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Entering the Black Box of Platform Orchestration: A metaphoric co-evolutionary framework for platform-based ecosystems

Dr. Parisot, Xavier

The Institute for Knowledge and Innovation, Bangkok University, Bangkok, Thailand
xavier.p@bu.ac.th

Dr. Thierry Isckia

Institut Mines-Télécom Business School, Evry, France
thierry.isckia@imt-bs.eu

Dr. Pierre Vialle

Institut Mines-Télécom Business School, Evry, France
pierre.vialle@imt-bs.eu

Abstract (194 Words):

Since the first empirical definition of business ecosystems (BEs), its central orchestration dynamic has been defined as co-evolutive. If the nature of the associated mechanisms is still debated, the co-evolutionary nature of inter-organizational innovation processes has been largely demonstrated. Platform-based ecosystems are characterized by a flexible and scalable architecture of cooperation designed to leverage collective intelligence. In such a context, platforms serve as a backbone for inter-organizational collaboration and facilitate interactions. But for a platform-based ecosystem to flourish inter-organizational co-evolutionary processes have to be triggered. To better understand how platform-based ecosystems achieve such goal, an empirical and theoretical characterization of the associated co-evolutionary processes is of utmost importance. However, current analogical transpositions of co-evolutionary mechanisms from biology to strategic management are still disparate and partial. To leverage our understanding of co-evolutionary mechanisms involved in biological complex adaptive systems, the application of a metaphorical transposition is necessary. The metaphorical transposition of coevolutionary mechanisms in organizational sciences enables the distinction between several mechanisms: mimicry, co-adaptation, and 3 different forms of co-evolutive mutualisms. This distinction allows a better understanding of platforms coordination processes, thus opening the way for the empirical identification of specific generative mechanisms and their related triggering factors.

Key-Words: Platform, Ecosystem, Co-evolution; Innovation Management; Strategic Management; Metaphor.

Introduction

Business ecosystems (BE) are new forms of organizational structures which are complex and adaptive systems – CAS (Isaac, 2017; Ntsondé & Aggeri, 2017). The focal complexity aspects appearing in BEs are self-organization, emergence, co-evolution and adaptation (Peltoniemi & Vuori, 2004). Koenig (2013) distinguishes 4 specific archetypal structures of BE. However, for all BE's structures to emerge, an organizational architecture must be set for the community to be able to work and interact in harmony. This architecture, necessary for BE's members co-evolution (Moore, 1993, 1996), is provided by keystone organizations or platform leaders through a coordination engine *i.e.* a platform (Iansiti & Levien, 2004, Cusumano, 2010; Camarinha-Matos, 2013; Evans & Schmalensee, 2016, Valkokari *et al*, 2017). The secret of coordination is to make those exchanges as frictionless as possible (Gray, 2014).

Since the emergence of organizational ecology (Hannan & Freeman, 1977) and evolutionary economics (Nelson & Winter, 1982) the principles of adaptation, variation, selection, retention and coevolution have largely spread among organizational sciences such as strategic management (SM). The principle of coevolution having been described for the first time in ecology (Ehrlich & Raven, 1964), its use in organizational sciences implies its transposition and characterization in the considered scientific field. However, although many studies in various disciplines of organizational sciences describe the coevolution phenomena, few define what the concept covers precisely (McKelvey, 1997, 2002). Several factors can explain this situation. 1) The plurality of paradigms in Ecology, Evolution and Genetics is at the origin of multiple perspectives presenting different mechanisms of coevolution (Urban *et al.*, 2008). 2) Coevolutionary mechanisms (CMs) characterized in Biology vary according to considered scale (Urban *et al.*, 2008). 3) Debates about the definitive conceptualization of the principle of coevolution in Biology persist and no compelling multi-paradigmatic synthesis has emerged so far (Janzen 1980, Schemske 1983, Thompson 1989, 1994, Pagel 2002). 4) Regardless of the considered paradigm / theory in Genetics, Ecology, or Evolution, CMs are only a subset of all evolutionary processes.

Consequently, prior to the importation of CMs in organizational sciences, this embeddedness across multiple complementary frameworks in Biology is analyzed and clarified. CMs are then connected to reveal feedback loops that regulate their operation. The generic structure thus created allows to infer that 42 concepts (and their associated mechanisms) are connected to evolutionary and CMs. The search of these concepts in 14 key references in organizational sciences applying biological importations demonstrates that they are never transposed all together. Each importation proposes a different combination of transpositions. Moreover, 10 concepts are never imported and the defining attributes of 5 concepts are always transposed partially. Since all scanned references operate analog imports, it is not surprising that some concepts cannot be imported.

To overcome the limits of these analogies, and establish a generic structure connecting evolutionary and CMs in organizational sciences, a metaphorical import is applied using the Domains-Interaction Model – DIM (Cornelissen, 2005). As the DIM allows the needed semantic and structural alignments to occur at the conceptual and theoretical levels, different paradigms and/or theories can be aligned in both the source and the target domains (Cornelissen & Kafouros 2008a&b). Metaphorical meanings are encoded for the concepts that were previously not or partially transposed and are aligned with each other. This metaphorical import then allows the construction of a generic structure combining evolutionary and coevolutionary mechanisms in the target domain of organizational sciences. This generic structure enables the distinction between several mechanisms: mimicry, co-adaptation, and 3 different forms of co-evolutive mutualisms. This distinction allows a better

understanding of platforms coordination processes, thus opening the way for the empirical identification of specific generative mechanisms and their related triggering factors.

Literature Review

Successful ecosystemic strategies in knowledge-intensive industries both in Western and, more recently, Asian countries, have increasingly attracted the attention of scholars on that topic in the last decade (Jacobides *et al.*, 2018). However, the focus of these inter-organizational relationships studies has evolved from the firm to the supply chain, the network, the platform to finally reach the ecosystemic level (Rong *et al.*, 2018). Moreover, the theoretical position adopted by the authors is more and more of evolutionary nature (Parisot *et al.*, 2018).

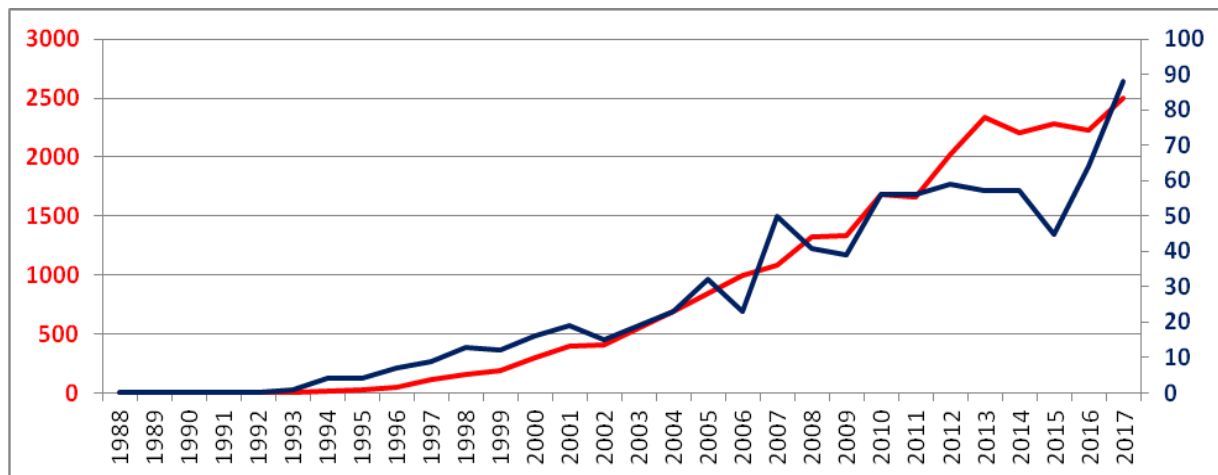


Figure 1. Evolution of publication numbers mobilizing coevolution principle in SM. (Red Curve: Total MS publications identified in Scholar Google; Blue Curve: Publications in 22 journals with the highest impact factors in MS¹).

As corporate success depends more and more on managing assets that lie outside organizational boundaries, keystone organizations or platform leaders provide stability by becoming ecosystemic managers (Iansiti & Levien, 2004). The orchestration dynamic of BEs has been characterized as coevolutionary in nature since the first observations (Moore, 1993, 1996). If the involved mechanisms are still debated (Parisot, 2013, 2015), the coevolutionary nature of inter-organizational coordination processes has been largely demonstrated (Tiwana *et al.*, 2010; Isckia *et al.*, 2018; Zang & Wang, 2018; Rong *et al.*, 2018).

In platform-based ecosystems (PBEs), platform leaders attract and aggregate third-party players and complementors that increase the platform value proposition (Gawer & Cusumano, 2008, 2014, Tiwana, 2013; Evans & Schmalensee, 2016, Reillier & Reillier, 2017; Parker *et al.*, 2016). Niche players are connected to the platform through shared or open-source technologies and/or interfaces. Counterintuitive intellectual property management can be applied to ensure the ecosystem stability and enhance small firms' ability to commercialize innovations created by large firms in unexpected markets (Azzam *et al.*, 2017). In such a context, the platform is an artifact designed to ensure the coupling of two core processes within the ecosystem: inter-organizational innovation and business

¹ The number of articles per year has been established using the following keywords: "Coevolution", "Co-evolution" and "Strategic Management" to ensure that the term is well-used in the required context. The same keywords were used to establish the number of articles published per year in the 22 journals with the highest impact factors in Strategic Management. This list is provided in Annex 1.

development (Isckia & Lescop, 2013; Isckia & Lescop, 2015; De Reuver *et al.*, 2017, Isckia *et al.*, 2018).

Orchestrating their platforms, keystone organizations ensure value creation, knowledge mobility, innovation appropriability, and network stability by applying especially mutualism mechanisms (Dhanaraj & Parkhe, 2006). If the platform provides architectural scalability and enhances collective intelligence, only the triggering of an inter-organizational co-evolutionary sequence leads to the development of a vibrant ecosystem (Moore, 1996; Parisot, 2015).

Several types of co-evolutionary mechanisms' triggering factors attached to BEs emergence have been already identified. Peltoniemi (2006) suggest 4 preconditions that need to be fulfilled in order to trigger co-evolution: 1) Scarcity of customers that induces selective pressure; 2) Conscious choice that enables the organizations to change; 3) Interconnectedness of the organizations that enables the organizations to have an effect on each other; 4) Feedback processes that carry the long-term consequences of coevolution. Loilier & Malherbe (2012) reported 3 types of capabilities characterized as "ecosystemic" and required for BEs' emergence. 1) Technological capabilities related to the innovation development; 2) Relational capabilities that promote interactions between BE's members and 3) Business capabilities to structure the value proposition. Ecosystemic capabilities are inter-organizational by nature. To trigger a coevolutionary sequence and activate these different mechanisms, ecosystem's members need to develop and coevolve their dynamic capabilities (Teece, 2007; Teece, 2017; Helfat & Raubitschek, 2018).

