The Concept of 'Co-evolution' and Its Application in the Social Sciences: A Review of the Literature

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1 Defining Co-evolution

The Oxford Dictionary online describes co-evolution as a term originating in biology, meaning "the influence of closely associated species on each other in their evolution". Ehrlich and Raven [10] first used the term co-evolution in reference to biological evolution when looking at the relationship between the patterns of evolution of plants and butterflies, stating that it describes the simultaneous, reciprocal evolution of interacting populations. In biology, co-evolution refers to the change of a biological entity triggered by the change of a related entity [42]. Each entity exerts certain pressures and influences over the other, affecting the evolutionary trajectory of each.

Reciprocity is an element of co-evolutionary relationships stressed by all definitions in the literature. The influence of one species upon another's evolution is inherently important to the idea of co-evolution, but some definitions also stress an element of selection or competition in this dynamic. Co-evolution has been characterized as a reciprocal evolutionary process between interacting species, driven by a process of natural selection [14,40]. Raven and Johnson [35] define co-evolution as the simultaneous development of adaptations in two or more populations, species or other categories, that interact so closely each is a strong selective force on the other. However, within the social sciences emphasis is placed more often on the concepts of adaption and change rather than selection and competition.

Basic definitions of co-evolution are relatively homogeneous across both the natural and social science literature, converging in the sense that two systems or entities co-evolve when they have a causal influence on each other's evolution [17]. However, interpretations and applications of the concept of co-evolution vary.

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E. Mitleton-Kelly (ed.), *Co-evolution of Intelligent Socio-technical Systems*, Understanding Complex Systems, DOI 10.1007/978-3-642-36614-7_3,

Interpretations range from the "specific, reciprocal, simultaneous evolution of traits between two closely related species" to "diffuse coevolution, meaning the adaptation of species to multiple features of their biotic and physical environment" [14, p. 708].

Co-evolution is a dynamic that has been most applied and explored in the field of evolutionary biology, however the concept has also been extended into diverse fields in the social sciences, applied as eithern an illustrative metaphor or as an interpretive frame that enables analysis of complex evolving phenomena. While the term was originally used only with reference to relations between biological species, it has now come to be used in reference to analogically similar dynamics between complex actors or systems that co-evolve [41]. This literature review focuses on the social sciences literature rather than natural sciences literature, and focuses on extended analyses of co-evolution as a dynamic of concurrent development and interaction, rather than its use in any metaphorical sense.

2 Co-evolution in the Social Sciences

Co-evolution now has a large range of applications in socio-economic contexts [31]. When applied within the social sciences, co-evolution usually refers to social co-evolution: the reciprocal evolution of two or more social systems or actors [18] and more specifically, as **reciprocal influence which changes the behaviour of the interacting entities within a social ecosystem** [26,29]. It has been used across a large range of disciplines such as computer science, economics, organizational theory, anthropology, archaeology, geography, history, sociology, and environmental sciences. It has also been used in more specific applications such as in IT legacy systems [25], and mergers and acquisitions [27,28]. Co-evolution can also refer to the reciprocal evolution of technologies and institutions, behaviours and institutions, populations of industries and universities, populations of producers and consumers (supply/demand co-evolution), organisations and their environments [18].

McKelvey [24] describes how various disciplines in the social sciences have been aware of the phenomenon of co-evolution without necessarily describing it using that term. For example, social psychologists have studied in detail the co-evolution of member attitudes and group norms, sociologists have observed the interaction and co-evolution of formal and informal systems in organizations, and economists have analysed the interaction between the behaviour of firms in creating industries and industry effects on firms [24]. Kauffman [19] argues that co-evolution is the central dynamic of all self-organizing behaviour. It allows dynamic system change to occur, and allows innovative structures to emerge.

Mitleton-Kelly was one of the first complexity theorists to apply the concept of co-evolution within the social sciences. She introduced the concept to the IT community in the UK in the late 1990s when it was the central concept of two EPSRC-funded (Engineering and Physical Sciences Research Council, UK) projects on IT legacy systems. The projects were part of the 'Systems Engineering for Business Process Change' EPSRC Research Programme. The concept is used in most of her publications, and specifically in [25, 26, 27, 28] and [29], in a wide range of applications from IT legacy systems, to mergers & acquisitions and organisational transformation. In 2011 it was also applied to a study on disaster risk reduction in West African States.

