stability of standards of living.

The rapid increase in world population in the past few decades (3 billion people in 1960, 4 billion in 1974, and almost 8 billion today) has kept lively debates on the impact of demographic growth on economic growth (and also on development or poverty). These issues are dealt with by researchers in economic history, growth theory, and development economics. Some argue that population growth has a negative impact on economic growth, while others, on the contrary, claim that its impact is negligible or positive. Recent empirical

studies suggest more nuanced views, according to which the correlation depends notably on the period considered (negative correlation in the 1980s but negligible in the 1960s and 1970s) and on the level of development of the country considered (see Birsdall, Kelley & Sinding 2001).

By asserting that a decline in material welfare (especially in food supply) lowers birth rate by influencing marriage behaviors, Malthus already stressed the impact of the economic situation on the family. The relationships between conventional economic factors (like incomes, demand on commodity markets, supply on the job market, etc.) and family behavior is at the heart of “family economics.” Family structure and organization, along with behaviors related to marriage, divorce, and child-bearing (see Ermisch, 2008 and Browning, Chiappori & Weiss 2014). One salient feature of family economics, differentiating it from other approaches to these topics in the social sciences, lies in the fact that since G. Becker’s seminal work (Becker, 1981), its explanatory framework has mainly borrowed from microeconomic analysis. For instance, decisions to marry are typically viewed as taking place on a “marriage market” where individuals compete against each other to find spouses (see MARKET). *Matching theory* (see Roth & Sotomayor 1990) provides a tool for analyzing the marriage market, even if it disregards the lack of perfect information that exists in the actual search for potential mates. It operates on the idea that marriage is expected to satisfy some *stability* characteristic, according to which (a) no married person prefers to be single and (b) no two single persons would prefer to be married to each other. Another example of family economics would be the view that the division of labor between spouses as a specialization can be explained by comparative advantage. Decisions to have children are typically seen as expressing a trade-off between the number of children and the how much parents invest in each of them – and investment which would determine their “quality” (see Becker & Lewis (1973)). A microeconomic model of this trade-off may be consistent with the empirical finding that an increase in income is associated with a decrease in birth rate – a crucial stage of the so-called “demographic transition” that occurred in Western Europe at the end of the 19th century. (For a criticism of this explanation, see Galor, 2005).

References

Becker, G. (1981) *A Treatise on the Family*, Cambridge: Harvard University Press

Becker, G. & Lewis, H.G. (1973) “On the Interaction between the Quantity and Quality of Children,” *Journal of Political Economy*, 81(2), pp. S279-S288

Birsdall, N., Kelley, A. & Sinding, S. (2001) *Population Matters. Demographic Change, Economic Growth and Poverty in the Developing World*, Oxford: Oxford University Press

Browning, M., Chiappori, P-A. & Weiss, Y. (2014) *Economics of the Family*, Cambridge: Cambridge University Press

Clark, G. (2007) *A Farewell to Alms. A Brief Economic History of the World*, Princeton: Princeton University Press

Ermisch, J. (2008) "Family Economics," in *The New Palgrave Dictionary of Economics*, 2nd ed., Steven N. Durlauf and Lawrence E. Blume. Palgrave Macmillan, 2008.

Galor, O. (2005) "From Stagnation to Growth: Unified Growth Theory," in Aghion, Ph. & Durlauf, S. (eds.) *Handbook of Economic Growth*, vol. 1A, chap. 4, Elsevier

Kelley, A. & Schmidt, R. (2008) "Economic Demography," in *The New Palgrave Dictionary of Economics*, 2nd ed., Steven N. Durlauf and Lawrence E. Blume. Palgrave Macmillan, 2008.

Malthus, Th. (1798) *Essay on the Principle of Population*, trad.fr. Theil, P. Paris: Gonthier, 1963

Roth, A. & Sotomayor, M. (1990) *Two-sided Matching*, Cambridge: Cambridge University Press

Synthesis

Even though the concept of population is widely used in both fields, the foundational role it plays in evolutionary biology is unparalleled by its role in economics. For example, Darwinian evolution is a population-level process; evolutionary biology relies on "population thinking." This dimension is absent from economic thought: microeconomics operates at the level of the individual agents and macroeconomics tends to consider macro-entities (states, firms, banks, etc.) rather than populations. Although natural selection and rationality share many conceptual characteristics (see FITNESS/UTILITY), a main difference is that natural selection is inherently populational, while rationality is individual-centered. This key difference is reflected by the distinct statuses of the population concept in the two fields. The theory of the evolutionary process in biology is *population* genetics, while the classical theory of economic change and equilibria ultimately relies on rational choice theory, based on the individual.

More precisely, while all evolutionary problems refer to some population component, economists dealing with population are mostly concerned with the issue of growth and its relationship to various geographical and social populations.

Another difference is that for economists, a population is always made up of human beings; when the economist handles a specific problem, the only question is determining the category to which the humans belong (country, social class, age class, etc.). In evolutionary biology, on the other hand, the nature of a population is an open question. Microevolution considers populations of a single species, while studies of coevolution or mutualism will focus on two species, or maybe more. Also, a single entity can be considered either as an individual - such as a beehive, or a mammal - or as a population, when the many sets of endosymbionts that fulfill important functions for this organism are taken into account.

Economists as well as evolutionary biologists study family, though economists question the impacts of various family decisions upon population structure and growth - i.e., the "demographic transition" - while for evolutionary biologists, families are understood from the viewpoint of genetic relatedness. The gene's-eye view supports a variety of attempts to

explain family dynamics (mate choice, inter sibling conflict, sexual conflict, etc.) biologically. Economists, however, do not take the genetic dimension into account. Moreover, biologists mostly examine the evolution and dynamics of family structures – usually avoiding the word “family,” which refers to a social institution - instead of its effects on population.

In evolutionary terms, the effects of population structure are an important issue in population genetics as well as behavioral ecology. Population size defines the amount of stochastic effects (random genetic drift, see CHANCE/UNCERTAINTY), kin structure governs the evolution of altruism (see COOPERATION, ALTRUISM), etc. In this case, a parallel concern may exist in economics, in studies where population features (age structure, assortative mating) become endogenous variables for economic growth.

Resource / Investment

Evolutionary biology (*P. Huneman*)

Although resource and investment are operative concepts in studies in evolutionary biology, they are only rarely explicitly treated as themes in themselves. The idea of resources is present in Darwin's formulation, while "investment" is mentioned by Fisher when he conceives reproductive value as hope of a yield on the investment it entails. Investment became a prominent concept in the 1970s, within the framework of research on the division of parental labor. It then became widespread in theories of behavioral ecology, where it is directly related to the concept of resources.

The elements an organism or a species population needs to survive and endure – water, air, space, light (for plants), prey – define its resources in the broadest sense. Any investigation of a population and its variations over time must take these resources into consideration. Resources may also account for the causes and evolution of behavior.

The theory of evolution by natural selection, in its beginnings, referred directly to the notion of resource scarcity. Population growth is limited by the availability and/or renewal of resources, variables that define the boundaries of an intra- and inter-species competition resulting in natural selection. Naturally, this idea constitutes Darwin's initial borrowing from Malthus's economics, generalized to biological nature.

In later developments in evolutionary biology, the idea of resources seems to have faded into the background. By centering the process of evolution by natural selection on population genetics and quantitative genetics, the Modern Synthesis places less emphasis on competition. Fitness values lead to evolution through natural selection, so that resource scarcity itself is only a distant cause. In principle, at least, it is not necessary for fitness.

But the resource notion is fundamental to the *ecology of populations and communities*. It is also reappearing under the aegis of *behavioral ecology*, which concerns organisms more than populations. For a given population, the available resources define its "*carrying capacity*," i.e., the maximum number of individuals able to live and reproduce with the resources in that environment. The resource consumption dynamic – above all, the resource renewal rate – has an essential impact on population trends. Therefore, the concept of resources concerns consumption more than it does production; like the "good" in economics, the resource in biology is what is consumed. In particular, the case of prey consumption is the subject of a research tradition that uses Lotka-Volterra equations to model prey-predator population cycles.

Generally speaking, in the field of ecology, resources are the object of interspecies interactions: competition is limiting other species' access, limiting other species' access to resources, etc. The notion plays a key role in population and community ecology, via the concept of "ecological niche" developed by Hutchinson in the 1950s (Hutchinson 1957). In the hyperdimensional space whose axes are the various environmental parameters (pH, temperature, light, etc.) the ecological niche of a species is the multidimensional subspace of resources that are accessible to and consumed by organisms in this species. The more

temporary notion of “adaptive zone” (Simpson) designates niches that can be occupied by species exploiting the same resources in the same way.

In this sense, the very idea of resource plays a large explanatory role in community ecology. Several models explain specific patterns of diversity using niche effects and theories associated with them, such as the “competitive exclusion principle,” also referred to as Gause’s law, stipulating that two species competing for the same limited resources cannot coexist - the best competitor excluding thereby the lesser competitor from the part of their two niches that they share. The verdict is not yet in on recent “neutral models” (Hubbell 2001), which denies this principle, but their predictive capabilities are certainly amazing.

Resource supply is also a typical problem for the field of *behavioral ecology*. It is centered on organisms, and studies the “decisions” they make about all aspects affecting their fitness: reproduction, life history, dispersion, parenting, habitat, etc. In fact, the point of *optimal foraging theory* - a problem that was a structuring theme for the field since the 1960s - is to determine the best resource acquisition strategy that would be favored by natural selection, on the basis of certain assumptions concerning constraints (developmental, genetic, etc.) and the function connecting fitness to resources. Time spent foraging (to feed self and family), movements, and quantities of resources brought back are all modeled. These models may be static or, if they account for the effect of new resources on the organism’s appetite, dynamic. To the degree that resources diminish as a function of foraging, and that organisms can always go look for new, untapped resources elsewhere – with the risk that they might not find anything – compromises between *exploitation* and *exploration* emerge to be studied.

As for the notion of investment, it is a more general concept. Behavioral ecology applies it for the purposes of explaining an organism’s behavior. The organism’s “decision” to behave in such-and-such a way is conceived as the “choice” of the optimal strategy (Grafen 2014). Effectively, if each possible strategy contributes to the organism’s reproductive success, and therefore to a measurable gain (or loss) in fitness, it nevertheless requires prior effort from the organism. This effort is measured in terms of energy expended, metabolism, etc. Trivers (1972) gave the concept a technical sense in the framework of a study of differences between males and females in parental care and reproductive strategies. The “parental investment” he writes of is defined as the portion of energy the organism is willing to devote to matters concerning reproduction and care for present descendants, compared to all the other portions of energy devoted to other activities: seeking mates, collecting resources, defending territory, later reproduction, etc. Parental investment is therefore the quotient of all of the expenditures beneficial to posterity, but costly to the organism’s survival and future reproduction. Due to the difference in gametes between the two sexes (anisogamy), males and females should generally make distinct parental investments, according to differences that vary among species and as a function of environments.

In addition to parental investment, other types can be defined: reproductive investment, social investment, etc. The concept is always relative: it expresses a comparison between what it earns, versus what it costs in future reproductive opportunities. A second comparison involves explaining and predicting which investment is prioritized, relative to other possible investments. In the most general sense, investment is evaluated in relation to potential growth in fitness, since an investment in one strategy always limits the number of offspring that might have existed without that strategy (i.e., it essentially costs in opportunity).

Behavioral ecology can be fine-grained enough to analyze the distribution between reproductive and parental investment. Parental investment gives rise to several additional questions; e.g., how investment is allocated between male and female offspring, which also depends on the environment. Reproductive investment prompts strategies that differ according to species (e.g., size of individuals, metabolism, etc.) and the environment (e.g., predator density, variability, etc.). In particular, an organism may “choose” to have a large number of offspring and take little care of them, or to have only a few, to whom one or both parents devote a significant investment (strategies called “k” and “R”) (Davies et al. 2012). The theory of life history traits studies the general distribution of investments over an organism’s lifespan – notably, it analyzes trade-offs between reproductive investment, parental investment, growth, etc. (Stearns 1992).

The type, quantity, and accessibility of existing resources are a factor limiting investment. They impose constraints on the profit from investment. In many cases, the idea is then to study general trends towards decreasing yield on investment, which plays a major role in determining the strategy selected. Generally speaking, investment, resources, and yield are all expressed in a single currency, fitness. The various models must then formulate a hypothesis about the conversion rates; that is, the way one type of resource can be converted into fitness and, in return, be invested in by the organism according to strategies to be explained.

The notion of resource, although rarely explicitly theorized, plays an important explanatory role in many ecological areas. It is simultaneously the subject of an explanation (in optimal foraging theory, theories of sexual conflict or parental allocation, etc.) and, in other cases, an element implicit to the explanation (as an investment-limiting factor, in behavioral ecology; as a component of the notion of niche in community ecology).

References

- Davies, N.B., Krebs, J.R. and West., S.A. 2012. *An Introduction to Behavioural Ecology*. London: John Wiley & Sons.
- Grafen, A. (2014) The formal darwinism project in outline. *Biology and Philosophy*, 29(2):155–174.
- Hutchinson, G.E. 1957. “Concluding Remarks” *Cold Spring Harbor Symposium. Quantitative Biology* 22: 415–427.
- Hubbell S. 2001. *The unified neutral theory of ecology and biogeography*. Princeton: Princeton University Press.
- Stearns S. (1992) *The evolution of life histories*. Princeton University Press.
- Trivers, R.L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man, 1871-1971* (pp. 136–179). Chicago, IL: Aldine.