If these first empirical descriptions reveal some of the coevolutionary triggering factors and mechanisms, the definition of these mechanisms still lack of clarity and the distinction between mechanisms of evolutionary nature and mechanisms of real coevolutionary nature remains blurred (Parisot *et al.*, 2018). Moreover, the connections between the evolutionary and CMs and the feedback loops that regulate them remain to be revealed. As Malerba already indicated in 2006: "*The challenge for research here is to go to a much finer analysis at both empirical and theoretical levels, and to move from the statement that everything is changing with everything else to answering questions such as the following. What is coevolving with what? How intense is this process? And most importantly, what are the specific feedback loops that link the variables that change together?*" (p.25).

Seminal definitions of coevolution being biological (Cf. Annex 2), their application in organizational sciences and SM implies their importation. Conceptual and or theoretical importation from Biology to SM can be analog (Tsoukas, 1991) or metaphorical (Cornelissen, 2005). This distinction is of utmost importance. Indeed, analog import implies the preservation of 1) the defining attributes of the concepts in the target domain as well as 2) the logical structure linking these concepts (Tsoukas, 1991) while metaphorical imports passes through the adjustment of 1) the defining attributes of the concepts to the context of the target domain (Cornelissen, 2005) and of 2) the links connecting concepts to each other (Indurkha, 1991, Cornelissen, 2005; Cornelissen & Kafouros, 2008a&b).

A previous analysis of the applied coevolution importations reveals that all applied importations are of analog nature and that no metaphorical transposition has been made (Parisot *et al.*, 2018). This choice of an analog import is most of the time implicit and never justified. The close analysis of these importations also reveals several weaknesses of the applied analog imports at the paradigmatic, theoretical and conceptual levels (Parisot *et al.*, 2018).

1. Paradigmatic level: Although these analogous transpositions should import all the concepts associated with one specific paradigm in the source domain (Tsoukas, 1991) of Biology (Cf. Annex 2 & 3), the concepts mobilized are connected to different paradigms

in Evolution, Ecology and, Genetics (Table 1). This use of multiple paradigmatic sources generates semantic, ontological, and structural issues (Parisot *et al.*, 2018).

- 2. Theoretical level:** Each paradigm in Evolution, Ecology and, Genetics brings together different theoretical perspectives (Cf. Annex 2 & 3). For example, theories of evolution are multiple and have evolved through several attempts of synthesis until the development of the synthetic theory of evolution (Cf. Annex 3).

Therefore, 1) combination of concepts from different theoretical frameworks, 2) lack of consideration of the theoretical origin of the imported concepts and 3) the logical structure connecting them in the source theory prohibit 1) accurate assembly of imports with the concepts of organizational sciences, 2) development of models matching organizational realities and 3) clarification of the feedback loops regulating evolutionary and therefore coevolutionary triggering factors and mechanisms.

In addition, a theoretical fragmentation also exists in the target domain of organizational sciences. The division between the proponents of adaptation and those of selection has long nourished it (Lewin & Volberda, 2003; Porter, 2006). Research developed on organizational ecology's foundations focus on uncontrollable environmental selection forces eliminating unfit organizations (Population Ecology of Organizations: Hannan & Freeman, 1977; Organizations and Environments: Aldrich, 1979; Institutional Theory: DiMaggio & Powell, 1983, and Evolutionary Theory of Economic Change: Nelson & Winter, 1982), while SM research assumes that managers influence the fitness and survival of organizations (Dynamic Capability Theory: Teece *et al.*, 1997; Interpretive Views of Strategy: Daft & Weick, 1988; Dutton *et al.*, 2001; Learning Theories: Levitt & March, 1988; and Strategic Choice Theory: Child, 1972).

Since coevolution analyzes the interactions between organizations and their environments, and the consequences of these interactions on the dynamics of organizational environments, it reconciles both perspectives. This reconciliation went through the creation of a new paradigm encompassing alternative theories. The Quasi-natural Organization Science (Mac Kelvey, 1997) "*view organizations from a microevolutionary perspective of selectionist naturally caused phenomena in interaction with macrocoevolution and intentionally caused phenomena.*" (p.351). The theory of organization–environment coevolution (Lewin *et al.*, 1999), based on the organization adaptation model proposed by March (1991), link "*firm-level exploration and exploitation adaptations to changes in the population of organizations.*" (p.535). In that view, "*organizations, their populations, and their environments [are] interdependent outcome of managerial actions, institutional influences, and extra-institutional changes (technological, sociopolitical, and other environmental phenomena).*" (p.535). In both cases, a new model is created using an analogical process which still do not integrates all the concepts associated to evolutionary and CMs in Biology (table 1).

- 3. Conceptual level:** The observed conceptual imports transpose definitions from several paradigmatic and / or theoretical frameworks. However, these different frameworks assign different defining attributes to the same concept. The coevolution concept especially is defined in SM using definitions borrowed from different paradigms in Ecology, Genetics and even Anthropology (Cf. Annex 4). The use of multiple paradigmatic sources to establish the defining attributes of coevolution in SM weakens the scientific strength of the applied imports and complicates the integration of coevolution phenomena in organizational sciences and especially in SM.

Moreover, for some concept the defining attributes are only partially imported. For example, the seminal definition of natural selection (Darwin, 1859) encompasses two

mechanisms which are the environmental selection (struggle for survival) and the sexual selection (struggle for reproduction). However, since organizations do not exhibit sexual reproduction mechanism, an analog importation is impossible. Therefore, the authors most of the time just ignore all defining attributes attached to the sexual dimension of the natural selection processes (Cf. Table 1). Similarly, biological definitions of the environment include biotope – abiotic and, biocenosis – biotic dimensions. If the biocenosis is always considered in SM, the biotope is frequently ignored (Cf. Table 1). These partial imports generate a confusion between 1) interactions involving organizations only and those involving organizations and objects of their physical environment/habitat and therefore between 2) interactions able to trigger coevolution with those only of evolutionary nature unable to trigger coevolution.

Finally, the meaning affected to the available analogical importations varies depending on the context in which they are operated (Parisot *et al.*, 2018).

The proposed examples for each level (paradigm, theory, concept) demonstrate the partiality and fragmentation of the applied importations in SM. Logical structures linking concepts in source domains are never respected. Only some elements allowing an efficient comparison of similar phenomena between the source and target domains are transposed. These biases decrease the value of the applied imports as 1) they prevent a clear distinction between coevolutionary and simply evolutionary phenomena, 2) they diminish the possibility to understand how the mechanisms associated with these two types of phenomena are entangled and 3) they do not allow access to feedback loop regulation mechanisms affecting these two types of phenomena. Paradigmatic fragmentation of CMs in the source domain of Biology (Cf. Table 1) combined with these weaknesses leads to heterogeneous, partial and disparate borrowings whose scopes and limits are variable and therefore questionable. This situation generates semantic, ontological, epistemological, and structural issues (Parisot *et al.*, 2018).

Following Jacobides *et al.* (2018), if the literature better characterizes PBEs, “*there is [still] little explanation of how firms mutually adapt*”. Therefore, platform orchestration co-evolutionary mechanisms remain poorly understood. Existing accounts of ecosystem dynamics are quite scarce in the academic literature and the few available descriptions of coordination mechanisms in PBEs (Dhanaraj & Parkhe, 2006; Pellinen *et al.*, 2012; Loilier & Malherbe, 2012) provide limited empirical support. From this point of view, platform orchestration is still a black box that needs to be illuminated. To overcome the limitations observed in previous attempts to theorize coevolution in organizational sciences, and to shed light on platform orchestration’s black box, we propose a metaphorical import of all the concepts attached to CMs. To achieve such goal, conceptual origins of coevolution and theoretical connections linking CMs in the source domain of Biology are considered and aligned with organizational sciences using a metaphorical process of importation.

Before the first description of the coevolution phenomenon (Ehrlich & Raven, 1964), three distinct paradigms already existed in Ecology: Community/Population Ecology (Shelford, 1913, Clements, 1916), Ecosystem Ecology (Elton, 1927; Tansley, 1935), and finally Evolutionary Ecology (Pimentel, 1961, Hutchinson, 1965) which emerges with the development of modern genetics and the synthetic theory of evolution also called neodarwinism (Huxley, 1942). If these three paradigms differ in their knowledge objectives, they study related phenomena at different scales (Cf. Annex 2 & Figure 2). This observation leads Naeem (2002) to unify these 3 paradigms and to integrate all ecological objects and phenomena in a holistic perspective. However, it does not specify how it redefines coevolution but retains all the mechanisms associated with each scale.

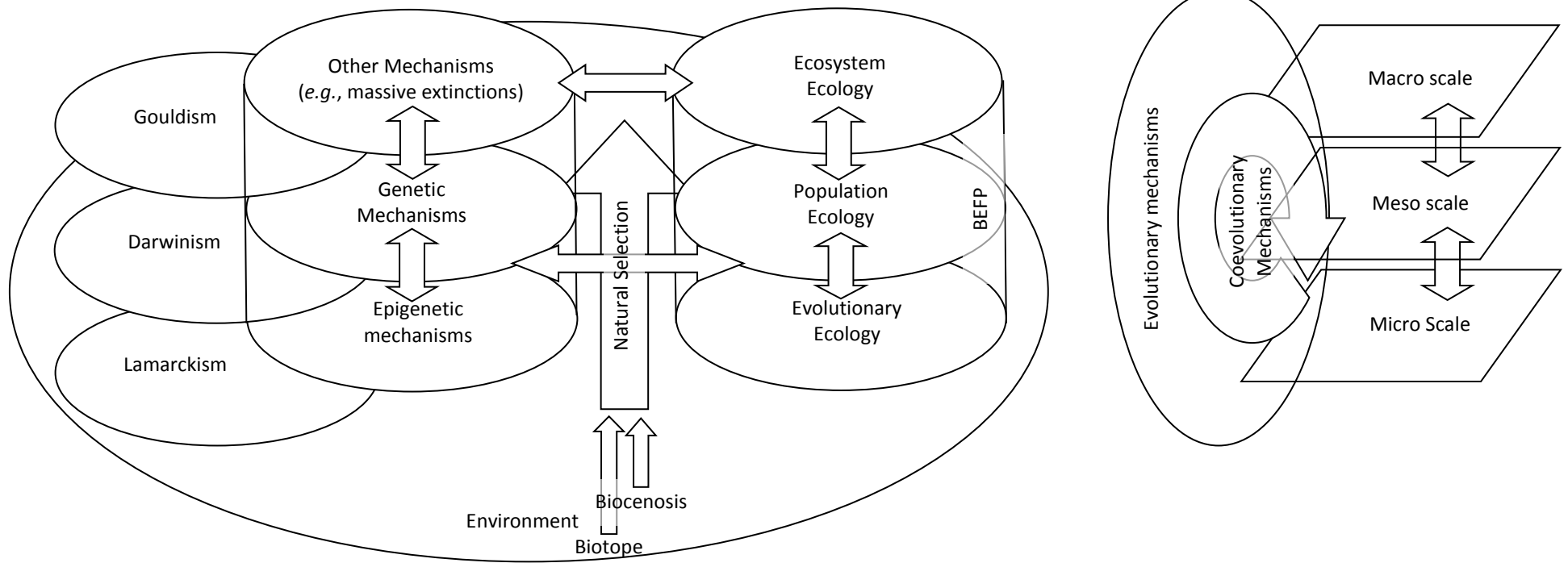


Figure 2: Coevolution paradigmatic fragmentation in Biology: Main connections between evolutionary, ecological and, genetic paradigms (Adapted from Parisot *et al.*, 2018).

Ehrlich & Raven (1964) report the first empirical description of the phenomenon of coevolution, but they do not define it. It is necessary to wait for the work of Janzen (1980) to obtain a first definition of the concept: "*the reciprocal evolution of interacting species*". This definition evolved to incorporate mechanisms taking place at different scales (Cf. Annex 4). In this context, the addition of defining attributes is based on empirical observation of concrete phenomena, which precludes the possibility of a charge of concept stretching (Gerring, 1999). The positivist posture common to all hard sciences avoids any confusion: there is a principle of coevolution underpinned by multiple mechanisms. Deductive inference here aims at defining the laws governing the mechanisms underlying the phenomena observed. To achieve such goal, it is necessary to identify all the mechanisms in order to test their connections and to establish which laws govern them. However, if the CMS emerge at individual and population levels, their long-term fixation involves the molecular level. This complex interaction between phenomena taking place at different scales explains why these laws still have not been established in Biology. In the absence of these laws, the diverse available definitions provide information on CMs.

Moreover, all these mechanisms being interconnected with those of evolution, understanding CMs implies to connect the paradigms of ecology with those of evolution using the laws of genetics. Three dominant paradigms describe the evolutionary phenomena (Cf. Annex 3): Lamarckism (1809), Darwinism (1859) and Gouldism (2006). Underlying these three evolutionary paradigms the laws of classical genetics (Mendel, 1866) explaining the character transmission processes, as well as synthesis aiming to connect these laws to Darwinism (Huxley, 1942), Lamarckism (Waddington, 1942) and later to molecular genetics (Kimura, 1983). In addition, recent advances in epigenetics demonstrate the existence of two systems of transmissions respectively associated with innate characters on the one hand and acquired characters on the other hand. The discovery of this double character encoding system validates both Lamarckism and Darwinism perspectives at the molecular level.

Evolution is possible because 1) there is variation in the genetic diversity of populations and 2) because changes in environmental conditions favor the most likely to survive to the changes. Genetic variation and natural selection are population phenomena. Four processes explain most genetic variations in populations. They form the basis of the cumulative change in the genetic characteristics of populations, leading to the descent with modification (Darwin, 1859) that characterizes the process of evolution:

1. Mutation: origin of new genetic abilities in populations through spontaneous changes that may be punctual (one nucleotide), genic or chromosomal. Meiotic recombinations are part of mutation processes. Because all genetic and epigenetic mutations modify DNA, they are all inherited and transmitted to the next generation.
2. Migration: The movement of individuals among subpopulations within a larger population affects the spatiality and temporality of interactions with the biocenosis and biotope.
3. Natural Selection: resulting from the difference in the individual's ability to survive and reproduce in the face of changing environmental conditions.
4. Random genetic drift: random, mostly neutral and punctual mutations regularly affect DNA sequences. These randomized variations affect allele frequencies across populations. (Kimura, 1983).

Evolutionary, ecological and, genetic mechanisms are interdependent and connected. A synthesis of the feedback loops connecting them (Figure 3) shows that they are not all expressed at all scales and that their consequences on the evolution of populations depend on their reciprocal interactions. In this context, emergence of CMs requires permissive genetic variations establishing mutually profitable relationships between individuals of two distinct species. Variations are of genetic nature and involve several types of mutation.

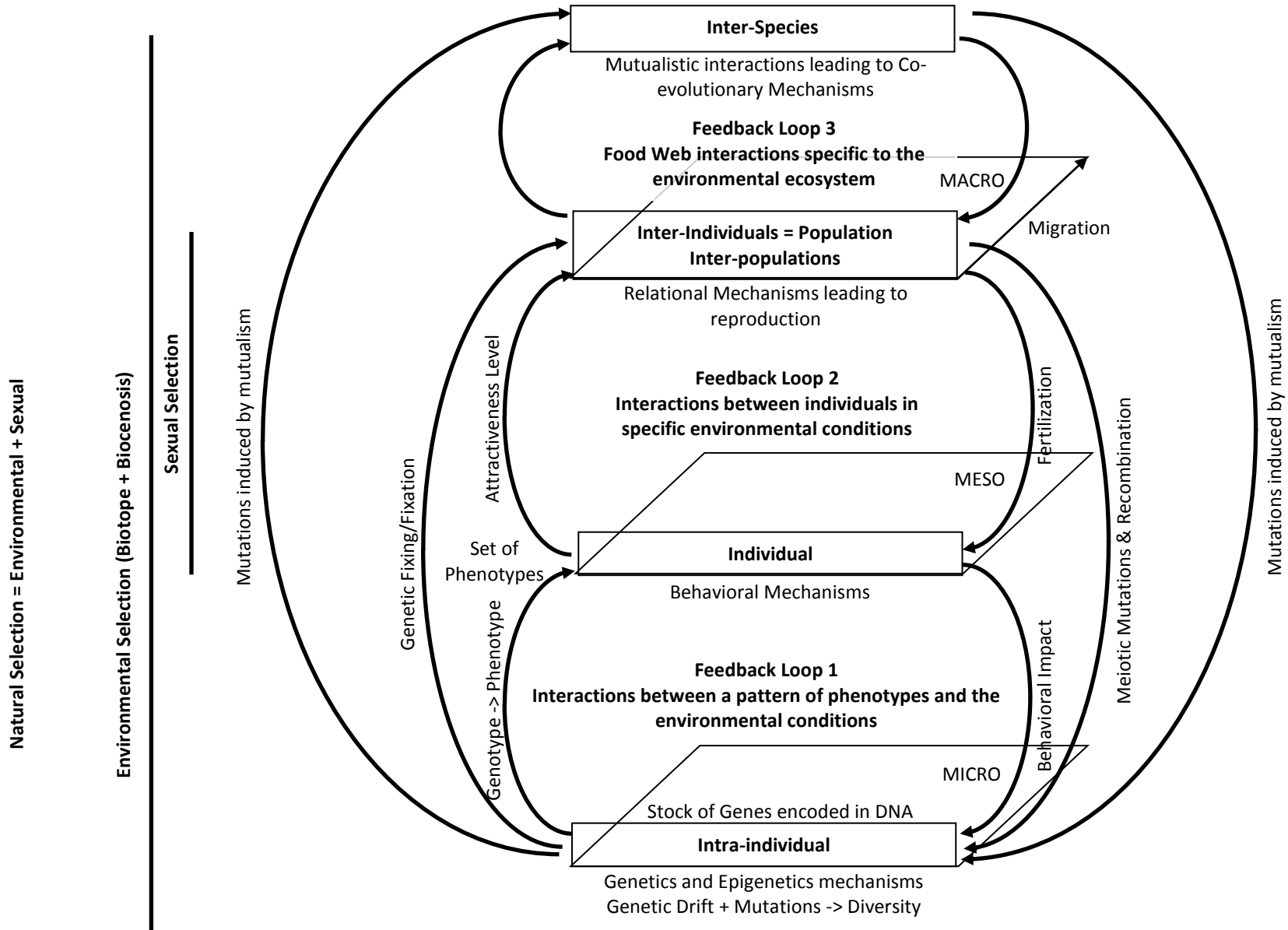


Figure 3: Evolutionary, Ecological and, Genetic Mechanisms and their main connecting feedback loops.

Feedback Loop 1

At the intra-individual scale, only genetic or epigenetic mutations affecting gamete's DNA generate DNA variations potentially transmitted to the next generation. Based on gene's pool composition, genotypes are converted in phenotypes. Individual behaviors are both causes and consequences of phenotypic patterns. On the one hand, since basic behaviors (hunger, thirst, sleep...) are genetically encoded and, psychological traits are substantively influenced by genetic factors (*e.g.* Bouchard, 2004), individual behaviors are partly the result of their heredity. The influence of environmental conditions on development and learning also contributes to the diversification of individual behaviors. On the other hand, individual behavior affects how genotypes are converted into phenotypes, *e.g.* bulimi leads to obesity. In addition, some behaviors may lead to the direct alteration of gamete's DNA, *e.g.* the inadvertent consumption of dioxin promotes epigenetic transgenerational inheritance of disease through DNA methylation epimutations (Manikkam *et al.*, 2012). Therefore, each phenotypic pattern is unique and the results of complex interactions between heredity, environment, and behavior.

Feedback loop 2

At the individual scale, phenotypic patterns lead to various combinations of physical characteristics and to different level of partner attractiveness. Individual's ability to attract partners and reproduce constitutes the sexual selection phenomenon which is one components of natural selection. Genotypic variation takes place during the production of gametes (meiosis). Rearrangements of genetic material from chromosome crossing over lead to the recombination of characters. Each gamete of each parent contains a unique combination of character from these meiotic mutations. During reproduction, fertilization assembles two unique sets of recombinant chromosomes that will give birth to an individual whose combination of genotypes will be different from that of both parents and will lead to the expression of a new phenotypic pattern. Again, interactions between heredity, environment and behavior will determine the attractiveness level of this individual (Pagel, 2002).