Economics (*B. Walliser*)

Resources are entities, natural or artificial, which are primitively available to economic agents. In the past, economics was often seen as the science of optimal allocation of resources (Robbins, 1932) (see OPTIMALITY). In fact, resources are directly consumed by agents or appear as factors of production, or inputs, that are combined to produce other goods through a production function. The usual inputs are natural resources, labor, capital and capital stock – human-produced goods. Moreover, classical economists considered the soil as a factor. Now, it is treated as a natural resource, like water, along with the others. Finally, financial resources, although they are immaterial, are incorporated into the list of factors more and more.

The natural resources are of geological (raw materials, energy) or biological origin (forests, fishes). They are classified as renewable (i.e., exploitable without reduction of future availability) or not renewable even if, in practice, the times required for renewal form a continuous loop. Conceptually, natural resources constitute a “natural capital” that evolves both spontaneously and by human exploitation. They are subject to specific property rights, and give rise to special rules of pricing. In practice, some are free (air) while others must be purchased (water). In the Hotelling model (1931), the theoretical price appears as the sum of the extraction cost and a scarcity rent.

Labor is a heterogeneous factor. Profession taxonomies treat it qualitatively; working hours treat it quantitatively. In microeconomic models, it is also characterized by a worker-effort rate which is not directly observable (but revealed by production). According to the neoclassical model, the wage equals the productivity of the worker. In macroeconomic models, it is aggregated in a global labor index by weighting its components by the corresponding wage. In any case, labor is simply renewed by the population of workers (and labor rights regulating the amount of time spent working).

The “economic capital” combines all physical resources consumed in production over a sufficiently long period (more than a year, in practice). Its nature may be material (machines, buildings) or immaterial (research & development, training, software). It looks especially heterogeneous and its solution requires complex aggregation problems. A fraction of the capital depreciates through time either from a technical point of view (wearing) or an economic one (obsolescence). Its price oscillates between its past cost and its future induced profit, which are equal only on a perfect market.

A production function, relating factors and products, is generally applied to a firm or a country. But it may also be applied to the labor production of an individual, comparing his material and symbolic consumptions (reproduction of the working force after Marx). The capital involved in this case is the “human capital”; i.e., the set of skills the individual has acquired (knowledge, know-how). This capital, incorporated within the individual and not directly observable, is generally measured by level of education.

Each final good is obtained from previous goods along a whole chain of goods beginning with resources acting as basic factors. The main resources being capital and labor, it is possible to compute, for a given good, its (direct and indirect) "content" in capital and labor. For instance, it is possible to calculate the respective percentage of capital and labor necessary to produce a car. Since capital is itself produced by labor, it is possible to retain the total labor incorporated in the good as the sole production factor. Labor appears then as the common yardstick to evaluate all other goods, in the Marxian tradition.

The economic capital is constituted by a stock of goods, and it can be decomposed in a sequence of instantaneous flux called investments. Each investment corresponds physically to a set of goods presenting some indivisibility (equipment). Its acquisition by an economic agent results from a decision which trades off a short-term cost and a long-term profit, the last being marred by high uncertainty. Moreover, the sequence of investments is subject to strong irreversibility effects, since the stock of goods is used for a long period before being replaced.

At a microeconomic level, investment is financed by each firm by borrowing and self-financing. At a macroeconomic level, by aggregation in the national accounting system, global investment becomes equal to global saving. Moreover, any investment is a production factor which gives rise to successive flows of (direct and indirect) production. The total production induced is higher (in value) than the initial investment, the amplifying factor being called the "Keynesian multiplier."

References

Hotelling, H. (1931): The economics of exhaustible resources, *Journal of Political Economy*, 39, 137:75.

Marx, K. (1872-75): *Das Kapital*, Verlag von Otto Meisner.

Robbins, L. (1932): *An essay on the nature and significance of economic science*, Macmillan.

Synthesis

In biology, spontaneously available natural resources play a primordial role, whereas in economics, natural resources are overshadowed by capital, made up of durable manmade resources. Nevertheless, there is no reason not to consider an anthill as a real-estate asset built to serve a society of ants.

In both fields, resources appear as stocks of goods that are renewed in two ways. On the one hand, available natural or artificial resources are spontaneously modified by regeneration or decomposition. On the other hand, they are modified by deliberately chosen investments that serve as flux. Nevertheless, the concept of investment has emerged only recently in biology. It is still loosely connected to the concept of resource.

Through investments, resources are the subject of a general problem of allocation, whether by organisms or species (in biology) or by rational agents (in economics). The outline of the problem – how to move from a stock of resources regulated by their cycle, their availability, etc., to a more or less optimal utilization of them downstream – is therefore common to both fields.

In economics, an economic agent is supposed to choose to invest according to self-interest, whether it is immediate or more long-term (profit for the company, usefulness to the consumer). Investments are categorized chiefly according to their nature, material or symbolic. In biology, the investment engaged by any individual or group is directly related to the adaptive value it yields, either directly or indirectly for its offspring. Behavioral ecologists tend to typify investment according to fitness yardsticks (survival, reproduction), spawning such concepts as “parental investment” and “reproductive investment.”

Biology has introduced the crucial notion of the niche as an abstract subset, a hyperspace containing the kinds of resources needed by a species, and that is physically instantiated in a territory. Economics uses the notion in a more occasional and analogical way, often in relation to an innovation that gives its initiator some relative advantage. In fact, the niche is an abstract place where interactions oscillating between competition and cooperation occur. These interactions can involve either species or agents.

Selection

Evolutionary biology (*J. Martens*)

In evolutionary biology, the notion of selection pertains almost exclusively to the principle of *natural selection* (Darwin 1859), where it refers to the process through which the most favorable/unfavorable traits are preserved/eliminated within biological populations. Together with the hypothesis of common descent, the principle of natural selection constitutes the cornerstone of our current conception of life, and plays a fundamental role in our explanations of adaptive diversity.

At the most abstract level, the process of natural selection depends on the satisfaction of three conditions (Lewontin 1970), namely: variation, differences in fitness and heritability. Each of these conditions, as is obvious, is highly general, and appears to be realizable—albeit to varying degrees of approximation—in many kinds of populations (from populations of bacteria to populations of computer algorithms). Some authors have claimed that this generality should be taken at face value, and that we shouldn't, at least on *a priori* grounds, exclude entities such as artifacts, human products, or socio-economic organizations from the domain of application of Darwinian theory. But this particular view—known as “Universal Darwinism” (Hodgson 2002)—tends to be quite marginal in the literature; and most philosophers and biologists insist, in contrast, on the importance of *restricting* our use of the concept of natural selection to certain *sorts* of biological populations—characterized by particular modes of inheritance and of reproduction (Godfrey-Smith 2009).

The notion of natural selection, as is well known, is intimately related to the notion of *competition*, which Darwin famously described as a “struggle for life” in the third chapter of the *Origin* (see COMPETITION). However, these two concepts should not be conflated, for the very idea of a “struggle for life” (i.e. the “Malthusian dimension” of biological interactions) is definitely more *general* than the concept of natural selection. The reason is simple: a struggle for life, understood in a Darwinian sense, will occur as soon as two or more individuals with different survival/reproductive prospects compete (directly or indirectly) for a limited ecological resource. This may happen, of course, between the members of the same species—in which case natural selection will ensue—but also between members of different species—in which cases the process shall be best conceived of as an instance of *competitive exclusion* (Matthewson 2015). The principle of natural selection, on the other hand, always *presupposes* some dimension of Malthusian (or ecological) competition, since the latter represents the minimal “glue” without which no Darwinian population is guaranteed to exist in the first place (cf. Godfrey-Smith 2009 p.48).

The very expression of “natural selection” has a strong evocative power. In the *Origin*, Darwin chose it expressly “to mark [the relation of natural selection] to man's power of selection”

(Darwin 1859, p. 61). But Darwin clearly insisted on the reality of the differences between the two processes. Thus, man's selection—such as the one exerted by livestock breeders to produce the best varieties of meat—always involves an element of *intentional* choice made by some conscious agent, whereas natural selection is primarily a blind process, which relies on the mechanical sorting of individuals (depending on their type and on the set of ecological constraints). Furthermore, natural selection is a *ubiquitous* process, “a power incessantly ready for action” (*ibid.*), whereas humans, in contrast, can only select between local varieties on a very short time scale. As a result, natural selection—by operating on the long run and at any time—has a much broader scope for action than artificial selection.

In spite of these differences, every instance of artificial selection constitutes a proper instance of natural selection. Natural selection, in effect, has two key dimensions: one concerning the origin of the variation, and the other concerning the source of the selective pressures (i.e., the ecological “demands”). When the intentional element is on the selective side, such as in the case of livestock selection, the epithet “natural” remains appropriate for describing the overall process; for what makes selection a *natural* process in this case (and not a *supernatural* process or a purely intelligent process) is, at bottom, the blind character of the variation on which this selection operates. However, when the variation *itself* is directed by some intention, as is the case where some design is devised and chosen by a conscious being (in order to fit a particular demand), things are getting more complicated; for then, there is no longer the need for a “natural,” i.e. external sorting process that would select *ex post* the fittest variation—indeed, the fittest is already given. Hence, the epithet “natural” (and, with it, the assimilation of this process to an instance of natural selection) becomes more questionable.

This latter point *might* seem to suggest the existence of a sharp difference between some sorts of artificial (intentional) selection and natural selection. But we must stress that this difference remains, at its roots, a matter of degree. Concretely, natural selection does not depend, for its realization, on the *internal* properties of the individuals (such as their mental states), but only on the existence of *external*, causal properties relating their heritable behaviors to their relative fitness. Thus, even in those cases where some intentional (internal) causes *constrain* the set of variations on which natural selection operates, the scope of natural selection (i.e. the remaining variation) can still be quite significant.

This articulation of the mechanisms of variation and of selection is also relevant to our understanding of the well-known distinction between *Lamarckian* and *Darwinian* mechanisms of evolution. In Lamarckian processes, the individuals transmit (some of) their *acquired characters* directly to their offspring, which implies that, in a population where both Lamarckian and Darwinian mechanisms are at work, the former inevitably alter the adaptive variation on which natural selection can act (though the *extent* to which Lamarckian processes are effectively at work in the living world remains an empirical—and controversial—question). Yet, this interference—when it applies—does not mean that the two sorts of mechanisms

should be considered as mutually exclusive: for both, after all, might still act *in concert* on the evolution of individual traits.

References

Darwin, C. (1859) : *On the Origin of Species*, London: Murray.

Godfrey-Smith, P. (2009) : *Darwinian Populations and Natural Selection*, Oxford: Oxford University Press.

Hodgson, G.M. (2002) : Darwinism in Economics: from Analogy to Ontology, *Journal of Evolutionary Economics*, 12, 259-281.

Lewontin, R. (1970) : The Units of Selection, *Annual Review of Ecology and Systematics*, 1, 1-18.

Matthewson, J. (2015) : Defining Darwinian Populations, *Philosophy of Science*, 82, 178-197.

Economics (*B. Walliser*)

Evolutionary economics (Nelson and Winter, 1982) is focused on the evolution of firms rather than evolution of individual behavior or institutions. More precisely, the triptych mutation-transmission-selection is generally applied to routines; i.e., basic processes of production, organization, or research that decentralize the functioning of the firm. If mutation is analogous to innovation (see MUTATION) and transmission to imitation or self-reproduction, selection is analogous to competition between firms, which form a heterogeneous population as concerns their importance and their specialty.

In fact, competition was already studied by classical economists as a mechanism acting through prices in the short term on the exchange of goods. In this case, it concerns firms already present on the market. Pure and perfect competition assumes that firms have perfect and complete information on the quality and price of goods, do not exert a market power on prices, and that prices are perfectly flexible (see COMPETITION). But numerous market failures (imperfect information, market power, viscous prices) lead to imperfect competition.

Competition at long term, however, is what exerts a true selective power on firms. Some firms are willing to penetrate the market since they expect sufficient profits despite a risky environment. Firms already present on the market try to survive by adapting their decisions (good differentiation, technology adjustment, alliance with other firms) to the global context. Often considered as wild competition, even if some institutional constraints exist, it leads many firms to merge or split up, to be absorbed or disappear (Dosi et al., 2005).

In short-term competition, firms are assumed to maximize their profit on the basis of empirical arguments alone. In long-term competition, according to the Alchian-Friedman thesis (Alchian, 1950), the only firms that can survive are precisely those that maximize their profit. A theoretical analysis shows effectively that optimizing firms alone can survive, but only under drastic conditions. Under softer conditions, a sub-optimizing firm may survive for a long period

(Chiappori, 1984). For instance, it would be enough for all firms to be simultaneously sub-optimizing, for reasons of complexity in the computation of optimal strategies.

In practice, the problem of long-term survival of firms can be grasped in two ways. In an absolute form, a firm may only survive if its profit is positive, preventing it from going bankrupt. In a relative form, a firm may only survive if its profit is higher than that of its competitors, allowing it to invest and preserve its market shares. Moreover, the “paradox of competition” states that if the optimizing firms are the only ones to survive at long term, they will concentrate and ensure a monopoly situation, effectively annihilating competition. But the paradox is solved when the State fixes antitrust rules that preserve enough firms.