As mentioned previously, genetic variation and natural selection are multi-scale population and generational phenomena. Genotypic variations lead to phenotypic diversity. Changes in environmental conditions lead to the selection of the fittest. The greater the genotypic and phenotypic diversity in a population, the greater the chances of having traits adapted to new environmental conditions. The larger the population size, the greater the genotypic and phenotypic diversity it contains. Individuals with traits most suited to new environmental conditions increase their probability of survival and reproduction. As a result, the frequency of their traits increases in the population until they become dominant (genetic fixation).

At this point, it is important to note that the natural selection phenomenon is passive. It results from complex interactions between individual traits present in a population, behaviors and, environmental conditions' changes. Movement of individuals among subpopulations within a larger population affects the spatiality and temporality of inter-individual interactions. It also affects the spatial and generational distribution of genotypic and phenotypic diversity in each sub-population. Therefore, migration affects the natural selection process.

Feedback loop 3

For their alimentation, populations of different species are part of interlocking and interdependent food chains (food web) specific to each ecosystem. In that context, privileged predator-prey relationships can lead to mutualistic interactions. Mutualism can take 3 different forms: parasitism, commensalism and symbiosis. Only symbiotic relationships benefits populations of both species (+/+). In commensalism, one species benefits from the

relationship while the other one is neither helped nor harmed (+/0). In parasitism one species benefits from the relationship while the other one is harmed (+/-). Mutualistic relationships emergence implies that individuals of two species that had no previous contact, already have traits facilitating their interaction (Pagel, 2002). This co-adaptation is punctual and does not involve any genetic evolution. Co-adaptation is a transformation event (physiological, morphological or behavioral) at a given time generating possibilities of mutualistic interactions or facilitating mutualistic interactions.

It is important to note that mutualistic interactions, although they can sometimes be mutually profitable, are always opportunistic and do not constitute self-help behaviors. Co-adaptations leading to mutualism do not therefore constitute a free or even altruistic effort towards another species, but rather an egoistic calculation whose sole purpose is to gain fitness.

Shifting from co-adaptation to coevolution is a process that takes place over a broad time scale (several generations) and includes a series of successive co-adaptations involving mutual genetic adjustments that make both species more suitable for each other. Moreover, “[...] *coevolution shapes species traits throughout mutualistic networks by speeding up the overall rate of evolution. [...] Coevolution results in higher trait complementarity in interacting partners and trait convergence in species in the same trophic level. [...] Convergence is higher in the presence of super-generalists, which are species that interact with multiple groups of species.*” (Guimaraes *et al.*, 2011).

Variations and Selective Pressures

To summarize, two processes are sources of genotypic and therefore phenotypic variations and diversity: 1) somatic mutations affecting non-sexual cells' DNA and 2) germinal mutations affecting gametes' DNA. If these two processes take place at the molecular (intra-individual) level, selective pressures affecting them exist at each level of the scale. At the intra-individual level, variations in environmental conditions affect genotypes conversion to phenotypes by modifying gene expression levels. At the individual level, changes in environmental conditions combined with behaviors also affect the level of gene expressions. In inter-individual interactions, the least attractive individuals have the lowest probability of transmitting their genes to the next generation. And finally, at the inter-species level, predator-prey and mutualistic interactions lead to the selection of the fittest traits on both sides. Co-adaptations can lead to mutualism and successive sequences of genetically fixed co-adaptations can lead to coevolution. Coevolution is therefore a very rare and specific phenomenon (Janzen, 1980, Thompson, 1989).

Analog import of coevolution from the source domain of biology to the target domain of organizational sciences requires connecting all the involved evolutionary mechanisms. However, the establishment of these connections is impossible in an analogical perspective because some parameters present in biology do not exist in organizations. This situation explains why applied analog imports are partial. Only comparable elements are transposed. Missing elements are nevertheless of vital importance to understand feedback loops regulating evolutionary phenomena and consequently CMs before their importation.

If a metaphoric import overcomes the weaknesses of the analog imports already applied, it involves the alignment of the structures linking the mechanisms and their associated concepts in the source field of Biology with the mechanisms and their associated concepts in the target field of the organizational sciences (Cornelissen, 2005). This is why the synthesis that has just been presented is a necessary preliminary step.

Methodology

To develop new concepts and new theories, the use of analogy and metaphor is common in organizational sciences (Grant & Osrick 1996). Despite their fragility, these imports are inevitable and essential as they provide an understanding whose scope implies their acceptance. To empower analogical and metaphorical imports in organizational conceptualization and theorization, a new field of study emerged in the 80s (Morgan, 1980) which examines their role, scope, limits and processes (Tsoukas, 1991; Cornelissen, 1995; Cornelissen & Kafouros 2008a&b).

Limitations of analogical imports justify the use of metaphorical imports in organizational science. In opposition to analogy, metaphor generates itself similarities between the source and the target domains where there was none before (Indurkha, 1991): "*metaphors generate inferences beyond the similarities required for their comprehension*" (Cornelissen, 2005, p.754). Since, analogies proceeds using deductive inference by rejecting dissimilarities, it does not integrate all the basic mechanisms involved in the production and understanding of metaphors. Tourangeau and Rips (1991) demonstrate that the context contributes to the determination of the transposition nature exploited by a specific metaphor. Outside this context, the nature of the transposition cannot be anticipated. They also suggest the existence of a mechanism that allows the receiver of the metaphor to assign properties that are not the result of comparison between the source and the target domains.

Cornelissen (2005) proposes the domain interaction model (DIM) which emphasizes the fact that the characteristics of the source can rarely be applied directly to the target because similarities that both domains share are often only metaphorical. The analogical approach (Tsoukas, 1991) would therefore be valid only in very rare cases. Cornelissen (2005) exploits some results obtained in cognitive psychology to demonstrate the existence of similar inherent structures between correlated domains. In the metaphor, objects in the source and target domains have equivalent structural positions and similar characteristics in their respective representations. This observation is related to the phenomenon of implementation of the metaphor that triggers the activation of higher order cognitive schemas in the source and target domains. A cognitive schema of higher order governs the assembly of semantic objects in the same field such as Biology or MS. It constitutes a network connecting objects associated with the same theme (for example, the semantic domain of ecology includes objects such as environment, biotope, biocenosis, population, ecosystem...). Once these higher-order cognitive schemas are activated, they guide the set of subsequent treatments connected to a specific metaphor. Each theory or concept corresponds to a representation included in a cognitive schema of higher order. Each of these schemas representing a specific network, the nature of the projection operated, from the schema corresponding to the source to the schema corresponding to the target (Gentner, 1983), is influenced by their particular crosslinks. The metaphorical process therefore takes into account the structural correspondences during the establishment of each new relationship between two domains considered, the circumstances and the nature of the pre-existing structures in each domain (development of a generic structure). Not only a correspondence is established between the source and target domains, a new metaphorical space is created which feeds on a process of going back and forth between two higher order cognitive schemas (development and elaboration of the blend). In this space, a new meaning is assigned to the transposed objects allowing the establishment of correspondences between the source and the target where apparently, there was none at the beginning (emergent meaning). When all the stages of the cognitive process of the metaphor are achieved, they go beyond those of the analogical process as they allowed transitions from abduction to deduction and from deduction to induction. These transitions explain why metaphorical cognitive processes are more powerful than analogical processes (Cornelissen, 2005).

To better benefit from the understanding of the CMs involved in biological CAS, the application of a metaphorical importation is necessary. Only a shift from analogy to metaphor allows the needed semantic, conceptual, theoretical and structural alignments of 1) coevolution associated concepts (Indurkha, 1991; Cornelissen, 1995), and of 2) feedback loops regulating evolutionary and CMs within the particular context of organization sciences. To achieve such goal, Cornelissen's (2005) domains-interaction model (DIM) phases have been applied step by step.

1. Development of a generic structure:

The prior presentation of evolutionary and CMs identified in Biology allows to establish a list of 42 associated concepts. The paradigmatic and / or theoretical origin of each concept is identified in order to specify which theoretical combinations are implicitly applied by the authors during their analogical imports (Table 1). Since the Domains-Interaction Model allows the needed semantic and structural alignments to occur at the conceptual and theoretical levels, different paradigms and/or theories can be aligned in both the source and the target domains (Cornelissen & Kafouros 2008a&b).

The 42 concepts associated to CMs in Biology are sought in 14 key references in organizational sciences proposing analogous evolutionary or co-evolutionary importations (Table 1). This search allows to distinguish:

- concepts that are imported analogically (Table 1)
- combinations of concepts that are imported analogically (Table 1)
- concepts that are not imported (Table 1 & 2)
- concepts whose defining attributes are partially analogically imported (Table 1 & 2).

Concepts that are not imported or whose defining attributes are partially imported determine the terms of the metaphor to encode. For each term, conceptual structures seen as parallel between the source and the target domains are specified.

For the concepts whose defining attributes are partially transposed, conceptual structures of references importing the same concept are aligned with in the target domain (Annex 5, 6 & 7).

2. Development and elaboration of the blend

Metaphorical elaboration of the meaning of each missing concept can be achieved using information blending from both the target and sources domains. Moreover, importation completion of concepts partially transposed can also be accomplished. In all cases, maturation of the blend implies back and forth movement between the source and target domains to ensure the proper alignment of the metaphoric meaning with other transpositions involved in the generic structure.

3. Emergent meaning

The meaning (ideas and conjectures) that emerges from the blend is not simply a composition of meanings that can be found in either the target or source concepts. If such blended meaning can be referred back to both the source and target domains, it emerges as a new perspective which makes sense in the metaphorical structure combining the concepts.

Preliminary Results

Concepts associated with evolutionary and CMs and inferred from the generic structure established for the source domain are listed in Table 1. Their paradigmatic origins are specified. The combinations of conceptual importations operated in the 14 references analyzed are presented in Table 1.