In evolutionary game theory, the foundation of evolution is the strategy followed by the players in a population. The evolution process is again expressed by the biological triptych mutation-transmission-selection. Although mutation is ensured by a random change of available strategies, and transmission by the permanence of ongoing strategies, selection is not described by any precise modalities, but only by its effects. It is stated that each strategy in the population reproduces according to its fitness, analogous to the utility it gains against the others’ strategies.

Mainly, the simplest model of Darwinian evolution applied to a game is the “replicator model.” It states that the frequency variation of a given strategy in the population is proportional to the difference between the utility obtained with that strategy and the mean utility obtained by the whole population. In its form, this model can be compared to the various learning models developed in game theory (see ADAPTATION/LEARNING). But it is at the very opposite of intentional selection models, such as those of expert pool players or college-admissions committees.

References

- Alchian, A. (1950): Uncertainty, evolution and economic theory, *Journal of Political Economics*.
- Chiappori, P.A. (1984): Sélection naturelle et rationalité absolue des entreprises, *Revue Economique*, 35(1), 87-108.
- Dosi, G., Kaniovski, Y., Winter, S. (2005): A baseline model of industry evolution, *Journal of Evolutionary Economics*, 13(4), 355-83.
- Nelson, R., Winter, S. (1982): *An Evolutionary Theory of Economic Change*, Harvard University Press

Synthesis

There are some important differences between the biological and the everyday uses of the term “selection.” In evolutionary biology, the term “selection” refers to a *population* process, which no plan or intention governs, while in ordinary language, it refers to an *individual*

process of intentional choice—though selective effects may also occur as unintended by-products at the population level. In economics, by contrast, the term “selection” is most commonly used in this second, ordinary sense, as when we speak of a consumer selecting between different goods. But as we have seen above, this term is also employed to describe the process of competition between firms on the market, a process which, to a certain degree, is analogous to the competition between organisms driven by natural selection.

Understood in this second sense, the selection occurring between firms is heavily constrained by the choices of consumers—which constitute the “limiting resource” for which they have to compete. Nevertheless, individual firms can still exert a significant amount of control over their market strategies in order to increase their profit. For instance, innovation or the acquisition of new technologies are usually the result of deliberate investments/strategies of the firms, such as investment in R&D departments or industrial spying. Hence, unlike the mechanisms responsible for the selective differences among organisms (such as genetic mutation), the mechanisms responsible for the production (or the reduction) of variations among the firms are rarely undirected (though accidental variations may sometimes happen). Because of this additional, *deliberate* selective component, economic evolution—like most forms of cultural evolution—will typically occur at a *much faster rate* than biological evolution.

Another noticeable difference between biological and economic selection is that firms can actually survive on the markets even when they are not the most efficient. This famous result, known as the “law” of comparative advantage, has been demonstrated by Ricardo (1817). In a nutshell, the idea can be formulated as follows: if two firms, capable of producing two sorts of goods X and Y, engage in a free market, then each will end up producing the good for which it has a comparative advantage, that is, the good for which its relative marginal production costs are minimized. Thus, even if one firm is more efficient in its production of *both* goods X and Y, one should expect that it will specialize in the production of the good (X or Y) for which it has a comparative advantage. Correspondingly, one should expect that the other, less efficient firm will specialize in the production of the other good, without disappearing or being eliminated from the market. This result has no clear theoretical counterpart in the domain of Darwinian theory.

There are many controversial aspects of the analogy between natural selection and economic selection. They deserve scrutiny, but cannot be addressed here in further detail. One of these is the above mentioned analogy between mutation (the most common mechanism behind the variation condition) and innovation is (see INNOVATION/MUTATION). Another is the application of the notion of fitness to the case of the firm. In the principle of natural selection, fitness plays a central role, and corresponds to a measure of both the survival and the reproduction of individuals. In evolutionary economics, increased profit is sometimes suggested as a measure of “fitness” for the firms. But this analogy is questionable, for successful firms do not really “reproduce” on the market; instead, they expand by making new investments and/or by adopting various strategies of diversification (either in buying other

firms or in creating subsidiaries). Thus, one could legitimately ask to which extent the study of the dynamics of selection in biological populations is relevant for our understanding of the dynamics of competition between firms on the markets.

References

Ricardo, D. (1817/1951) : *On the Principles of Political Economy and Taxation*, Cambridge: Cambridge University Press.

Strategic Interactions

Evolutionary biology (*P. Huneman*)

The concept of strategy has no uncontroversial definition in evolutionary biology, though it is used pervasively, especially in behavioral ecology. Its use comes from the evolutionary theory of games, a field initiated in the 80s, by Maynard-Smith in particular. He introduces the concept as “the specification of what an individual would do in any situation in which it may find itself.” (Maynard-Smith 1982) But in the practice of biological modeling, the situations are defined in a specific context, where there is a limited amount of their types. Often each situation allows for few alternative actions, such as fighting or fleeing when encountering a threat. Individuals are of given types defined by the strategy they play, and they reproduce accordingly.

In each situation, various strategies will yield various payoffs. These pay-offs may be unconditional, or they may depend upon which strategy is adopted by other individuals interacting with the focal individual in the same situation. In the first case, the individuals play against nature; some strategies will be unconditionally optimal (see OPTIMALITY). In the latter case, a payoff matrix stipulates the payoffs of all strategies, in any possible interaction. This defines a game. Games and strategies, namely precisely what we call strategic interactions, are important concepts in this second case.

Games can involve players playing pairwise one against the other, or they can involve a player pitted against all the others. That case is known as “playing the field,” and the opponents can be characterized as an average value of a quantity. Games can also be symmetrical or asymmetrical. In symmetrical games, contestants are in the same position regarding the possible strategies; in asymmetrical ones, their position is different (for example, tall vs. small, male vs. female etc.).

The payoffs are measured in fitness gains or loss. (The issue of the manner in which fitness itself is defined and measured is exogenous to the game.) Therefore, natural selection can be the driving force of the dynamic that leads to the prevalence of some strategies over others. According to the basic logics of natural selection, since the reproduction of individuals at each generation is determined by fitness, the individuals playing strategies with highest fitness payoff will increase in frequency, and hence these strategies will dominate others (see SELECTION) : the reproduction of strategies across generations, modulated by fitness payoffs, makes the game an evolutionary game.

Evolutionary game theory questions the maintenance of strategies rather than their origin. Individuals play one strategy that belongs to a set of strategies, considered as givens by the biologist. The origin of the strategy set, and the reasons why it is the way it is, constitute additional questions. Our theory may not solve them (although resorting to developmental constraints may help explain the answer (see CONSTRAINTS/TRADE-OFFS)). Thus, behavioral ecology asks why organisms implement certain strategies rather than other competing strategies, or which strategies should be expected in a given ecological context. Natural selection is explanatory, even though such assumptions can prove wrong in many particular cases.

Rather than “strategy” itself, the crucial concept in the theory is the Evolutionarily Stable Strategy. An ESS is as a strategy such that once it is adopted by a population, no mutant (i.e., individual switching to another strategy) can invade the population. In strategic interactions, no strategy has constantly and absolutely the highest payoff, in a way that necessarily natural selection would bring it about. Thus, the existing strategies are the ones that are preserved against invasion, given that mutants keep occurring in reality (at least for genetic reasons). Strategies can be *pure*; namely, they determine which action to take in each situation. But often, several pure strategies can yield a pattern with no ESS. Therefore, the presence of one strategy in the population cannot be expected. Instead, there can be a “*mixed strategy*,” that combines two strategies played stochastically with a given probability. The ESS may often be a mixed strategy. When there are two strategies, a population with all individuals playing the mixed strategy that is the ESS is equivalent to a population with a stable polymorphism, where the proportions equal the probability coefficients in the model. (Beyond two pure strategies, they stop being equivalent.)

“Strategies” do not require any cognitive ability from the individuals; they can be seen as genetically hard-wired. Individuals do not decide to behave in such or such a way, they just implement a strategy. They cannot be seen as having a purpose for such a strategy. The dynamics of strategies in population, according to fitness payoffs, determines which strategy(ies) will be present in the population, when an equilibrium is reached. Hence, natural selection is what decides between strategies in a population, according to the payoff matrix.

Because they are not a decision or action in the strict sense of the term, “strategies” are not confined to behavior. They mean the same thing as “phenotypes.” Reproduction timing, plant growth styles, tree size, skin color, etc., can be considered as strategies, and evolutionary game theory is used to understand what phenotypes should be expected. In this way, games make it possible to model all aspects of the ecology of a given species population.

However, given that strategies prescribe conditional actions, some information must be provided to the individual, concerning the situation. Information can be pure chemical interactions (i.e., soil composition gradient, etc.) or environmental cues. Hence the symmetry or asymmetry of information plays a crucial role, as well as the manipulation of cues by the players (see INFORMATION) (Skyrms 2010).

In the context of the simplest models, individuals are playing one definite strategy, and then their offspring reproduces the strategy. To justify calling upon natural selection, the theory assumes that strategies are highly heritable, which means that some genetic differences should result in the adoption of one strategy rather than another. The fact that strategies are comparable to phenotypes means that the biologist thinks in terms of strategies when he or she can't or doesn't want to describe the details of the genetic make-up of phenotypes. However, taking the genotypic basis in account is a matter of degree: in some cases, it constrains the phenotypes available so much that the model has to specify some features of the transmission genetics involved. For instance, it is crucial to consider the genetic basis when studying sex ratios, anisogamy, every trait related to sexual reproduction, or when the strategies are supported by diploid genotypes so that the heterozygous strategy can't be pervasive even if it would be the ESS.

Other assumptions of the simplest models that start with haploid asexual individuals, such as infinite population, random mixing, etc., are loosened in more sophisticated and realistic models.

Moreover, individuals with cognitive abilities can learn strategies, which impacts on evolutionary dynamics. They learn the payoffs of their acts and modify their future actions accordingly, so that they acquire a type of strategy that they can transmit. Different learning rules are possible for this modification, and some are evolutionarily stable (i.e., non invadable by mutated learning rules).

Learning is at the same time a consequence of evolution by selection, since learning evolved, and analogous to evolution, since strategies are learned according to their fitness payoff (see ADAPTATION/LEARNING). As a result, the relations between development (acquisition of strategies) and evolutionary games are complicated (Gintis 2009) . These relations are ruled by a theorem according to which the evolutionarily stable learning rules are rules for ESSs (except in some specific cases) (Harley 1981).

References.

Gintis H. (2009). *Game Theory Evolving*, Princeton University Press.

Harley CB. (1981) Learning the evolutionarily stable strategy. *Journal of Theoretical Biology* 89(4):611-33.

Maynard-Smith, J. (1982) *Evolution and the Theory of Games*, Cambridge : Cambridge University Press.
Skyrms B (2010). *Signals: Evolution, Learning, & Information*. New-York: Oxford University Press.
Weibull J (1995) *Evolutionary Game Theory* Cambridge M.I.T. Press

Economics (*B. Walliser*)

Strategic interactions between several players are at the very foundation of game theory (von Neumann-Morgenstern, 1944). Interactions are said to be strategic as soon as the result of some player's action not only depends on that action, but on others' actions as well. Prototypical examples of games were the parlor games, and especially chess, the chess-player being the Drosophila of a game theorist, according to Simon. But the notion of a game has been enlarged to any form of social interaction between rational players. It covers social situations of military conflict, economic competition, and political confrontation.

For any game, it is assumed that several agents are immersed in a common physical environment called nature. Each player has prior *opportunities* summarized in an action set limited by individual and social constraints, while nature is endowed with a state set. The combination of all players' actions and of the nature's state leads to some global result expressed in physical terms. This result can be assessed by each player through his *preferences*, summarized by a utility function that depends directly on the result and indirectly on the players' actions and nature's state.

Moreover, each player is endowed with personal *beliefs* which are oriented on all the elements of the game. At any time, they concern both the production law of nature's states, the players' action sets and the players' utility functions. Moreover, at each period, a player may observe the present actions and result, and may infer from them some information on past states and actions. Relying on their *cognitive rationality*, they revise their beliefs according to new information in virtue of belief revision rules. When beliefs are probabilistic, the usual revision rule is the Bayes rule.

Finally, the players obey some exogenously imposed *game rules*. In fact, these rules often stay implicit, since they are already incorporated in the players' characteristics. They may constrain possible actions. They are then assumed to be always satisfied, since a player playing a forbidden action is eliminated. They may influence the utility, if a player playing a forbidden action is fined or discredited. In addition, they even impact heavily on players' beliefs by limiting the amount of information they can freely gather.

Games are categorized according to the individual characteristics they introduce. For instance, when considering the action sets, static games are distinguished from dynamic ones according to whether players play simultaneously only once or play sequentially several times. Likewise,

when comparing the players' utility functions, distinctions are made between twin games, zero-sum games, and symmetrical games. Finally, perfect and imperfect information games are differentiated according to whether players have perfect information about the structure and full observation of the development of the game.

In *classical game theory*, players are endowed with a strong *instrumental rationality*. Each player chooses the action which maximizes his own utility function, the others' actions, and nature's state being fixed. However, a conjoint maximization can only be realized by defining equilibrium notions which ensure players' coordination. Hence, the equilibrium notions are defined from the point of view of the modeler by a set of constraints. A lot of equilibrium notions have been defined; each leads to a variable number of equilibrium states for a given game.