Concepts connected to CMs		Nelson & Winter (1982)	Hannan & Freeman (1993)	Baum & Singh (1994)	Van de Ven & Garud (1994)	Moore (1996)	Mckelvey (1997)	Lewin <i>et al.</i> (1999)	Koza & Lewin (1998)	Lewin & Volberda (1999)	Hite & Hesterly (2001)	Malerba (2006)	Porter (2006)	Mittleton-Kelly & Davy (2013)	Jacobides <i>et al.</i> (2018)
Concepts Mobilized (42)	Source Paradigms Mobilized	18/9	20/8	11/9	13/6	26/12	18/8	18/8	11/8	18/8	10/8	9/8	24/8	23/9	12/6
Evolution	Lamarckism, Darwinism, Gouldism	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Variation	Lamarckism, Darwinism	✓	✓		✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Selection	Lamarckism, Darwinism	✓	✓	✓	✓	✓	✓	✓	✓	✓			✓	✓	✓
Retention	Lamarckism, Darwinism	✓			✓		✓	✓		✓			✓		
Mutualism	Ecology 4 paradigms		✓	✓		✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Parasitism	Ecology 4 paradigms		✓			✓							✓		
Commensalism	Ecology4 paradigms		✓												
Symbiosis	Ecology 4 paradigms		✓			✓			✓				✓	✓	
Mimicry	Ecology 4 paradigms	✓	✓	✓									✓	✓	
Ecosystem	Ecology 4 paradigms		✓			✓							✓	✓	✓
Adaptation	Lamarckism, Darwinism, Gouldism	✓	✓	✓	✓	✓		✓	✓	✓	✓		✓	✓	
Fitness	Lamarckism, Darwinism	✓	✓				✓	✓		✓			✓		
Co-adaptation	Lamarckism, Darwinism		✓			✓		✓	✓	✓	✓		✓	✓	✓
Coevolution	Lamarckism, Darwinism			✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Micro-coevolution	Molecular Genetics				✓		✓	✓		✓				✓	✓
Macro-coevolution	Population Genetics				✓		✓	✓		✓				✓	
Gene	Molecular Genetics	✓	✓				✓							✓	
Genotype	Molecular Genetics														
Phenotype	Molecular Genetics														
Mutation	Molecular Genetics	✓				✓	✓	✓	✓	✓	✓		✓	✓	✓
Mitosis	Molecular Genetics														
Somatic Mutation	Molecular Genetics														
Meiosis	Molecular Genetics														
Germinal Mutation	Molecular Genetics														
Recombination	Molecular Genetics	✓	✓												
Genetic Drift	Synthetic theory of Evolution, Neutralist evolutionary theory														
Genetic Fixing	Population Genetics												✓		
Punctuated equilibria	Gouldism		✓			✓	✓	✓		✓					
Environment	Ecology/Evolution/Genetics	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Biotope	Ecology 4 paradigms					✓	✓	✓	✓					✓	
Biocenosis	Ecology 4 paradigms			✓		✓	✓	✓					✓	✓	✓
Trophic level	Ecosystem Ecology					✓									
Natural Selection	Darwinism	✓	✓			✓	✓	✓	✓	✓		✓	✓	✓	
Environmental Selection	Darwinism	✓			✓	✓	✓	✓					✓	✓	
Sexual Selection	Darwinism														
Selection Pressure	Darwinism	✓	✓	✓	✓	✓	✓	✓		✓		✓	✓	✓	✓
Reproduction	Ecology, Lamarckism, Darwinism, Molecular & Population Genetics	✓													
Migration	Darwinism					✓		✓			✓				
Species	Ecology, Lamarckism, Darwinism, Molecular & Population Genetics	✓	✓												
Generation	Ecology, Lamarckism, Darwinism, Molecular & Population Genetics	✓	✓		✓	✓	✓					✓			
Genealogical	Ecology, Lamarckism, Darwinism, Molecular & Population Genetics						✓	✓		✓					
Feedback loop	Ecology, Darwinism, Molecular & Population Genetics	✓		✓		✓	✓	✓		✓	✓	✓	✓	✓	

Table 1. Concepts connected with evolutionary and CMs in 14 key references in organizational sciences applying analogical importations from Biology.

1. Development of a generic structure:

Among the 42 concepts associated to evolutionary and CMs in Biology, no more than 24 are imported simultaneously in the same analogy. Biological concepts are imported from different paradigms and/or theoretical frameworks in 3 domains of Biology: Evolution, Genetics and Ecology. The inferred paradigms and/or theoretical frameworks are:

- Ecology: Evolutionary, Community and, Ecosystem Ecology (Cf. Table 1 & Annex 2),
- Genetics: Mendelian Genetics, Epigenetics, Neutralist theory of evolution (Cf. Annex 3).
- Evolution: Lamarckism, Darwinism, Neo-Darwinism, Gouldism (Cf. Annex 3),

Since, no multi-paradigmatic synthesis encompassing all these frameworks exist in Biology, a preliminary alignment of the structures seen as parallel between these inferred relevant domains was needed (Figure 2) to reveal how key evolutionary and CMs interact in Biology (Figure 3).

Ten concepts are missing in all the references analyzed. The biological defining attributes of 5 concepts are always imported partially and the missing parts are always the same among the 14 references analyzed (Table 2).

No importation		Partial importation		Missing Defining Attributes
1	Genotype	1	Gene	Introns/Exons Generational transmission
2	Phenotype			
3	Mitosis	2	Mutation	Distinction between somatic and germinal mutations
4	Somatic Mutation			
5	Meiosis	3	Genetic Fixing/Fixation	Increase of one allele frequency at the population scale
6	Germinal Mutation			
7	Recombination	4	Environment	Biotope
8	Genetic Drift			
9	Sexual Selection	5	Natural Selection	Sexual selection
10	Sexual Reproduction			

Table 2. List of concepts that cannot be transposed analogically or only partially (Adapted from Table 1)

All the missing concepts involve DNA, and / or sexual reproduction. This isn't surprising since no analogical comparison is possible with organizational phenomena. Unfortunately, the missing concepts are also all involved in the feedback loops regulating evolutionary and coevolutionary mechanisms (Figure 3). A similar situation has already been largely discussed for the same concepts in the context of BEs (Fréry, 2010; Parisot, 2013, 2015). However a metaphorical meaning can be elaborate for each missing concept upon information transferred from both the target and sources domains (Cornelissen, 2005).

Partial importations aren't surprising either. Only the comparable defining attributes of each concept are transferred. Defining attributes which are not matching organizational phenomena are just put aside.

2. Development and elaboration of the blend & 3. Emergent metaphorical meaning

To elaborate the blend, information of both source and the target domains are aligned. Back and forth movement between domains are applied to ensure the proper integration of the emergent metaphoric meaning with other transpositions involved in the generic structure. If

the development and the elaboration of the blend and the emergent meaning steps proceed from different cognitive schema, they are presented together in the results to improve the clarity.

Since the concepts whose defining attributes are partially transposed constitute key connective elements in the biological generic structure (Figure 3), their blending is operated first. The blending and emergent meaning of the missing concepts are realized based on the metaphorical defining attributes affected to previous key connective elements.

Gene/Genotype/Phenotype

Nelson and Winter (1982) propose the organizational routine as an analogical equivalent for the gene (Annex 5). If they mobilize the notions of genotype and phenotype, they don't really distinguish their analogical meanings from that of the gene (Annex 5). It is likely that this fusion of meanings in this seminal reference partially explains the recurrent lack of importation of genotype and phenotype concepts in the following works. Alternative analogies have been however proposed later. Mitleton-Kelly and Davy (2013) compared the gene with organizational skills and Parisot *et al.* (2018) with the core competences of the firm (Table 3). Moreover, Nelson & Winter (1982) connect gene and behavior directly (Annex 5) without taking connective and intermediary concepts into account (genotypes, phenotypes and their interactions with the environmental conditions).

In Genetics, DNA is the physical medium of genetic information. Gene is one unit of information encoded in DNA. Genes are not translated permanently into proteins. Genotypes represent different specific DNA sequences *i.e.* different versions of the same gene. The redundancy of the genetic code allows the encoding of the same protein with different gene DNA sequences. Therefore, most changes do not alter the composition of the protein. However, if several genotypes can lead to them same phenotype, one genotype can encode several phenotypes. This situation is due to the fact that the DNA sequence of genes contains coding parts (exons) and non-coding parts (introns). The translation of the gene's DNA into RNA is followed by a step of splicing the introns and assembling the exons. Several combinations of assembling exons being possible, one gene does not code for one protein but several. A new genotype appears when mutations affecting gene's DNA sequence modify the composition of the protein and when this change affects its function or its efficiency to perform its function. The phenotype is the physical character arising from the expression of the genotype. By extension, the notion of phenotype is also used to account for all the observable characters of an individual. Environmental conditions changes affect both genotypes and phenotypes.

Within the organizational context, each firm has a stock of routines (genes). All are not exploited permanently. Operationalization of each routine (generational transmission) implies the control of several skills. Different set of skills (genotypes) can lead to the same routine (gene) with diverse level of performance (phenotype). Variable combinations of the same skills can generate different routines (one gene -> several proteins). The level of performance of the routine (phenotype) depends on the influence of other routines with which it is combined (pattern/set of phenotypes) and, on the impact of the organizational environment (natural selection) on combinations of routines. Ability of routine combinations to perform in specific internal and external organizational environments determines which of them will tend to become predominant over time. At the organizational scale, core competences and dynamic capabilities derive from the expression of specific combinations of routines. Therefore, changes (mutation) affecting routine function or its efficiency to perform its function generate variations both at the routine and organizational levels.

Natural Selection / Sexual Selection / Somatic-Germinal Mutation / Reproduction

In Biology, natural selection includes environmental selection and sexual selection (Cf. Annex 6). It results from the difference in individual's ability to respectively survive and reproduce in changing environmental conditions. Sexual selection tends to reduce genetic diversity through attraction and reproduction with individuals exhibiting similar patterns of phenotypes and perceived as the fittest. Sexual reproduction tends to increase genetic diversity through two combined phenomena. 1) Chromosomal recombination occurs during the process of gamete's production (meiosis) and generates new genotypes at a low frequency. 2) The fertilization process combines two gametes *i.e.* one from each parent. The greater is the genetic diversity within the population, the greater the likelihood of combining genotypes of different nature for each gene. Only genetic and epigenetic mutations affecting gamete DNA (germinal mutations) are transmitted to the next generation. Mutations affecting the DNA of all other cells in the body (somatic mutation) are not transmitted (Pagel, 2002). The genetic diversity generated through germinal and somatic mutations (variation) is affected by environmental conditions changes and differential sexual attractiveness (selection). Individuals exhibiting the best fitness in the new environmental conditions increase their likelihood to survive and to transmit their genetic traits (retention)

In the organizational context, routine variations arise both inside and outside the firm. The ability of the firm to identify, attract, interact (Lorenzoni & Lipparini, 1999) and, ally (Kale & Singh, 2007) partners presenting complementary routines, assets, or knowledge, in short its connective capacity (Lichtenthaler & Lichtenthaler, 2009), determine its opportunities to combine internal and external routines. In the Darwinian perspective of natural selection (1859), sexual selection is essentially based on traits favoring the attraction of partners presenting the desired fitness. Accessible external routines (germinal mutation -> external variation) that are recognized, assimilated (selection), and applied (retention), participate in the evolution of internal ones. This process involves the absorptive capacity of the firm (Cohen & Levintal, 1990). The reverse process involving desorptive capacity leads to the same result for the partner.

Internal routine variations are connected to 3 other dynamic capabilities which are inventive, transformative and innovative capacities (Lichtenthaler & Lichtenthaler, 2009). The inventive capacity refers to organizational ability to internally generate new routines (somatic mutation -> variation). It comprises the process stages of knowledge generation and knowledge integration into the organizational base of existing routines (Nonaka, 1994; Smith *et al.*, 2005). The transformative capacity refers to organization capability of retaining routines internally over time. It comprises the process stages of maintaining the knowledge in the organizational base and subsequently reactivating this knowledge (Garud & Nayyar, 1994; Walsh and Ungson, 1991). Knowledge is easier to maintain and reactivate when the organization has more prior knowledge in a specific field (Garud & Nayyar, 1994). Benefits from prior knowledge indicate path-dependencies in knowledge retention (McGaughey, 2002; Pandza & Holt, 2007). Finally, the innovative capacity refers to the organizational capacity to match its innovations with the context of the market (Khilji *et al.*, 2006).

Environment/Biotope/Biocenosis

In Biology, the environment includes the biotope (physical habitat associated with a particular set of interacting organisms) and the biocenosis (interacting organisms living together in a specific habitat). Physical resources are drawn from the biotope while the biological resources are drawn from the biocenosis. The nature of the surroundings or conditions in which living beings live, operate and interact generate specific selective pressures. Any changes in the physical composition of the environment may affect the species that exploit it and may lead to the disappearance or appearance (by migration) of

species. All species being interconnected through the food web, any changes affecting a species generates a selective pressure on those that depend on it for its survival. Variations in the composition of the biotope and/or the biocenosis explain the evolution of most part of the selective pressures that species undergo and constitute evolutionary mechanisms. Co-evolutionary mechanisms are affected by the variations in selective pressure when they touch directly one or both species involved.

In the organizational context, raw material scarcity and geographic location (biotope) constitutes examples of sources of selective pressures. However, the distinction between elements of the physical / natural environment and, elements of the organizational environment (biocenosis) of the firm are never clearly stated in the analyzed references. Nevertheless, physical / natural and organizational environments interact constantly, and these mutual influences affect deeply the overall selective pressures applied to the firm.

Generic structure in target domain

Based on the preliminary results of blend elaboration and on emergent metaphorical meanings, a first draft of generic structure linking all the concepts inferred from the source domain and transposed in target domain is proposed (Figure 3).

Blend elaboration and metaphorical meanings remain to be enriched from both the theoretical and the empirical perspectives to reach maturity. However, CMs regulating feedback loops start to emerge and become entangled.

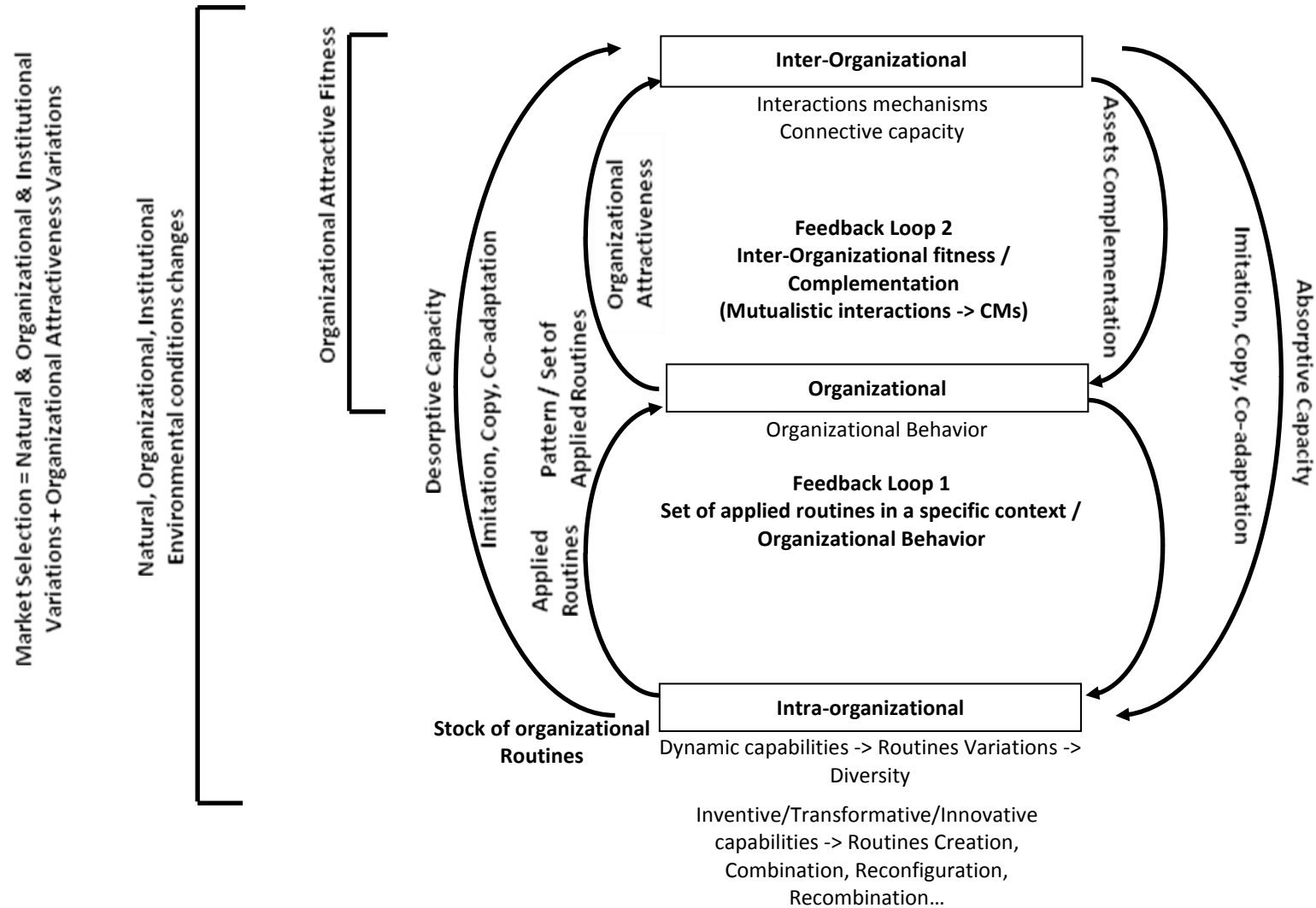


Figure 3: Generic structure in SM: Mechanisms connecting the imported evolutionary, ecological and, genetic mechanisms and their connecting feedback loops.

Conclusion

The metaphorical transposition of evolutionary and CMs with their associated concepts enables:

- 1) the metaphorical transposition of the associated concepts (mutation, migration, selection, genetic drift, selective pressure, genotype, phenotype, inheritance) and simultaneously their semantic and structural alignment,
- 2) the empowerment of the conceptual connections between evolutionary and CMs and the clarification of evolutionary and CMs entanglement in organizational sciences,
- 3) the distinction between 2 evolutionary mechanisms (imitation / co-adaptation) and 3 forms of coevolutive mutualism (Parasitism / Commensalism / Symbiosis),
- 4) a better specification of the CMs encountered in PBEs.

This metaphorical theorization is a preliminary contribution to a more fine-grained understanding of platform-based ecosystem coordination processes and, paves the way for further empirical characterization of yet unidentified generative mechanisms and their associated triggering factors.

Moreover, this transposition allows to specify the pre-requisites needed to pursue the empirical identification of CMs in PBEs:

- 1) Since CMs are hidden generative mechanisms, critical realism constitutes the optimal epistemology to apply
- 2) CMs should be considered in a diachronic perspective (McKelvey, 1997)
- 3) CMs arise only between different populations of organizations and/or communities
- 4) Intra and inter-organizational scales must be both simultaneously considered since CMs operate within and across organizational scales

Finally, by clarifying the differences between imitation, co-adaptation and, 3 forms of coevolutive mutualisms, this metaphorical theorization allows to better distinguish evolutionary mechanisms from CMs in PBEs and more largely in strategic management.

This distinction is of the utmost importance regarding the countless confusions existing in the current literature (Parisot *et al.*, 2018).

This metaphorical theorization contributes to a more fine-grained understanding of platform-based ecosystem coordination processes and, paves the way for further empirical characterization of yet unidentified generative mechanisms and their associated triggering factors.

In knowledge-intensive industries, business is increasingly led by BEs and PBEs. To help organizations build or join these ecosystems, strategic management must move from description to prediction and, produce theoretical models able to support ecosystemic generative mechanisms identification through empirical validation. This article proposes this type of model.

When information from both the source and the target domains are aligned, metaphorical meaning of the imported concepts emerges logically.

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Annex 1: List of the 22 Scientific Journals with the highest impact factors in Strategic Management by alphabetical orders used to measure the number of publications' evolution on coevolution. The indicated impact factor is for 2018.

1. Academy of Management Learning & Education (2.86)
2. Academy of Management Perspectives (4.68)
3. Advances in Strategic Management (0.22)
4. American Marketing Association (7.33)
5. Business Horizons (2.58)
6. Business Strategy Review (0.03)
7. California Management Review (3.30)
8. European Business Review (0.94)
9. European Management Journal (2.36)
10. European Management Review (1.25)
11. Harvard Business Review (0.72)
12. Journal of Business Strategy (0.52)
13. Journal of Management and Strategy (0.9)
14. Leadership & Organization Development Journal (1.07)
15. Long Range Planning (3.22)
16. M@n@gement (0.33)
17. MacKinsey Quaterly (0.50)
18. Management Decision (1.52)
19. Scandinavian Journal of Management (1.34)
20. Strategic Management Journal (5.48)
21. Strategic Organization (3.08)
22. Technology Analysis & Strategic Management (1.50)

Annex 2: Brief introduction of the dominant paradigms in Ecology and their definitions of coevolution (adapted from Parisot *et al.*, 2018).