As for the resolution of a game, no distinction is made by the modeler between a global strategy and a local tactic. However, a strategy is differentiated from an action. By definition, a strategy is the set of actions that a player intends to play in all circumstances in which he may have to move. The combination of a strategy for each player (and states for nature) leads to a given (random) result and a given utility for all players. Hence, for each equilibrium notion, equilibrium states can be computed either in actions or in strategies, and these states may differ.

In particular, a dynamic game can be represented by a game tree in which the players play sequentially and get a utility for each path. This tree is considered as fixed, since no new action and no evolution of utility is considered. In such a tree, a strategy indicates what a player intends to do at each node, i.e., for any past history of the game. More precisely, it indicates the intended response of the player to past moves of the other players and often takes the form of a promise or a threat. However, such a response may not be credible, since the player may lose the advantage in applying it after the others have already played.

In other respects, two types of actions can be considered for any player. He can be allowed to just play a "pure" or "mixed" action, i.e., a probability distribution on the action set (an action is played after a draw in a probability distribution). In a dynamic game, a probability distribution can be defined equivalently on actions or on strategies. In any case, all equilibrium notions can be defined either in pure strategies or in mixed strategies. Of course, the equilibrium states in pure strategies are specific cases of the equilibrium states in mixed strategies.

In *evolutionary game theory*, players have a bounded rationality due to limited cognitive skills. They consider simplified action sets, have reduced utility functions, and adopt incomplete beliefs. Moreover, they compute their intended strategies with restrained computing capacities and do no more optimizing. For instance, they are content with "satisficing" (Simon, 1982) in the sense that they retain the first considered action which achieves better partial

goals than given aspiration levels. However, in a dynamic setting, they are able to learn and evolve through time (see ADAPTATION/LEARNING).

References

Simon, H. A. (1982): *Models of Bounded Rationality*, MIT.

Von Neumann J., Morgenstern, O. (1944): *Theory of Games and Economic Behavior*, John Wiley.

Synthesis

The notion of interactions between several entities is at the foundation of biology as well as economics. To prevent triviality, it concerns some influences which are limited in time and localized in space. The notion of strategic interactions is more precise in assuming that the influences are not unilateral and have an impact on each concerned entity. This impact is ultimately measured by utility in economics and by fitness in biology, and depends on the concerned entities as well as on their common environment.

Whatever their content, all strategic interactions are considered as well as analyzed by game theory. The evolutionary version of this tool, initially constructed to represent economic interactions, turns out to be well adapted to biological interactions in a population. The same taxonomies of actions (pure or mixed) or of games (symmetrical, zero-sum) are relevant in both cases. The same equilibrium notions (or variants of them) between various characteristics of entities are able to show how they stabilize.

However, the very notion of strategy, which summarizes the support of the interactions, differs profoundly from economics to biology. In economics, a strategy is an intended action (i.e., a mental state) voluntarily implemented by some agent, whether or not it is consciously computed by him. In biology, a strategy is always unconscious and involuntary and concerns a physical entity often more temporally extended than an action, namely a phenotypic trait subject to natural selection.

A problem with game theory, especially for biology, is the stationary nature of the game structure along a dynamic play. In particular, the strategy set is given once and for all, and cannot be exogenously enriched or modified. Mutant strategies can indeed be imagined, but they result randomly by proximity or combination from an overall fixed strategy set. Such random processes are unable to reflect unexpected phenomena such as biological mutations or economic innovations.

Time scales

Evolutionary biology (*S. De Monte*)

Evolutionary theory deals with changes in the properties of biological ensembles (organisms within a species for microevolution, species themselves for macroevolution) over the course of physical time. The timing of changes can also be measured in terms of rhythms intrinsic to the biological ensemble, such as those defined by the succession of generations or by the rate at which genetic mutations occur. These “endogenous” times can often be converted into physical time, and this is essential for interpreting observed patterns, such as, for instance, a phylogenetic tree.

When general mechanisms underlying evolution are studied, processes are classified in terms of the relative time scale upon which they occur, abstracting the process away from the particularities of the entities subjected to selection. For instance, neutral drift gives rise to the same change in allelic frequency per generation when one considers organisms with very different life cycles, such as microbes and humans, as long as the probability of mutation per generation is the same.

The slower time scale associated with individual characters is that of gene persistence, which in Monod's words constitutes the “unvarying bearer of hereditary traits,” underpinning the consistency of characters along an evolutionary trajectory [Monod, 1970]. Because of their invariance, genes have been seen as the key players of evolution [Dawkins, 1976]. However, different time scales emerge in relation to different levels of description of the biological system. Fast evolutionary changes can occur in a few generations, but time scales relevant to macroevolution, that considers major clade divergence, can be as long as hundreds of millions of years.

A hierarchy of time scales is naturally established when looking at the processes involved in biological evolution [Simpson 2011]. Macroevolution is the slowest process, leading to gradual phyletic evolution as a consequence of gradual adaptive changes. On an intermediate time scale, speciation creates the diversity of life forms upon which natural selection can act as an optimizing process. On a shorter time scale, “quantum evolution” denotes changes that are heavily driven by stochastic fluctuations (drift, see MUTATION/INNOVATION), and which could account for drastic modifications of traits associated with catastrophic events, for instance. Other time scales have been more recently connected to those of evolutionary processes, notably the fast time scales of ecology and the even faster one of behavior.

The theory of evolution of biological species has been developed – since long before the discovery of the genetic mechanisms underlying heritability and generation of variation – with the aim of explaining how a great variety of life forms came to be established (see DIVERSITY).

The Darwinian theory of the origin of species referred to processes on the geological time scale, evident from fossil records, and did not rely – unlike Lamarck's theory – on changes occurring during the lifespan of one individual.

The image of evolution as an extremely slow process (compared to generation time) was confirmed by rooting the origin of phenotypic variation in mutations of the genetic code. The effects of these mutations are indeed seldom evident at the level that is directly subject to natural selection, that of the organism, so that in general evolution proceeds thanks to rare events that first create novel adaptive types.

More recently, however, much attention has been devoted to rapid evolutionary effects, such as the development of drug resistance in parasites or the biotic response to environmental changes. Evidence has been put forward indicating not only that large phenotypic modifications can be established on the time scale of a few generations, but also that the pace of evolution is not necessarily uniform and may accelerate due to environmental stresses.

As a consequence of shortening the time scales relevant for evolution, one must include other processes occurring at comparable rates in the description of the biological system, notably environmental fluctuations, behavior, epigenetics (non-genetic inheritance).

Altogether, the search for mechanistic explanations prompted the need to account for different time scales in interaction with each other. No comprehensive solution to this problem has been found, although specific assumptions sometimes allow processes acting at separate time scales (e.g., pertaining to different levels of biological organization) to be disentangled and described separately.

A paradigmatic example of a process involving several time scales is speciation, or the splitting of one species into two or more genetically separated populations. Speciation as an evolutionary process is the long-term outcome of the interplay of mechanisms acting on shorter time scales, such as population dynamics or ecology. These faster time scales can either be endogenous to the organism or species or imposed by an external force (which might be seasonal, for example). Therefore, they can sometimes be decoupled from the slower dynamics of species divergence. Adaptive dynamics models for evolutionary branching, for instance, rely on a time-scale separation between trait substitution (due to the ecology of the system) and trait mutation (supposed to happen on a slower time scale) [Brännström et al. 2013].

In the last thirty years, evolution by natural selection has been invoked as a major mechanism also acting in the realm of the social sciences, where cultural evolution has been compared to biotic evolution. Memes (cognitive units) have been proposed to play for cultural evolution a similar role as genes for biotic evolution [Dawkins, 1976]. In this analogy, behavior is considered to be inherited through cultural transmission and to obey the same principles of mutation and selection. In an evolutionary perspective, these points of view include all

changes occurring on a time scale faster than one generation and blur the border between fields such as evolutionary biology, the cognitive sciences, and economics.

References

Dawkins, R. (1976): *The Selfish Gene*, Oxford University Press

Monod, J. (1970) : *Le Hasard et la Nécessité: Essai sur la philosophie naturelle de la biologie moderne*

Simpson, C. (2011): How many levels are there? How insights from evolutionary transitions in individuality help measure the hierarchical complexity of life. In, *The Major Transitions in Evolution Revisited*, Brett Calcott & Kim Sterelny eds. MIT Press

Brännström Å., Johansson J., von Festenberg N. (2013): The Hitchhiker's Guide to Adaptive Dynamics, *Games*, 4, 304-328

Economics (*B. Walliser*)

In economic theory, three notions of time were gradually introduced. "Objective time" is the physical time constituting the medium for all material phenomena considered by the modeler? "Subjective time" is the psychological time associated with each agent. It is the yardstick for ordering the events of his memory and expectation exercise. "Mental time" is the operating time required for the agent's reasoning in order to make a decision. Of course, subjective time is often interpreted as a personal mental simulation of objective time. Likewise, mental time is often considered as an objective time devoted to the treatment of subjective information.

Each kind of time is evaluated on some time scale, which is introduced by the modeler either to collect empirical data or to parameter a theoretical model. The time scale may be continuous, in which case it is unique, or discrete, in which case several elementary periods can be chosen. When considering the year, for example, the period is a natural one (in most models) or even the phases of an agent's life (in the nested generations model). It is more conventional when it concerns historical periods such as successive governments or regimes of law. But whatever the period, several variables are considered simultaneously, and are implicitly considered as comparable throughout this period.

When observing the empirical evolution of a given magnitude, different periodic movements can be recognized by breaking its trajectory down into overlapping periodic components. In more theoretical terms, the "spectral decomposition" of this trajectory can reveal a trend, and cycles with shorter and shorter periods. The trajectory is affected by short-term perturbations around a long-term tendency. Moreover, each harmonic may receive an autonomous explanation with specific causal factors. The best example concerns the economic activity of some country, measured by a set of macroeconomic indicators. It reveals a gradation of cycles which are produced by different mechanisms (see CYCLES).

Now consider the evolution of several interacting magnitudes. They do not change according to the same rhythm. In the simplest case, with reference to a given exogenous period, the magnitudes can be ordered along three time scales. Fast variables adjust within each period,

slow variables adjust from one period to the other, and fixed variables do not move. Take a firm, for example: technologies are assumed to evolve more slowly than the prices of produced goods, which vary more slowly than the quantities of goods. Apply this to an economy: institutions are assumed to evolve more slowly than the human population, which varies more slowly than agents' preferences and beliefs.

In a model, relations between magnitudes let us link variables of different temporality. In the short term (within a period), slow variables (and environmental ones) impose constraints on fast ones. In the long term (between two periods), fast variables (and environmental ones) induce a change of slow variables. When using an equilibrium mode of reasoning, it is possible to define a sequence of short-term equilibrium states converging towards a long-term one. For instance, a decision-maker chooses a short-term decision depending on his preferences and beliefs. But in the long term, he adjusts his beliefs to new information (belief revision) and his preferences to past experience (habituation, addiction).

Finally, nested time scales are frequently paired with nested organizational levels (see ORGANIZATIONAL LEVELS). For instance, the two basic organization levels are the microscopic level of agents' behavior and the macroscopic level of global aggregates and phenomena. The interactions between these levels are similarly situated on two different time scales. In the short term, the agents act independently and jointly fix the social effects and the institutions (i.e., from the *bottom up*). In the long term, the socio-economic structures influence the agents by retroaction (i.e., from the *top down*). For instance, agents gradually define prices, and even trade rules imposed at long term.

Synthesis

In biology, just as in economics, various time scales are introduced in order to describe the transformation speed of different variables, such as traits or prices, of a given system. These interlacing time scales help explain the direct influence of slow variables on fast ones and the retroactive influence of fast variables on slow ones. Specifically, different kinds of equilibrium notions may be defined, depending on the time scale over which a process ultimately converges.

Of course, in the shift from economics to biology, the hierarchy of time scales as a whole is transposed to longer periods. In economics, individual strategies evolve at short term, prices or investments at medium term, and institutions or technologies at long term. In biology, individual behavior rules change in the short term, population demography or ecological conditions in the medium term, and species distribution in the long term. A given kind of economy is restricted, at least, to a given civilization, while the transformation of living organisms is an open-ended process.

Time scales may be imposed by conditions – especially physical – that are external to the system at hand. The period of the year affects both economic activity and biological behavior. But time scales may also be endogenously determined by internal processes. In economics, the activity cycle is the result of production and consumption exchanges. In biology, individual growth is

linked to the metabolism of an organism. More subtly, economic time scales are affected by biological constraints such as population growth.

Moreover, time scales are directly related to levels of organization (see ORGANIZATIONAL LEVELS), since systems evolve more slowly than their constituent elements. In economics, a firm keeps its main features and functions even if its members get older or change. In biology, an organism keeps its integrity even if its cells are steadily renewed. However, in both disciplines, a system may also change profoundly by using the same basic entities in different structural ways.

Efforts to disentangle processes arising at different organizational levels and associated time scales are often hampered by the existence of multiple interactions and feedback loops across them, such as those between institutions and agents or those between evolution and ecology, for example. Such interactions can result in a trajectory that is substantially different from what would be predicted by the simple superposition of the different processes. For example, they may cause sudden and unforeseen changes that can be interpreted as critical transitions (see CRISIS).