Paradigms	COMMUNITY/POPULATION ECOLOGY	ECOSYSTEM ECOLOGY	EVOLUTIONNARY ECOLOGY	BIODIVERSITY ECOSYSTEM FUNCTION PARADIGM
Founders	Shelford V.; Clements F.E.	Elton C.S.; Tansley A.G.; Lindeman R.L.	Pimentel D. ; Hutchinson G.E.	Naeem S.
First Description	1913	1927	1961	2002
Definition	"Ecology is the science of communities. A study of the relations of a single species to the environment conceived without reference to communities and, in the end, unrelated to the natural phenomena of its habitat and community associations is not properly included in the field of ecology." Victor Shelford (1913)	"Integrated study of living (biocenosis) and non-living (biotop) components of ecosystems and their interactions within an ecosystem framework. This science examines how ecosystems work and relates this to their components such as chemicals, bedrock, soil, plants, and animals."	"Consider both historical and contemporary influences on patterns of variation and study variation at all levels, from within-individual variation (e.g., ontogenetic, behavioral) to variation among communities or major taxonomic groups." Fox <i>et al.</i> 2001	"The BEFP concerns two issues [...]. First [...] the biota plays an essential role in ecosystem processes. The second [...] claim is that diversity plays a significant role in such processes. Put simply, the existence of life alters the environment and the diversity of life determines the manner in which life alters the environment, much as if diversity were a catalyst to life's biogeochemical activities." Naem, 2002, p.
Knowledge Objective	Examines how interactions among species and their environment affect the abundance, distribution and diversity of species within communities	Determining the underlying causes of the fluxes of materials (e.g., carbon, phosphorus) between different pools (e.g., tree biomass, soil organic material)	Understanding adaptive significance and the "evolvability" traits	Integration of previous ecological paradigms in a holistic approach
Methodology	Qualitative and Quantitative analysis and the community level	Quantitative holistic approach of systems analysis	Molecular qualitative and quantitative analysis at the individual, community, population and species levels	Quantitative & Qualitative
Scale	Méso	Macro	Micro	Micro/Méso/Macro
Coevolution Definition	"The evolution of two or more species due to mutual influence" (Wilson, 1992, p.163)	"Multi-species coevolution affects emergent community structure or ecosystem functioning." (Caldarelli <i>et al.</i> , 1998).	"Coevolution is the process of reciprocal evolutionary change between interacting species, driven by natural selection." (Thompson, 2001, p.1)	Integrative
Key References	Shelford, V. (1913). <i>Animal Communities in Temperate America</i> . University of Chicago Press, Chicago. Clements, F.E. (1916). <i>Plant Succession</i> . Publication 242, Carnegie Institute of Washington, 512 pp. Elton, C.S. (1966). <i>The Pattern of Animal Communities</i> . Chapman & Hall, London.	Elton, C. S. (1927). The nature and origin of soil-polygons in Spitsbergen. <i>Quarterly Journal of the Geological Society</i> , 83(1-5), 163-NP. Tansley, A. G. (1935). The use and abuse of vegetational concepts and terms. <i>Ecology</i> , 16(3), 284-307. Lindeman, R. L. (1942). The trophic-dynamic aspect of ecology. <i>Ecology</i> , 23(4), 399-417.	Pimentel, D. 1961. Animal population regulation by the genetic feedback mechanism. <i>American Naturalist</i> 95:65–79. Hutchinson, G. E. (1965). <i>The ecological theater and the evolutionary play</i> . Yale University Press. Fox, C. W., Roff, D. A., & Fairbairn, D. J. (Eds.). (2001). <i>Evolutionary ecology: concepts and case studies</i> . Oxford University Press.	Naeem S., (2002) Ecosystem consequences of biodiversity loss: the evolution of a paradigm, <i>Ecology</i> , Vol.83, n°6, p.1537-1552.

Annex 3: Brief introduction of the dominant paradigms in Evolution and Genetics and their main evolutionary mechanisms (adapted from Parisot *et al.*, 2018).

Paradigm	Transformist theory of evolution Lamarckism	Theory of evolution by natural selection Darwinism	Synthetic theory of evolution Neo-Darwinism	Theory of punctuated equilibria Gouldism	Laws of Heredity (Transmission of Characters)	Epigenetics	Neutralist theory of evolution
Founders	Jean-Baptiste de Monet, Chevalier de Lamarck	Charles Darwin	Sir Ronald A. Fisher, John B. S. Haldane, Sewall Wright, Theodosius Dobzhansky, Julian Huxley, Ernst Mayr, Bernhard Rensch, George Gaylord Simpson et George Ledyard Stebbins	Stephen Jay Gould	Gregor Johan Mendel	Mark J. Baldwin Conrad Hal Waddington	Motoo Kimura
First Description	1809 Zoological Philosophy	1859 The origin of species	Huxley, J. 1942 Evolution: Modern Synthesis	1972/2002 The structure of the theory of evolution	1866 Experiments in Plant Hybridization	Baldwin M.J. 1896 A new factor in Evolution Waddington C.H. 1942 Canalization of development and the inheritance of acquired characters	1983 The neutralist theory of evolution
Evolutionary Mechanisms	1) An organ develops under the effect of a frequent solicitation during the generations. 2) The species are transformed as a result of individual variations that are perpetuated through reproduction: Transformism. 3) Acquired characters are passed on to the next generation.	1) The species are gradually transformed as a result of individual variations giving them strengths or weaknesses that make them able to survive natural selection processes. 2) No transmission of acquired characters. Natural selection of the characters most adapted to the conditions of the environment then transmission of the latter via sexual reproduction. 3) Natural selection comes from two mechanisms: sexual selection (struggle for reproduction); selection by variation of environmental conditions (struggle for survival)	1) Evolution is not a transformation of isolated individuals but of groups of individuals of the same species (populations). 2) Evolution proceeds by random mutations of genetic inheritance and natural selection of differences due to chance. 3) There is a spontaneous genetic drift by mutation. 4) Environmental variations over time generate favorable or unfavorable selection pressures. 5) The characters are transmitted physiologically according to the mode of reproduction of the species. 6) Mutations can affect the physiological attractiveness thus generating a sexual selection of populations.	1) Evolution proceeds in a very irregular way with stops, resumptions, accelerations. 2) The appearance of new species results from evolutionary explosions between which the species evolve little.	1) Law of uniformity of the first generation hybrids: A character can present several different forms (genes / alleles). Living organisms inherit two factors (genes / alleles) for each trait. Dominant factors (genes / alleles) mask recessive factors, which explains the uniformity of first-generation hybrids. 2) Law of disjunction of alleles: The pairs of factors (genes / alleles) are disjoined independently during the formation of gametes (meiosis). 3) Law of independent segregation of multiple characters: Factors (genes / alleles) are recombined independently during fertilization.	1) Phenotypic diversity is superior to genotypic diversity. Many phenotypes are the result of epigenetic coding. 2) Two epigenetic coding mechanisms have been identified: 1- methylation of DNA; 2- compaction of certain chromosomal regions. 3) Epigenetic inheritance has a greater sensitivity to the environment and a lower stability than that of DNA modifications. 4) Germinal epimutations affect epigenetic inheritance in the next generation.	1) Genetic variations do not lead to functional modifications of the DNA molecules and cannot give rise to the selection to which they are neutral. 2) The variability of the molecules, reflecting the variability of the species, occurs with a regularity that is incompatible with selective pressures varying in intensity over time and with the species. It is therefore chance that presides over the fate of variations and not natural selection.

Annex 4: Common definitions of coevolution referenced by authors of articles theorizing coevolution in organizational sciences and MS (adapted from Parisot *et al.*, 2018).

References	Definitions	Source
Ehrlich, P., & Raven, P. (1964). Butterflies and plants: A study in coevolution. <i>Evolution</i> , 18, 586-608.	"[interspecific combinations of organisms] evolved in part in response to one another" Ehrlich & Raven, 1964, p.604 quoted by Porter, 2006, p.480	Population Ecology
Roughgarden, J. (1979) <i>Theory of Population Genetics and Evolutionary Ecology: An Introduction</i> . Macmillan. New York.	"[...] evolution in which the fitness of each genotype depends on the population densities and genetic composition of a given species itself and the species with which it interacts"	Evolutionary Ecology
Bateson, G. (1979). <i>Mind and nature: A necessary unity</i> . New York: Bantam Books.	"A stochastic system of evolutionary change in which two or more species interact in such a way that changes in species A set the stage for the natural selection of changes in species B. Later changes in species B, in turn, set the stage for the selecting of more similar changes in species A." p.277	Anthropology
Janzen, D. (1980). When is it coevolution? <i>Evolution</i> , 34(3), 611-612.	"One population evolves in response to another population, which has itself evolved in response to the first population." p.611 "In summury, I plead for the retention of the usefulness of 'coevolution' by removing it from synonymy of usage with 'interaction', 'symbiosis', 'mutualism', and animal-plant interaction'." p.611	Population Ecology
Van Valen, L. (1983). How pervasive is coevolution. In M. Nitecki (Ed.) <i>Coevolution</i> , p.1-19. Chicago: University of Chicago Press.	"[...] mutualistic evolution [...]" Van Valen, 1983, p.2	Evolutionary Ecology
Futuyama, D., & Slatkin, M. (Eds.). (1983). <i>Coevolution</i> . Sunderland, MA: Sinauer Associates.	"[the] key feature is that the selective factor that 'stimulates evolution in one species is itself responsive to that evolution'" Futuyama & Slatkin, 1983, p. 6 quoted by Porter, 2006, p.480	Evolutionary Ecology
Thompson, J. N. (1989). Concepts of coevolution. <i>Trends in Ecology & Evolution</i> , 4(6), 179-183.	"[...] coevolution is reciprocal change in interacting species [...]"	Evolutionary Ecology
Kauffman, S. (1993) <i>The Origins of Order: Self-Organisation and Selection in Evolution</i> . Oxford University Press	"[Biological] ecosystems are not totally connected. Typically, each species interacts with a subset of the total number of other species, hence the system has some extended web structure." p.255	Evolutionary Ecology
Caldarelli, G. <i>et al.</i> (1998) Modelling coevolution in multispecies communities. <i>J. Theor. Biol.</i> 193, 345–358	Community coevolution: "Multi-species coevolution affects emergent community structure or ecosystem functioning"	Ecosystem Ecology
Strauss, S.Y. <i>et al.</i> (2005) Toward a more trait-centered approach to diffuse (co)evolution. <i>New Phytol.</i> 165, 81–90	Diffuse coevolution: "The evolution of two species in response to each other is altered by the occurrence of a third species"	Evolutionary Ecology
Yip, K. Y. <i>et al.</i> (2007). An integrated system for studying residue coevolution in proteins. <i>Bioinformatics</i> , 24(2), 290-292.	"Coevolution (covariation/correlated mutation) is the change of a biological object triggered by the change of a related object." p290	Genetics

Annex 5: Definitions of ‘Gene’, ‘genotype’, ‘phenotype’ in both the source and the target domains and available analogies in the 14 references analyzed.