Concluding remarks 1. The relevance of the studied analogies according to their field origin and system characteristics

(B. Walliser)

As is the case when comparing any two fields, all formal analogies between economics and biology are grounded on some correspondence between two systems. More specifically, they are anchored in certain well-defined properties of these systems which look similar for some, dissimilar for others. According to a common ontology, these properties can be classified on the basis of either the *structure* of the interrelated entities; their *behavior* with respect to each other and their environment; or the mode of *evolution* of these entities and relations. Concepts and relations can be considered at a qualitative level or receive a mathematical expression.

Any analogy originates in one of the two fields being compared and is then transferred to the other. It can likewise be initiated by a phenomenon studied in an intermediary field, such as game theory. Finally, it may even arise from a concept or relation taken in a general ontological frame, either literary or mathematical. Any analogy is characterized by the depth of the interpretation it suggests. Although some appear to be rather formal, others are more substantial and may even turn into integral ones (see the introduction). This depth is analyzed along the preceding partition of properties in three classes.

In the following chapter, organizational levels and time scales in each field are compared first. The analogies are then examined as concerns the origin of the concept involved: one of the compared fields, the theory of decision or of games, or in some ontological frame. The analogies are further evaluated as concerns their semantic depth, with regard to the type of properties of the entities concerned: their structural properties, their behavioral characteristics, their modes of evolution. Their relevance is finally related to the anteriority of the corresponding fields; their practical use is examined, and the future of possible analogies is outlined.

Connections between analogy-related entities

The hierarchy of *organizational levels* considered in evolutionary biology is sustained by a large consensus. It distinguishes the infra-cellular level, the cellular level (including genes), the organism level, and the population level. The hierarchy considered in economics is more controversial. The basic distinction is between the microeconomic level of elementary agents (consumers, firms) and the macroeconomic level of a national community. An infra-economic level that is merely conventional is sometimes added: the mental states of the agents in neo-

classical economics, or the routines of the firm in evolutionary economics. An intermediary meso-economic level may be applied to social agents like labor unions. A supra-economic level concerns the international economic system.

As a consequence, the connection established among disciplines between the *organizational levels* may vary according to the economic school of thought. In neo-classical economics, the “global ontology” is directly articulated on biology through individuals. It distinguishes the infra-individual level (mental states), the individual level (humans), the level of organizations (firms), and the level of the global system (institutions, prices). In evolutionary economics, the “production ontology” is shifted by one level with regard to the preceding one, and distinguishes the routine level (related to the cell/gene one), the organizational level (related to the level of organisms) and the level of the whole industrial system.

Likewise, a hierarchy of *time scales* is widely accepted in evolutionary biology. It distinguishes the evolution speed of cells, of organisms’ behavior, of organisms’ population, and finally of ecological systems and species. In evolutionary economics, acceptance of a similar hierarchy is less clear. It distinguishes the evolution speed of individual behavior, of organization functioning, of goods prices and of institutions (and technologies). But other time scales are introduced, involving industrial structures or technologies, for instance, even if technologies evolve at a time scale which is not typically an economic one. The connection between the temporal hierarchies of both fields is then harder to establish.

Finally, within each field, the link between organizational levels and time scales is somewhat tenuous. In evolutionary biology, the infra-cell level does not correspond to a single time scale, since it involves distinct physical and chemical phenomena. Conversely, the species time scale does not correspond to an organizational level since it deals with the structure of organisms induced by mutations. In economics too, mental states (beliefs, preferences) can be associated with time scales, but they are highly disparate (belief revision, preference evolution). Likewise, the time scales for prices and institutions, belonging to the upper organizational level, may differ significantly.

Analogies rooted in one basic field

One category of analogies groups concepts initially introduced in one field and transposed to the other. More rarely, concepts may be proposed independently in both fields and later connected. Any concept has a prior technical definition in its original field. The interpretation of the definition is then broadened, and adopts a spectrum of meanings. Only a few of them are transferred in the analogical process. Finally, in its adoptive field, the concept usually retains only a subset of the enlarged interpretations. In any case, when migrating from one field to the other, an analogical concept may or may not keep its native denomination.

Most of the concepts that shifted from evolutionary biology towards economics originate in the neo-Darwinian trilogy. *Mutation* refers to a genetic restructuring process which brings in an idea of exogenous novelty in the same spirit as *innovation* in economics. *Heredity* qualifies a reproduction process of individual traits passed down from one generation to the other. It is comparable to the fuzziest notion of *transmission* of acquired skills by economic agents. *Selection* reflects a process of discrimination between biological organisms, summarized by the survival of the fittest. It matches the more explicit process of sorting out the more efficient economic agents.

Concepts that moved from economics to biology mainly came from neoclassical exchange theory. *Market* qualifies an institutional procedure of pair-wise transactions between sellers and buyers. Its counterpart in biology concerns the results of exchanges between cells or organisms. *Competition* is a mechanism inducing economic agents to adapt to the market by acting on the quality and price of goods. It is comparable to the competition between animal species for the acquisition of food. *Investment* is a voluntary human action to acquire equipment, the material foundation of many markets, while *natural resources* denote the undifferentiated environment of animals.

Two other concepts were introduced by one field and adopted by the other, but with a smaller scope and a fuzziest interpretation. *Adaptation* and *learning* refer to the ability of a biological organism to fit into its environment by a spontaneous change of its internal physical structure. In economic organizations, the modification of the structure chiefly involves mental states, and is partially voluntary and conscious. *Information*, in economics, refers to the content of a message transmitted from one agent to another. In biology, *information* has been adopted to designate the genetic program coded by proteins during cell replication, as seen primarily from the modeler's point of view.

Analogies derived from decision and game theory

A second group of analogies connects economic and biological concepts that originated in decision theory and game theory. These theories are widespread, and are themselves the outcome of studies worked out in microeconomics of the strategic interactions between agents. But the concepts have already achieved an important step towards generalization that facilitates their transfer. In biology, their meaning is strongly restricted in order to adapt to the field, although their prior interpretation is still detectable. Moreover, the concepts generally keep their original name, at least when they were already present in the field, which is the case for economic ones.

As concerns decision theory, the main concept is the concept of *utility* an agent assigns to the consequences of a choice he made or intends to make. It is connected to the evolutionary concept of *fitness*, which expresses the long term benefit of a trait possessed by an organism

or species more quantitatively, by examining its reproductive success: the average number of offspring. The concept of *altruism*, also present in both fields, merely qualifies a property of an agent's utility/fitness function: whether the individual is benevolent or not with regard to others. The notion of physical or social *constraint* imposed on an agent or an organism complements the notion of utility/fitness. It leads the actor or organism to make some *trade-off* between alternative motivations, summarized in benefits versus losses.

As concerns game theory, the main concept is the concept of *strategic interactions*. It characterizes any situation in which some agent or organism is subjected to the consequences not only of his own action, but to that of the others as well. The twin notions of *communication* and *signaling* refer to information exchanges between an agent or organism and another one and/or the environment, regarding the preparation of a decision or action. The notion of *cooperation* indicates that the concerned entities are in a situation where they are inclined to act in a direction that improves the outcome for all, in spite of their partially opposed interests.

Two more concepts, *equilibrium* and *optimality*, are supported by both economics and evolution, but they are applied to entirely different domains. The *equilibrium* notion was first introduced in physics. In game theory and economics, an *equilibrium state* denotes some stable situation of coordination between the agents' actions, from which they do not depart if initially there. *Equilibrium* was only later applied to biology in order to characterize the result of the behavior of interacting organisms. The *optimality* notion in game theory characterizes both the behavior of a single player who maximizes his utility, and the situation of a set of players in which no one player can do better without hurting some other ("Pareto optimality"). In evolutionary biology, the second meaning is more commonly applied to the fitness landscape of a set of organisms.

Analogies grounded in ontological frames

A third group of analogies involves concepts that originated in frameworks developed outside the two basic fields. On the one hand, a logical or mathematical framework may be structured into weakly interpreted models. Of course, any mathematical corpus stems itself from constituted fields, but its domain of application may either be narrow (quantum theory) or be quite broad (systems theory). On the other hand, a qualitative ontology may be expressed in ordinary language. Again, it is inspired by specific fields, but it is subject to a general conceptualization and even intends to be universal. In any case, these two primitive languages leave their names on the concepts imported by economics and evolutionary biology.

Three concepts based on mathematical frameworks develop patterns of different kinds. The notion of *randomness* makes it possible to model stochastic phenomena such as mutations or innovations, but also to represent uncertainty faced by an economic agent. The concept of *cycle* characterizes the periodic character of the evolution of a biological or social system,

these cycles following a wide range of periods. Finally, the methodological idea of *classification* reflects the need to construct structural or genetic taxonomies of species as well as of goods or agents, with the knowledge that a taxonomy built by the modeler is influenced by some earlier ones built by a society.

Three other concepts were borrowed from literary frameworks with a soft common interpretation for each of them. The notion of *development* merely indicates that the structure of any natural or social system evolves through time, possibly by growth and complexification. The concept of *crisis* suggests more precisely that the system's structure may be reaching or even crossing its viability frontier, leading eventually to a catastrophe in which the system disappears. Finally, the idea of *diversity* insists on the necessary heterogeneity of the composition of a system or a population, since it constitutes a source of innovation that may allow the system to survive.

Two more concepts concerning the general ontology used throughout both fields originated elsewhere. Both were already considered in the first section. Embedded *organizational levels* are distinguished in any empirical field, making it possible to designate the boundaries between two fields. The frontier between biology and economics is conventionally situated at the level of organisms, to which humans belong. Likewise, embedded *time scales* are distinguished in any field, but they overlap from one discipline to the other. Between biology and economics, species vary more slowly than institutions, but cells vary faster than firms.

Analogies in structure

An analogy that is primarily formal deals with the network of interactions between entities by which they ensure their *communication*, whether these interactions involve biological organisms or human beings. *Communication* can concern physical or symbolic interactions, one-way or two-way transmissions, occasional or permanent channels. These interactions have a visible part, the content and diffusion of messages in the environment, and an invisible part, their "interpretation" by the actors and the symbolic impact on them. Such an analogy was first grounded on a behaviorist approach, no longer very popular in either field, content with rebuilding the communication network and measuring its impact by the observable responses it produces.

This analogy looks more substantial when the entities concerned proceed to an interpretation of the messages that is partially observable. For economic agents, this interpretation is initiated by a comparison of the message to initial beliefs, leading to a gradual revision of those beliefs. For biological organisms, this interpretation can be reduced to the recognition of predetermined messages that appeal to prewired actions. Such a difference is present in the distinction between a *signal*, which asks for an explicit and bilateral interpretation, and a

stimulus, which just calls for a specific response. Although both transfer some information, the first is the result of bilateral intention while the second is an effect of crossed stimulation.

Such an analogy is never integral if one considers that human beings are able to think reflexively about their partners and opponents. It concerns beliefs about the others' behavior rules as well as about their bilateral relations. Of course, some animals are endowed with representations, for instance on the possible reactions of predators or preys to their messages or actions. But they hardly constitute more than a crude picture of some causal aspects of the interaction. Humans alone are able to understand the *competition* process driving their relations. Humans alone are able to define a kind of *cooperation* on the basis of common knowledge of the situation and of the institutions governing them.

In summary, if humans enter into *strategic interactions* and are profoundly reflexive, their relations become completely "eductive," since each player simulates the other players' reasoning. Conversely, if such reflexivity is out of reach, game theory remains a useful tool, even if some of its ramifications are not operative. It reduces either to classical game theory, for which equilibrium states are computed by an outside device, or to evolutionary game theory, for which equilibrium states are obtained as asymptotic states. This is why game theory is so widespread in evolutionary biology. The idea of sophisticated reasoning is replaced by bounded belief and bounded rationality, acting in the long term, or even by external *selection*.

Analogies in behavior

Another formal analogy between biological organisms and human beings works perfectly at the behavioral level of the corresponding entity. It expresses the necessity for the two types of entities to face their environment by using at best their specific skills. It is modeled by the *optimization* of some objective-function depending indirectly on their actions, under some physical and social constraints. When some structural conditions are satisfied, this function may be revealed *ex post*, knowing the implemented actions as well as the well-defined context. It is often sufficient to adopt an instrumentalist view of an agent's behavior, asserting that they act "as if" they were optimizing some implicit function.

Such an analogy acquires more substance if it is assumed that a decision results from a deliberation process, involving *trade-offs*, but differing in the two cases. For human beings, the calculus process is grounded on only a few mental states (beliefs, preferences). For biological organisms, it is reduced to mechanical responses to external stimuli. Such a behavioral difference is well reflected by the distinction between subjective *utility* defined as the degree to which humans' preferences are satisfied and objective *fitness* defined as the number of offspring of a biological organism. The first notion results from a strategy computed

by a decision-maker while the second results from behavioral traits shaped in an organism by natural selection.

But such an analogy never becomes integral, if one accepts that human beings, contrary to organisms, are endowed with consciousness. Such consciousness induces some self-reflexivity when dealing with the mental states and the deliberation process itself. Some higher animals must be able to have mental states, since they form expectations and feel satisfaction. But the last are not self-reflexive and only serve as intermediary variables in a process which remains mainly causal. It follows, for instance, that only humans can proceed to voluntary *investments* while organisms just manage at best with *natural resources*. It appears too that only humans are able to show some true *altruism* while organisms are conditioned to do so.

In sum, if human beings are considered as fully conscious, their behavior differs profoundly from that of other animals. Conversely, if such consciousness is only partially involved, the two types of behavior may look rather similar. This is precisely the case when humans are subject to bounded rationality and are induced to imitation and *learning*. As concerns cognitive rationality, the agent's expectations are no longer rational, but adaptive, without second-order thoughts. As concerns instrumental rationality, the agent's actions are no longer optimizing, but may be "satisficing" (reaching some "aspiration levels"). Moreover, external *mutations* or *innovations* compensate for the lack of sophisticated consciousness.

Analogies in evolution

A last formal analogy concerns the way in which behaviors of elementary actors evolve through time. The overall *development* of the system results from the evolution of all factors, combined to get more or less original macroscopic effects. More precisely, this analogy describes the transformation of rules for individual behavior, stochastic individual distributions, and rules for interaction between individuals into collective regularities. Such a transition can be explicitly described when the collective phenomenon appears as a simple aggregate of individual phenomena. But this transition stays implicit when an emergent phenomenon is observed and cannot be computed by the modeler from individual characteristics.

The analogy looks more substantial when the respective evolutions present some analogies, as is the case for institutions. Institutions are viewed as collective devices able to coordinate the members of a group in order to face common forms of uncertainty more efficiently. For human beings, typical economic institutions are the State, a market, a contract, or just money. For other animals, usual institutions include languages, social rules or even property rights. Institutions aggregate to constitute a symbolic basis for the *culture* of any society, but stay

more or less implicit. *However*, some institutions look very similar across fields: for example, *markets* for the exchange of goods or *allocation rules* for the distribution of goods.

But such an analogy never becomes integral, since human institutions are for the most part voluntarily designed by the representatives of a group and seek optimality. For instance, they act as Lewisian conventions (Lewis, 1969) since they are sustained by common knowledge of the advantage in respecting them. Conversely, some animal societies are able to adopt common rules by an unconscious process and to respect them as if forced by natural and external constraints to adopt them. These spontaneous social rules result from random innovations in given situations; they become enforced in stable situations or adapted to new situations. They survive (through natural selection) as stable *equilibria* without making any claim that they are *optimal*.

In sum, some of the main social phenomena have emerged by a shared will of members of a society to solve explicitly a collective problem. Conversely, if such a voluntary design is not achievable, human or animal societies are regulated by numerous social rules which appeared spontaneously and are instantiated by pure reinforcement. For instance, the driving rules on the road result from a more or less sophisticated learning process. But finally, even spontaneous rules are progressively made explicit and further sustained by law. When the environment changes, they undergo some phases of *development* and some kinds of *crisis*, leading to changes in their content as well as their status.

Frequency of analogies

In the general evolution of the universe, biological phenomena emerged before economic ones, even if they now coexist. In principle, economics should be more complex than biology, since it relies on characteristics already present in biological organisms and adds original characteristics which are irrelevant in biology. But at the same time, economics only deals with specific activities of production and exchange of goods made by restrictive individuals. What can be said is simply that the social sciences as a whole are more sophisticated than biology, since they incorporate more complex factors. They have to cope with more observations stemming from more fundamental laws and principles.

No integral analogy can be stated between biology and social science fields like economics, because of the emergence of “thought” during the evolution process. Under certain favorable circumstances, human beings develop a reflexive, conscious, and voluntary behavior that is completely unknown in biology. Hence, only weaker analogies between the fields can be explored, concerning lower-level properties that can be explained in a causal way. For instance, although languages are already available at this level for animals, they are devoted only to a mechanical communication of warning messages that does not need any profound interpretation mechanisms.

Substantial analogies are for the most part sustained by the fact that biology and economics face similar problems with possibly different solutions. They consider the optimal adaptation of heterogeneous entities to the scarcity of their available resources. However, adaptation is more spontaneous in biology and more voluntary in economics (Hayek, 1973). Likewise, optimality of adaptation appears essentially at a collective level in biology, and stays at an individual level in economics (Lagueux, 1993). In fact, this precise concern is examined by game theory with an “eductive” interpretation, able to accept an intentional deliberation process and an evolutionary interpretation that assumes bounded rationality.

Some formal analogies can finally be shown between both fields, at least in privileged domains. However, many biological or economic phenomena are too specific to give rise to relevant analogies. For instance, sexual reproduction, genetic mutations, and even species differentiation are particular biological phenomena with no clear counterpart in economics. Symmetrically, the existence of firms or prices can be considered as typically economic phenomena. On the other hand, some general phenomena studied by systems theory apply in almost all fields. This is the case for cycles, randomness, optimality, and externalities which are just basic properties of variables or relations.

Past use of analogies

A first class of analogies appear as true heuristic devices, able to transfer an original interpretation from a source domain to a target domain. Moreover, this new interpretation suggests original properties for the target domain, properties that can then be tested. The best example is the correspondence of (subjective) *utility* with (objective) *fitness*. It once gave rise to heated debates, even if the positions are now stabilized. Both properties are considered as maximized and both are represented by different specifications (selfish or altruistic ones). But the first behavior is individual and intentional, while the second is collective and deterministic, and they are linked by an “as if” principle.

A second class of analogies consider the already accepted similarity of two domains in order to apply some specific concepts and relations from the first to the second. This was especially done with certain notions derived from game theory, once a general reinterpretation of game theory was accepted in biology. The best example is the application of the notion of *cooperation* to the behavior of animals for the exploitation of resources. The same concepts and tools are invoked as for humans, especially the reference to the Prisoner’s Dilemma. But here again, cooperation is considered as voluntary in the primitive situation and selected in the animal situation.

A third class of analogies act essentially as a means of facilitating the understanding of a phenomenon already studied in other domains. The phenomenon belongs to a well conceptualized framework with a large spectrum of application. The best example is the

notion of *cycle* which is almost universal and can be attributed to (four) well-defined formal causes. For any cycle, it then becomes possible to point out its most probable cause and propose the corresponding model. Of course, the analogy is essentially formal and the possible interpretations of the cycle are only superficially substantial.

Hence, analogies are used at various depths in the literature, but the prevalent ones all ultimately give rise to similar formal models. This does not prevent the underlying interpretation from remaining more or less unformalized and differing from one field to another. In that respect, the dream of universal Darwinism is just the suggestion of a class of formal models but with different meanings, depending on the field. Analogies favor content homogeneity in the fields by developing similar models, as can be observed in economics and biology. Even more, they favor the homogeneity of their methodology by making a more drastic separation between the content of models and their interpretation.

Future of analogies

As a specialization of biology, evolutionary biology looks far more dynamic than economics. It follows that evolutionary biology is essentially idiographic, since it tries to give an account of the unique evolution path of species; economics, by contrast, remains nomothetic when it tries to exhibit the plurality of basic empirical regularities. The dynamic aspect of biology is particularly pregnant in the three principles of Darwinian theory, inheritance and selection being profoundly time-dependent while mutation brings in an element of novelty. Economics and game theory also incorporate some dynamic principles, but they are generally extended from static ones. Hence, economics would benefit by developing biological analogies with a dynamic flair.

Regarding relations between entities, contemporary economics is built around the idea of a set of implicit or explicit contracts between traders exchanging goods. Conversely, the communication between biological organisms is achieved by a variety of specialized networks (nervous, sensorial, endocrinal, immune) through which some kind of information circulates. Here again, messages are transmitted by various physical channels such as structural adjustments, electric circuits or chemical reactions. But, at least between cells, different networks ensure different functions, with some obvious similarities with signals operating between economic agents.

Regarding the entities' behavior, economics continues to think in terms of conflict and coalition, the latter sustained by both interest and trust. Conversely, the functioning of a biological entity is conditioned by a superposition of positive and negative retroactions which enforce its coherence and stability in some given environment. Here again, all basic laws determining behaviors, distributions, and interactions of and between biological entities are ultimately physical ones. But the same formal ingredients may explain why some economic

systems develop or decline, specialize or homogenize, coalesce or dissolve, and finally survive or die.

Regarding the entities' evolution, economics revolves essentially around the idea of innovation and accumulation/obsolescence of physical as well as symbolic capital. But the metabolism of a biological organism gives many examples of dynamic mechanisms enabling an entity to survive and reproduce. Of course, metabolism appears rather simple, structurally, since it reduces to a set of chemical reactions in a dissipative open system. Functionally, however, some molecules are specialized in structural building blocks, energy storage, energy transport, genetic coding, cellular signalization, and in catalysis. The process presents some substantial similarities with those of a firm.

References

Hayek, F. (1973): *Law, Legislation and Liberty*, Routledge.

Lagueux, M. (2014): Rationality and natural selection in economics, in M. Lagueux: *Rationality and explanation in economics*

Lewis, D. (1969): *Conventions, a philosophical study*, Harvard University Press

Concluding Remarks 2.

Economics and evolutionary biology: an overview of their (recent) interactions

J. Martens

Over the past fifty years, the conceptual exchanges between evolutionary biology and economics have been greatly intensified. From these exchanges, three disciplines have emerged, namely: evolutionary game theory, evolutionary economics and evolutionary behavioral economics. In this postface, we propose a brief survey of these approaches, by focusing on the kind of explanatory schemes that they involve. We then conclude with a few thoughts relative to the future of the relations between economics and biology.

Evolutionary game theory

Evolutionary game theory is, *par excellence*, a transdisciplinary approach (see STRATEGIC INTERACTIONS). First originated from the transfer of game theory models to evolutionary biology (Price and Maynard Smith 1973), this framework has been mostly used—in both economics (Friedman 1998) and evolutionary biology (Weibull 1995)—to account for the dynamics of social interactions involving a strategic component, such as territorial conflicts in animals, or technologic arm races between firms. In both of these disciplines, the *goal* of game theoretical-models is very similar, and consists in determining which evolutionary outcomes are reached in presence of such interactions (equilibria, cycles, and chaotic dynamics). But the *processes* represented by these models are completely different. Thus, in biology, the analog of rational choice is a *populational* process of natural selection—i.e. a blind process “choosing” among the different types of individuals according to their average fitness¹³—whereas, in economics, the changes in frequency of strategies are associated with *individual* learning, a process by which agents with a limited form of rationality adjust their behavior according to past and current information (e.g. information about payoffs, opponent’s play, etc.) (see ADAPTATION/LEARNING).

Because of this discrepancy, the analogy between the core *applications* of evolutionary game theory—economic and biological—is best interpreted as a “formal” analogy rather than as a “substantial” analogy (*sensu* Walliser, this volume). But the conceptual overlap between these two applications remains nevertheless quite significant. Thus, as just mentioned, both

¹³ At the individual level, the phenotypic strategies are merely “implemented” by the organisms—in their genotypes—with no assumption being made about their cognitive capacities.

share a *common purpose*, which is to explain the state or the dynamics of a given population where the payoffs of each member depend on its own action/phenotype and that of its partner(s). Furthermore, both share a *common domain of objects*, as the different kinds of individuals to which they apply can be compared according to their *degree of cognitive autonomy*—that is, according to their ability to respond, adaptively, to the strategic environment(s) with which they are confronted. To illustrate, one could well think of an ontological continuum relating the various members of this domain. Such a continuum would begin with the simple individuals deprived of any sort of agency—having mere genetically fixed strategies—and end with the perfectly rational agents of traditional game theory (von Neumann & Morgenstern 1947). Between the two, one would then have an indefinite number of individuals with various degrees of cognitive autonomy (that is, with more or less limited forms of rationality), each representing a certain trade-off between selection and learning.

Viewed in this light, the relationship between the economic and biological applications of game theory differs markedly from most of the transdisciplinary analogies found in the other areas of science. The reason is that, in evolutionary game theory, the degrees of cognitive autonomy provide a relatively *homogeneous* scale for comparing the different objects to which it applies. By contrast, many “formal” scientific analogies (such as the formal analogy between Newton’s law of gravitation and the gravity model of migration in urban geography, for instance) do not permit this kind of comparison, since their objects and processes are strictly *heterogeneous* (gravity vs. migration, planets vs. persons).

This relative homogeneity, however, needs to be qualified in at least three important ways. First, no cognitive structure is universally shared by *all* of the members of the different populations that can be formalized by evolutionary game theory. Thus, a bacterium and a human are hardly comparable from a cognitive point of view, though both can be envisaged as cognitive “agents” in the broadest sense of the term. Second, game-theoretical models are typically applied at *different levels of organization* possessing heterogeneous features. For instance, a population of bacteria and a population of humans count both as instances of biological populations; yet the former is made of unicellular entities and the latter made of multicellular entities; and surely, we may expect a greater influence of learning than of natural selection over evolutionary change in the second of these populations. Last, evolutionary game theory is commonly used to represent strategic interactions between entities existing at *higher* levels of organizations, such as firms competing in a duopoly scenario, or labor unions vs. governments; but in those cases, it is far from obvious what the nature of our “ontological continuum” could be. Hence, even though cognitive autonomy provides an interesting (though speculative) currency to assess the respective importance that selection and learning may have in a given evolving population, it should not be overstated.