Concepts	Definitions in the source domain	Analogy	Definitions in the target domain
Gene	Fundamental unit of inheritance determining one specific trait transmitted from one generation to another (Pagel, 2002).	Routine: "[...] <i>these routines play the role that genes play in biological evolutionary theory. They are a persistent feature of the organism and determine its possible behavior (though actual behavior is determined also by the environment); they are heritable in the sense that tomorrow's organisms generated from today's (for example, by building a new plant) have many of the same characteristics, and they are selectable in the sense that organisms with certain routines may do better than others, and, if so, their relative importance in the population (industry) is augmented over time.</i> " (Nelson & Winter, 1982, p.14)	"[...] <i>general term for all regular and predictable behavioral patterns of firms [...] this term to include 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.</i> " (Nelson & Winter, 1982, p.14)
		Skills: "[...] <i>in an organizational context, it is important that there are a wide range of skills represented by employees to maintain an ability to adapt to the uncertainty of the market and other contextual constraints and shifts.</i> " (Mitleton-Kelly & Davy, 2013 p.54)	None
		Core competences: "[...] <i>core competencies of the company would be a good analogical equivalent capable of translating organizational genes.</i> " (Parisot <i>et al.</i> , 2018)	None
Genotype	Specific Gene/Set of genes responsible for the expression of one particular trait (Pagel, 2002).	Genotypes -> Routines (Nelson & Winter, 1982, p.160)	None
Phenotype	Observable physical characteristics for one specific trait resulting from the interaction between its genotype and the environmental conditions (Pagel, 2002).	" <i>In biological evolution, differential reproduction rates of phenotypes possessing different genetic inheritances drive the selection dynamics. In models of economic selection, expansion of profitable firms relative to unprofitable ones plays an analogous role.</i> " (Nelson & Winter, 1982, p.142)	None

Annex 6: Definitions of ‘Natural Selection’ in both the source and the target domains and available analogies in the 14 references analyzed.

Definitions in the source domain	Analogy	Definitions in the target domain	Reference
Results from the difference in the individual's ability to survive and reproduce in changing environmental conditions (Pagel, 2002)	<p>"[...] economic 'natural selection'[:] Market environments provide a definition of success for business firms, and that definition is very closely related to their ability to survive and grow. Patterns of differential survival and growth in a population of firms can produce change in economic aggregates characterizing that population, even if the corresponding characteristics of individual firms are constant." (p.9)</p>	<p>"Supporting our analytical emphasis on this sort of evolution by natural selection is a view of 'organizational genetics' - the processes by which traits of organizations, including those traits underlying the ability to produce output and make profits, are transmitted through time." (p.9)</p>	Nelson & Winter (1982)
	Isomorphism (p.93)	<p>"[...] units subjected to the same environmental conditions, or to environmental conditions as mediated by a given key unit, acquire a similar form of organization [...]" (p.93)</p>	Hannan & Freeman (1993)
	<p>"[...] processes of either adaptation or selection (or combination of the two)." (p.379)</p>	<p>"[...] organizations tend to become isomorphic with their environments through processes of either adaptation or selection (or combination of the two)." "Community ecology investigates the evolution of patterns of structure represented in the interactions among populations and considers the system-level consequences of these interactions for the dynamics of coacting sets of populations (Astley, 1985; Hannan and Freeman, 1989). Community-level interactions moderate population dynamics by altering the selection pressures that organizations face" (p.379)</p>	Baum & Singh (1994)
	<p>"Variation [...] Selection [...] Retention [...]" (p.425)</p>	<p>"Variation is the creation of a novel technical or institutional form within a population under investigation. Selection occurs principally through competition among the alternative novel forms that exist, and actors in the environment select those forms which optimize or are best suited to the resource base of an environmental niche (Hannan and Freeman, 1977:939). Retention involves the forces (including inertia and persistence) that perpetuate and maintain certain technical and</p>	Van de Ven & Garud (1994)

	<i>institutional forms that were selected in the past (Aldrich, 1979)." p.425</i>	
<i>"[...] 'species' are seen to be subject to genetic mutation and selection that gradually transforms them." "[...] ecological and evolutionary interactions that occur across an entire ecosystem [...]" (p.11)</i>	<i>"[...] in a market economy a Darwinian selection occurs in which the fittest products and companies survive. More recently, as businesses have been dissected into processes through the quality and reengineering movements, some now maintain that the fittest processes and systems of processes drive out the weak. In either instance, the 'species' are seen to be subject to genetic mutation and selection that gradually transforms them." (p.11)</i>	Moore (1996)
<i>"[...] variation, selection, retention, and struggle [...]" (p.359)</i>	<i>"Through the interaction of four processes (variation, selection, retention, and struggle) the Darwinian theory of natural selection explains order in the biological world in the context of competitive forces impinging on organisms (Darwin 1859, Dobzhansky et al. 1977, Lewontin 1979, Kauffman 1993). As the twentieth century ends, Darwinian evolutionary theory is properly seen as composed of multilevel micro- and macroevolutionary explanations (Depew and Weber 1995)." (p.359)</i>	Mac Kelvey (1997)
None	<i>"Survival of the firm is realized in changes in the firm's wealth creation performance over time. We hypothesize wealth creation to be an interdependent outcome from returns to (1) exploitation, (2) exploration, and (3) legacy. Legacy embodies returns to reputation, market position, scale, and capabilities reflecting firm-specific history of exploitation and exploration adaptations." (p.537)</i>	Lewin et al. (1999)
None	<i>"Exploitation and exploration alliances vary on three related, although, nonexhaustive principle attributes. These attributes function as selection mechanisms, facilitating the success and failure of individual alliances. However, in the aggregate these attributes drive the evolution of the population of alliances: Absorptive capacity [...] Control [...] Identification [...]" (p.259-260)</i>	Koza & Lewin (1998)

Literature review encompassing several analogies.	Literature review encompassing several definitions.	Lewin & Volberda (1999)
None	"Coevolution is set in motion when resource challenges require networks to adapt because network adaptation then ameliorates the resource challenges, which consequently increases the firm's chances of successfully progressing to subsequent stages." (p.283)	Hite & Hesterly (2001)
None	"During its evolution an industry undergoes a process of transformation that involves knowledge, technologies, learning, the features and competences of actors, the types of products and processes, and the institutions. An industry also changes its structure, where the term structure here means not market structure, but rather the network of relationships (competitive and cooperative, market and non market, formal and informal) among actors that affect innovation and performance in an industry."	Malerba (2006)
Literature review encompassing several analogies.	Literature review encompassing several definitions.	Porter (2006)
Literature review encompassing several analogies.	Literature review encompassing several definitions.	Mitleton-Kelly & Davy (2013)
None	None	Jacobides <i>et al.</i> (2018)

Annex 7: Definitions of the ‘Environment’ in both the source and the target domains and available analogies in the 14 references analyzed.

Definitions in the source domain	Analogy	Definitions in the target domain	Reference
<p>Surroundings or conditions in which living being lives and operates. Encompasses the Biotope (abiotic) & the Biocenosis (biotic) (Pagel, 2002).</p>	<p>Distinction between internal and external environments. Environment -> Price Vector involving Economy, Market, Organizations, Competitive stimuli, Product Demand, Supply, Institutions, Knowledge...</p>	<p>"[...] <i>no theory of long-run evolutionary change logically can take the environment of the individual species (collection of firms) as exogenous. Hence, the notion of fitness (profitability) contributes much less to the understanding of the long-run pattern of change than might at first glance appear. What does play a crucial though obscure role is the character of the whole evolving system's interactions with the truly exogenous features of the environment, represented in the current model by product demand and factor supply curves.</i>" (p.20)</p>	<p>Nelson & Winter (1982)</p>
	<p>"[...] <i>fundamentally comprised of other organizations and populations (DiMaggio and Powell, 1983) [...]</i>" (p.380)</p>	<p>"<i>A coevolutionary approach requires that sets of coacting organizations and their environments be the object of study and changes in all interacting organizations be allowed to result not only from the direct interactions between pairs of organizations but also by indirect feedback through the rest of the system (Roughgarden, 1983)</i>" (p.380)</p>	<p>Baum & Singh (1994)</p>
	<p>"[...] <i>actors in the environment [...]</i>" (p.425)</p>	<p>None</p>	<p>Van de Ven & Garud (1994)</p>
	<p>"[...] <i>comprising all the organisms of a particular habitat as well as the physical environment itself [...]</i>" (p.11)</p>	<p>"[...] <i>there are complementary forms of evolution that play vital but grossly underrated roles in both biology and business. They encompass the ecological and evolutionary interactions that occur across an entire ecosystem, comprising all the organisms of a particular habitat as well as the physical environment itself.</i>" (p.11)</p>	<p>Moore (1996)</p>

"[...] organisms and [...] abiotic environment [...]" (p.359)	"In fact, evolution is mostly coevolution. 'The true and stunning success of biology reflects the fact that organisms do not merely evolve, they coevolve both with other organisms and with a changing abiotic environment' (Kauffman 1993, p. 237; his italics)." (p.359)	Mac Kelvey (1997)
Organizations, Institutions, Geopolitic, Economy, Social Movements, Natural Environment.	"The theory assumes that organizations, industries (populations) and environments (institutional and extra-institutional) coevolve, that their rate, pace, and patterns of change are distinct and interdependent, and that the direction of these changes is not unidirectional." (p.536) "Extra-institutional influences, such as geopolitical, economic, and natural environmental changes, as well as social movements that affect the deep structure enveloping the enterprise and market competition." (p.536)	Lewin et al. (1999)
Based on Lewin et al., 1998 and Mac Kelvey, 1997.	Based on Lewin et al., 1998 and Mac Kelvey, 1997.	Koza & Lewin (1998)
Literature review encompassing several analogies.	Literature review encompassing several definitions.	Lewin & Volberda (1999)
Implicit	Network	Hite & Hesterly (2001)
Implicit	"[...] the network of relationships (competitive and cooperative, market and non market, formal and informal) among actors that affect innovation and performance in an industry."	Malerba (2006)
Literature review encompassing several analogies.	Literature review encompassing several definitions.	Porter (2006)
Literature review encompassing several analogies.	Literature review encompassing several definitions.	Mitleton-Kelly & Davy (2013)
Literature review encompassing several analogies.	Literature review encompassing several definitions.	Jacobides et al. (2018)