Evolutionary economics

Evolutionary game theory is not the only “evolutionary” approach built on an analogy between biology and economics. The so-called field of “evolutionary” economics¹⁴ (Dopfer 2005) also derives from an (apparent) analogy between the two disciplines (though, in this second case, the analogy goes exclusively from biology to economics). Originally sketched by Alchian (1950), and later championed by Nelson and Winter (1982), evolutionary economics has been developed in reaction to the dominant, neoclassical paradigm, and proposes an original account of the *nature* of economic change—drawing on earlier works by Schumpeter (1934) on the importance of innovation (vs. price) in the dynamic of competitive markets. The main tenet of this approach is quite intuitive, and consists in positing a fundamental analogy between the processes of natural selection and the process of economic competition.¹⁵

In neoclassical economics, a central assumption is that any market satisfying the condition of pure and perfect competition should ultimately “clear” at some point in time; that is, the price system should reach a unique equilibrium (Arrow & Debreu 1954). Yet, as many economists (and not only evolutionary economists) have noticed, *real* markets rarely satisfy this idealization; for in the real world, the rationality of individual agents (firms and consumers) is always limited; and the choices of these agents are always made in the absence of complete information. To explain the dynamic of market change, the founders of evolutionary economics have thus proposed an alternative framework in which the competition between firms is envisaged *on the model of* a Darwinian competition. In this framework, the process driving economic change on competitive markets is fundamentally analogous to natural selection: the firms which are the most efficient are the ones which are favored by this process of selection, and the others are left with no other option than *either* to imitate the most successful firms *or* to go bankrupt. The innovations are analogous to mutations (see MUTATION/INNOVATION), and the “evolutionary success” of the firms is measured in terms of increased profit.

A further analogy in evolutionary economics is the parallel—introduced by Nelson and Winter (Winter 1964; Nelson and Winter 1982)—between the role of the genes within organisms and the role of the so-called “routines” within firms. In Nelson and Winter’s terminology, routines refer to “characteristics of firms that range from well-specified technical routines for producing things, through procedures for hiring and firing, ordering new inventory, or stepping up production of items in high demand, to policies regarding investment, research and development (R&D), or advertising, and business strategies about product diversification and overseas investment” (Nelson and Winter 1982, p.14). Like genes,

¹⁴ This appellation is a bit unfortunate, for evolutionary economics has not much in common with the other “evolutionary” approaches in social sciences (like evolutionary psychology). But to follow the common use, we will stick with this appellation.

¹⁵ In the most radical versions of this theory (e.g. Hodgson 2002), economic competition is envisaged as an *instance* of natural selection (see Walliser, this volume).

routines are persistent features which are involved in every aspect of the firm's organization. They determine the possible behaviors of the firm on markets (the firm's "environment") and are ultimately responsible for their economic success. Sometimes, an innovation occurs which supplants an old, less efficient routine. But innovations do not necessarily lead to increased profits, and can also be responsible for the death of a whole organization (like with deleterious mutations).¹⁶

Because of its exclusive emphasis on the process of economic competition, evolutionary economics is (for the most part) of little relevance for the evolutionary biologist. But it is certainly instructive to stress the general differences between, on the one hand, evolutionary economics and, on the other hand, evolutionary game theory.

To begin, there is an obvious difference concerning the *direction* of their analogies: in the case of evolutionary game theory, the approach is bi-directional—i.e. transdisciplinary—whereas in the case of evolutionary economics, the analogies are "one-sided". This difference reflects another important aspect of their respective methodologies: while evolutionary game theory puts a great emphasis on abstraction (many details are neglected, such as the relation between the genotype and the phenotype) as well as on idealization (many unrealistic assumptions are made about the infinite size of the populations, the strategy set, etc.), evolutionary economics aims at providing a precise and realistic description of the way firm competition is working in real markets (e.g. by considering how the R&D departments influence the dynamic of innovation and competition in particular populations of producers).

Unlike the models used in evolutionary economics, which are often very detailed and derived from empirical data, models in evolutionary game theory, by contrast, are mostly analytic in their structure. This explains why evolutionary game theory constitutes a powerful tool to derive *testable* predictions about the evolution of populations, but also why the predictive power of evolutionary economics appears quite limited. This lack of predictive power goes with the relative scarcity of formalism in evolutionary economics; yet, in spite of these differences, the two disciplines possess overlapping domains (as noted above, evolutionary game theory can perfectly account for strategic interactions between firms—especially when some amount of "firm-level selection" and learning is involved). Thus, even though both differ in what concerns their methodological and epistemological aspects, evolutionary economics and evolutionary game theory remain somehow (though only loosely) related—not only as possible ways of applying analogical schemes in scientific explanations, but also as possible sources of complementary insights into the process of economic competition.

¹⁶ In Nelson and Winter's view, the most successful routines tend to be copied by the other firms present on the same markets, based on their average success.

There are, nevertheless, some limitations that are specific to evolutionary economics. Two of them deserve a quick mention here. First, the analogy between mutation and innovation is very imperfect (see MUTATION/INNOVATION), for unlike innovation—which is an intentional and adaptive process—mutation is fundamentally *undirected* (though there may be adaptive constraints on some mechanisms of variation) and usually *rigid* (mutants are not plastic “problem-solvers”). Second, the very notion of fitness, when applied to firms, is very hard to define, for there is no real equivalent of biological fitness in economics. Of course, the notion of an increased profit provides a natural criterion for success *in economics*; but it is not analogous to the process of reproduction in biology (successful firms do not “reproduce” in any biologically meaningful sense of the term). Hence, evolutionary economics does not really derive from a substantial connection between natural selection and economic competition—in fact, its whole methodology is better seen as a *sui generis* representation of economic processes.

Evolutionary behavioral economics

The third connection between evolutionary biology and economics emerged in the last third of the XXth century, and concerns the use of evolutionary hypotheses in the field of *behavioral economics* (Robson and Samuelson 2010). Historically, behavioral economics has developed in the 1960s-1970s to account for the systematic violations of the strong model of rationality posited by neoclassical economists.¹⁷ The main influence of this discipline was cognitive psychology (Allais 1952; Kahneman and Tversky 1979; 2000). But in the 1990s-2000s, several theoreticians suggested that an evolutionary stance could well explain some of the observed departures from strong rationality reported in the literature (Rogers 1994; Waldman 1994; Bergstrom 1996; Robson 2002). Today, there is still no real consensus about the relevance of evolutionary theory for economic and psychological matters. But it seems reasonable to assume that natural selection has had at least a *non-negligible* influence on some of the cognitive structures underlying our current preferences (Gintis 2009).

At first, one might find odd that most of the evolutionary explanations found in behavioral economics have to do with *deviations* from rationality (e.g. violations of Bayes rule); for given the strong analogy between rational choice and natural selection, and given the non-negligible role that natural selection has (presumably) played in the evolution of our cognitive architecture, one should expect these deviations to constitute instead a challenge to *both* economic rationality and biological optimality—and not solely a challenge to economic rationality. However, two reasons can be invoked to explain this apparent oddity.

¹⁷ Examples of such departures include violations of instrumental rationality, such as preferences reversal, time inconsistent preferences or loss aversion, but also violations of cognitive rationality, such as violation of Bayes’ rule and multiple statistical biases.

First, the best solution to a given decision problem is not always “accessible to” natural selection.¹⁸ For example, implementing a sophisticated device for probabilistic reasoning might well—assuming it is available—be optimal in some situations involving a choice under uncertainty. But if there are not enough variations to sustain the evolution of this system, or if the developmental/ecological constraints somehow prevent its implementation, then evolution will fail to produce individuals which behave according to the relevant (in that case probabilistic) principles. Of course, this does not mean that such an optimal device could never appear in natural populations (assuming the proper variations are present); but even so, it would not necessarily follow that this device should be favored by natural selection. After all, implementing a sophisticated decision machinery is cognitively expensive; and, if cheaper alternatives are on the market, one should expect natural selection to favor instead “fast and frugal” heuristics which, *on average*, will do a better job—perhaps at the price of some “irrationalities” (Gigerenzer and Goldstein 1996).

Second, one might question the implicit assumption—made in behavioral ecology—that natural selection always favors individual organisms who behave in conformity to the axioms of rational choice theory. Though surprising, this line of thought has recently found some support in the work of evolutionary biologists, who have shown that animals often exhibit irrational behaviors *that are nevertheless consistent with the fitness maximization hypothesis* (Houston *et al.* 2007; McNamara *et al.* 2014).¹⁹ Admittedly, one might wonder whether the behaviors described in those studies are truly “irrational” in the first place (Kacelnik 2006; Huneman and Martens 2017; Okasha 2018). But the very possibility that it *could* sometimes be biologically optimal to be irrational (in the strict sense of decision theory) remains an interesting conjecture.

A good putative example of such a “parting of ways” between rational choice and natural selection concerns the evolution of irrational risk aversion. In behavioral economics, several empirical and theoretical studies have indeed reported the existence of violations of the principle of expected utility, originally derived by von Neumann and Morgenstern (1944) to account for decision under risk. The most famous of these results is the so-called Allais paradox, who showed that an agent could actually exhibit patterns of risk-averse preferences which violate the *independence axiom*—a central piece of expected utility theory (Allais 1953).²⁰ Since Allais’ works, several models have been proposed (Machina 2008) to account for these “non-standard behaviors”, the most well-known being the so-called “prospect

¹⁸ This point does not rely on the nature of the situation considered—deterministic or stochastic.

¹⁹ The most common examples are violations of transitivity or non-independence of irrelevant alternatives.

²⁰ The independence axiom stipulates that, if an agent prefers lottery A to lottery B, then for any lottery C and any probability p , the agent should prefer the compound lottery (A, p ; C, $1 - p$) to the compound lottery (B, p ; C, $1 - p$). In the Allais paradox, the agents prefer a lottery A with a sure monetary outcome to a lottery B with an unsure outcome (but with a higher expected utility), and yet reverse their preferences when confronted to a pair of compound lotteries D and E which are such that (i) both obtain, respectively, by mixing A and B with a lottery C in identical proportions (p ; $1 - p$), and where (ii) neither guarantees a sure monetary outcome.

theory” (Kahneman & Tversky 1979). But recently, a few authors have suggested that these departures from expected utility theory could actually admit an *evolutionary rationale* (Robson 1996; Okasha 2011).

The core suggestion of these authors, put roughly, is that natural selection, under specific ecological circumstances, can lead to the evolution of irrational risk preferences (irrational according to the standard of expected utility theory). To illustrate this possibility, Okasha (2011) considers a simple scenario, in which an animal is confronted with a choice between one of two possible foraging strategies—A and B (the fitness values have been slightly modified here). In his example, strategy A is “safe”, and guarantees the animal with a payoff of 4 offspring, whereas strategy B is “risky”, and provides the animal with either 10 offspring or 0 offspring, with probabilities 0.5 each. Because strategy A has a lower expected fecundity than strategy B, an animal “seeking” to maximize its expected fecundity (as prescribed by the direct application of the principle of maximization of expected utility to biology) should obviously “prefer” the second, riskier strategy. But as Okasha rightfully notes, this particular expectation fails to correctly predict what happens when natural selection is at work. For natural selection—depending on the *sort* of ecological risk that the individuals are facing (and assuming further that A and B correspond to heritable genotypes in the population)—will, on many occasions, favor the strategy with the *lowest* expected fecundity. Thus, if the risk faced by every member of the population is “idiosyncratic”, that is, if any two individuals of type B have an *independent* chance of getting either 10 or 0 offspring, then (provided the population is large) natural selection will favor the riskier strategy. However, if the risk is “aggregate”, that is, if *all* of the B individuals either get 10 or 0 offspring at some point in time, then natural selection will obviously favor the risk-averse strategy A, *which has yet the lowest expected fecundity*.²¹

Turning now to the case of human preferences, one might legitimately wonder if this sort of evolutionary pattern might not further explain a significant portion of the “irrational fears” or “pessimism” that economical agents often manifest in the face of risk. For now, empirical data are still lacking on these issues, which remain largely speculative (though see Okasha (2018), p.216, for some brief but interesting thoughts over the parallel between behavioral finance and evolutionary biology). But, in the light of these previous theoretical results, it would be interesting to know if the kind of risks faced by human agents, say, in economic contexts (e.g. investors facing aggregate vs. idiosyncratic financial risks on specific markets) could affect their decisions in a way predicted by the model, or whether those risks correlates with important biological factors (like hormone levels).²²

²¹ An example of idiosyncratic risk would be a situation where each individual of type B has an independent chance of being caught by a predator. By contrast, an example of aggregate risk would be a situation where all of the individuals of type B have the same chance of ending simultaneously with either the bad or the good outcome—e.g. an unexpected harsh winter after the foraging season (Starrfelt and Kokko 2012).

²² On this latter point, see Kandasamy *et al.* (2014).

A common point to the various evolutionary approaches in behavioral economics is that they all involve biological hypotheses relative to the *causes* of economic behaviors. In this sense, these explanations are best described as *integrative*, since they conceive of economic phenomena as a part of a broader causal network involving both biological and economic factors.²³ However, “integrative” is not to be understood here as a synonym of “reductive”; for evolutionary behavioral economics usually relies on different *kinds* of evolutionary processes to explain the various patterns of economic behavior (like genetic and cultural forms of selection).

An illustration of such a pluralistic attitude can be found in the evolutionary approaches of ‘strong reciprocity’—a kind of social interaction that has become one of the hottest topics in behavioral economics in the past three decades. In behavioral game theory, strong reciprocity refers to a (conditional) form of altruistic cooperation, where there seems to be no apparent benefits for the cooperating agents (Gintis 2009). Many alleged instances of such altruistic behavior have been reported in experimental studies, such as in experimental applications of the dictator game and the ultimatum game (see ALTRUISM).²⁴ However, none of these observations fits with the game-theoretical models posited by neoclassical economists, which predict that the agents should consistently behave in a self-regarding manner.²⁵

To account for the sort of “other-regarding” preferences that these experiments reveal, behavioral economists have proposed several evolutionary explanations—including group selection hypotheses. Most often, these explanations integrate both genetic and cultural sorts of evolutionary influences. Hayek (1960), for instance, was a precursor in positing the existence of a process of *cultural group selection* to explain how moral norms promoting strong reciprocity could have evolved in human populations. More recently, Richerson and Boyd (2005) developed a model in which strong reciprocity emerges as the product of a *coevolution* process between *genetic* and *cultural* group selection. In this “mixed” explanatory scheme, genetic group selection is supposed to be a weak force—due to a high migration rate between the groups—but cultural group selection is supposed to be quite powerful (this is

²³ In one sense, integrative explanations could be envisaged as a *limit case* of analogical explanations (like the “integral” analogies discussed by Walliser in his “preliminary reflections“ in this volume), for they apply precisely when the explanandum of one discipline (in this case: economic behaviors) shares all of the relevant aspects—plus some, non-relevant aspects—of the explanandum of a broader discipline (biological behaviors).

²⁴ In the dictator game, an experimenter gives a subject a fixed amount of money; and the latter has to choose between (a) sharing this amount of money with an unrelated and anonymous recipient or (b) keeping the whole amount. In the ultimatum game, the experimental setting is identical, except that the recipient now has the possibility of declining the offer—which leads to a mutual payoff of zero. Typically, the agent shares about 25% of the initial endowment in the dictator game (altruistic cooperation) and about 40%-50% of the initial endowment in the ultimatum game. Small offers in the ultimatum game are almost systematically rejected by the recipients (altruistic punishment).

²⁵ In both the dictator and the ultimatum games, classical game theory predicts that the agent should keep the whole amount of money. In the ultimatum game, it also predicts that the recipient should accept any offer, even the smallest.

because, in most human groups, conformist norms tend to keep individual variations at a low level; while the newcomers adopt the most common behaviors in the group).

Often, reputation (indirect reciprocity) is included in these models to explain why individuals sometimes incur an apparent cost to reward or punish an anonymous fellow (Fehr *et al.* 2002). But some evolutionary models do not assume group selection at all, and explain the evolution of strong reciprocity by the sole action of individual selection. André and Baumard (2011), for instance, have developed an ecological market model in which only individual selection is at work: in their model, strong reciprocity (i.e. inequality aversion) evolves in a population of proposers and responders (playing a Dictator game) where the responders have the ability to choose the “best offers” among the proposers. The hypothesis of cultural group selection is therefore neither the only nor necessarily the best explanation to the evolution of strong reciprocity.

What’s next?

At this point, one could be tempted to conclude that, of the three perspectives sketched above, the third one (i.e. the evolutionary stance in behavioral economics) is the most *promising*. This position has been defended, interestingly, by Hammerstein and Hagen (2005), who noted that, during the past history of evolutionary game theory and evolutionary economics, “the interdisciplinary discourse was limited”, whereas in behavioral economics, the testing of evolutionary hypotheses promoted “the joint exploration of empirical and theoretical questions of mutual interest by biologists and economists” (p.604). In favor of this claim, Hammerstein and Hagen emphasize—rightfully—that most of the analogies involved in evolutionary game theory or evolutionary economics are markedly one-sided and domain specific (that is, used either by biologists for biological purposes, or by economists for economic purposes). Yet, although this theoretical assessment is certainly correct, it is important *not* to derive from it the much stronger view that the “integrative” explanations of evolutionary behavioral economics would be—in some way—*intrinsically superior* to the analogical explanations of evolutionary game theory and evolutionary economics.²⁶

Evolutionary game theory, for sure, is no longer as popular or lively than it was at its beginning in the 1970s. But, far from being outdated, it is now part of the “normal science” conducted in many areas of evolutionary theory and economics. Thus, even though the communication between economists and biologists may have been somehow limited in the past,²⁷ it does not mean that the development of theoretical analogies has no longer its place

²⁶ This is *not*, however, a conclusion that Hammerstein and Hagen (2005) endorse explicitly in their paper.

²⁷ Hammerstein and Hagen illustrate this lack of communication by pointing to the parallel development of signaling theory (see COMMUNICATION/SIGNALLING) in economics and evolutionary biology—as the

in the future of interactions between biology and economics. In scientific research, analogies are often fruitful in suggesting new directions of inquiry, and are even more valuable when they provide a general framework for modeling different sorts of phenomena. Evolutionary game theory possesses exactly this form of generality, because it can be used to represent different sorts of evolutionary processes (e.g. learning, cultural and genetic selection) within a single formal language. This particular way of “integrating” or “combining” multiple evolutionary processes into a single, dynamical perspective is not “integrative” in the sense of evolutionary behavioral economics. But it remains essential for the conduct of an interdisciplinary research; for without it, behavioral scientists (especially those with an evolutionary bent) would not be able to address the multiple aspects of the strategic behaviors within a common language.

Evolutionary economics is, obviously, a bit more specific, for the analogies on which it relies do not serve a real purpose outside of economics. But even so, this approach has proven quite useful in drawing attention to many key aspects of market economics that were previously neglected (thus, the *dynamical* character of competitive markets was mostly overlooked by neoclassical economics, yet the evolutionary analogies pointed by Nelson and Winter have largely helped to shed light on its significance). Today, the analogical scheme of evolutionary economics is admittedly no longer very popular among the community of economists, a disaffection that *may* be due, to some extent, to the rather loose and imprecise character of its central analogy (i.e. the analogy between Darwinian competition and market competition). But this disaffection might well be due, more prosaically, to the quite general trend affecting the life-history of *any* scientific hypothesis—at some point, evolutionary analogies may just have been “drained” of their original explanatory power.

In conclusion, we cannot predict how exactly the interplay between economics and evolutionary biology will continue to evolve in the near future. But our guess is that the collaborative enterprises between biologists and economists will probably take a large variety of forms, and *not only* the sort of “integrative” trend that is currently characteristic of evolutionary behavioral economics. Thus, rather than merely following the flow of these newest approaches, scientists would probably gain by focusing more on the articulation and the combination of the main explanatory schemes (integrative *and* analogical) at the interface between evolutionary biology and economics.

References

Alchian, A. A. (1950) : Uncertainty, Evolution, and Economic Theory, *Journal of political economy*, 58(3), 211-221.

authors note, evolutionary biologists didn't seem to be aware, at first, that such a theory had already been developed by economists a few years earlier.

Allais, M. (1953) : Le Comportement de l'Homme Rationnel Devant le Risque, Critique des Postulats et Axiomes de l'École Américaine, *Econometrica* 21, 503-46.

André, J. B., & Baumard, N. (2011) : The Evolution of Fairness in a Biological Market, *Evolution*, 65(5), 1447-1456.

Arrow, K. J., & Debreu, G. (1954) : Existence of an Equilibrium for a Competitive Economy, *Econometrica: Journal of the Econometric Society*: 265-290.

Bergstrom, T.C. (1996) : Economics in a Family Way. *Journal of Economic Literature*, 34(4), 1903-1934.

Boyd, R.W. & Richerson, P.J. (2005) : *Not by Genes Alone: How Culture Transformed Human Evolution*, Chicago: University of Chicago Press.

Dopfer, K. (Ed.). (2005), *The Evolutionary Foundations of Economics*, Cambridge University Press.

Fehr, E., Fischbacher, U., & Gächter, S. (2002) : Strong Reciprocity, Human Cooperation, and the Enforcement of Social Norms, *Human Nature*, 13(1), 1-25.

Friedman, D. (1998) : On Economic Applications of Evolutionary Game Theory, *Journal of Evolutionary Economics*, 8(1), 15-43.

Gigerenzer, G., & Goldstein, D. G. (1996) : Reasoning the Fast and Frugal Way: Models of Bounded Rationality, *Psychological Review*, 103(4), 650.

Gintis, H. (2009) : *The Bounds of Reason: Game Theory and the Unification of the Behavioural Sciences*, Princeton: Princeton University Press.

Hammerstein, P., & Hagen, E.H. (2005) : The Second Wave of Evolutionary Economics in Biology, *Trends in Ecology & Evolution*, 20(11), 604-609.

Hayek, F. A. (1960/2013) : *The Constitution of Liberty*, The definitive edition. Routledge.

Hodgson, G.M. (2002) : Darwinism in Economics: From Analogy to Ontology, *Journal of evolutionary economics*, 12(3), 259-281.

Houston, A. I., McNamara, J. M., & Steer, M. D. (2007) : Do We Expect Natural Selection to Produce Rational Behaviour? *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 362(1485), 1531–1543.

Huneman, P., & Martens, J. (2017) : The Behavioural Ecology of Irrational Behaviours, *History and philosophy of the life sciences*, 39(3), 23.

Kacelnik, A. (2006) : Meanings of Rationality, in S. L. Hurley & M. Nudds (eds.), *Rational animals*, 87–106, Oxford University Press.

Kahneman, D., & Tversky, A. (1979) : Prospect Theory : an Analysis of Decision Under Risk, *Econometrica: Journal of the econometric society*, 263-291.

Kahneman, D., & Tversky, A. (eds.) (2000) : *Choices, Values, and Frames*, Cambridge University Press.

Kandasamy, N. et al. (2014) : Cortisol Shifts Financial Risk Preferences, *PNAS*, 111(9): 3608-3613.

Machina, M. (2008) : Non-expected Utility Theory, in S. N. Durlauf & L. E. Blume. (eds.), *The New Palgrave Dictionary of Economics*, Basingstoke: Palgrave Macmillan.

- McNamara, J. M., Trimmer, P. C., & Houston, A. I. (2014) : Natural Selection can Favour 'Irrational' Behaviour, *Biology Letters*, 10(1), 20130935.
- Nelson, R. & Winter, S. (1982) : *An Evolutionary Theory of Economic Change*, Belknap Press of Harvard University Press.
- Okasha, S. (2011) : Optimal Choice in the Face of Risk: Decision Theory Meets Evolution. *Philosophy of Science*, 78(1), 83-104.
- Okasha, S. (2018) : *Agents and Goals in Evolution*, Oxford University Press.
- Robson, A. J. (1996) : A Biological Basis for Expected and Non-expected Utility, *Journal of economic theory*, 68(2), 397-424.
- Robson, A.J. (2002) : Evolution and Human Nature, *The Journal of Economic Perspectives*, 16(2), 89-106.
- Robson, A.J., & Samuelson, L. (2010) : The Evolutionary Foundations of Preferences, in J. Benhabib, A., Bisin & M. Jackson (eds.), *Handbook of Social Economics*, 221-310, 1B.
- Rogers, A.R. (1994) : Evolution of Time Preference by Natural Selection, *The American Economic Review*, 460-481.
- Schumpeter, J.A. (1934) : *The Theory of Economic Development*, Harvard University Press.
- Smith, J.M., & Price, G. R. (1973) : The Logic of Animal Conflict, *Nature*, 246(5427), 15-18.
- von Neumann, J. & Morgenstern, O. (1947) : *Theory of Games and Economic Behavior*. Princeton: Princeton University Press.
- Starrfelt, J., & Kokko, H. (2012) : Bet-Hedging—a Triple Trade-off between Means, Variances and Correlations, *Biological Reviews*, 87(3), 742-755.
- Waldman, M. (1994) : Systematic Errors and the Theory of Natural Selection, *The American Economic Review*, 482-497.
- Weibull, J. W. (1997) : *Evolutionary Game Theory*, MIT press.

Table of contents

Introduction (P. Huneman)

Preliminary analyses. Analogical reasoning between economics and biology (B. Walliser)

Keywords in economics and evolutionary biology : twenty-five Concepts.

Adaptation/Learning (J. Gayon, B. Walliser)

Altruism (J.-B. André, M. Cozic)

Chance/Uncertainty (P. Huneman, B. Walliser)

Classification (P. Huneman, B. Walliser)

Communication/Signalling (J.-B. André, M. Cozic)

Competition (J. Gayon, M. Cozic)

Constraint/Trade-off (P. Huneman, M. Cozic)

Cooperation (J.-B. André, M. Cozic)

Crisis (S. De Monte, B. Walliser)

Cycles (S. De Monte, B. Walliser)

Development/Growth (J. Gayon/M. Cozic)

Diversity (S. De Monte, M. Cozic)

Equilibrium (S. De Monte, B. Walliser)

Fitness/Utility (P. Huneman, B. Walliser)

Heredity/Transmission (S. De Monte, B. Walliser)

Information (J. Martens, B. Walliser)

Market (J.-B. André, M. Cozic)

Mutation/Innovation (J. Gayon, B. Walliser)

Optimality (P. Huneman, M. Cozic)

Organizational levels (J.-B. André, M. Cozic)

Population (P. Huneman, M. Cozic)

Resource /Investment (P. Huneman, B. Walliser)

Selection (J. Martens, B. Walliser)

Strategic interactions (P. Huneman, B. Walliser)

Time scales (S. De Monte, B. Walliser)

Concluding remarks 1. The relevance of the studied analogies according to their field origin and system characteristics (*B. Walliser*)

Concluding remarks 2. Economics and evolutionary biology: an overview of their (recent) interactions (*J. Martens*)