McKelvey also applied this term to organisational management and he outlines five basic types of co-evolution, each involving a different relationship between the interacting and evolving entities, providing an example of how this type of co-evolution may operate in the social world [24, p. 3]:

- Co-evolution between the mutation or change rate of an entity and its environment: "The more the Internet develops the more people develop Internet skills; the more they develop their skills the faster the Internet develops, and so on".
- Predator vs. prey co-evolution: "The faster large firms buy up start-up firms, the faster start-ups and IPOs materialize; the more start-ups and IPOs there are, the more large firms can buy them up, and so on".
- Super-normal co-evolution: "The more that firms see MBAs as preferred, the more MBAs will be hired; the more MBAs are hired, the more they will tend to prefer hiring additional MBAs, and so on".
- Co-evolution, restricted population size and inbreeding: "The more a small discipline uses its members as referees the more narrowly restricted are the ideas in their papers – the more intellectually inbred it is; the more restricted are the ideas (the more inbred), the more narrowly the membership allowed into the population, and so on".
- Symbiotic co-evolution: "The more that a large firm hires surrounding suppliers, the more they survive and grow; the more that the suppliers survive and grow, the easier it is for the large firm to survive and grow in its competitive context, and so on".
- Macro and micro co-evolution: A firm's ability to effectively macro co-evolve with competitors depends on how its internal micro co-evolutionary processes are progressing.

Use of the concept of co-evolution in the social sciences can be organised into four main research clusters: (1) evolutionary economics, (2) socio-technical systems analysis, (3) human culture and cognition, and (4) socio-ecological evolution. These four fields comprise the bodies of literature that have applied co-evolutionary analysis in the most rigorous and extensive manner, and the remainder of this chapter will review this literature in turn.

3 Co-evolution in Economics

Research that approaches economic analysis from a co-evolutionary perspective examines the mutual interactions and adaptations that occur between the market, relevant social and economic institutions, and the operations and growth of companies or organisations. For example, within the established field of evolutionary economics, co-evolution is defined by one article as the dynamic interaction and developmental interplay between industrial sectors, institutional frameworks, networks and structures of agglomeration, "or, more simply, between firms and dimensions of their social and economic environments" [41, p. 282]. Similarly, co-evolution is now used in organisational science to describe both the behaviour of agents within organisations and the interaction of organisations with the wider environment they are embedded in [24].

Lewin and Volberda [21] propose that research into economic and organisational co-evolution should incorporate the following suggestions:

- To study organisational adaptations over a long period of time;
- To examine organisation adaptation within its historical context;
- To consider multi-directional causalities within and across organisations as well as between and across elements of the economic system;
- To incorporate mutual, simultaneous, lagged and nested effects of co-evolution, rather than just immediate or progressive adaptions;
- To incorporate analysis of the changes that occur at different levels of the organisation;
- To accommodate economic, social, and political macro-variables.

Prud'homme van Reine and Dankbaar [34] incorporate many of these research concerns, using the concept of co-evolution in reference to the interaction between corporate cultures and regional cultures. The paper investigates why some geographical and cultural regions in Europe are able to respond and adapt to change by evolving in line with new development paths while others remain locked in traditional patterns. The authors argue that under certain conditions, interaction between corporate cultures and regional cultures can become a virtuous circle, in which corporate performance and regional performance reinforce each other. Cultural change is a result of the interaction between companies and regions when tensions such as that between regional embeddedness and openness to outside influences are negotiated successfully: "Successful regions are regions that are handling the potential tensions in a balanced way. This requires mutual orientation in the actions of companies and regional actors and the development of change competencies on both sides" [34, p. 1865].

In the context of the economy, Arthur [3] argues that economic forms co-evolve with the behaviours of individual economic agents and group entities. Elsner [11] also describes the co-evolution of economic institutions and company/firm sizes, arguing that both have causal impact on the other. The economy emerges out of the interactions of individual agents whose behaviour constantly evolves, and whose strategies and actions are always adapting in turn to economic structures and rules [4].

A similar dynamic is reported by Song and Thakor [38], who look at the co-evolution of banks and markets, focusing on the way the structures and strategies used by banking finance systems influences development in the 'real' sector and vice versa. While the dominant view is that banks and markets compete, with development in one sector occurring at the expense of development of the other, Song and Thakor argue that they in fact mutually co-evolve. They posit that economic analysis needs to focus on the relationship between markets and banks, rather than just focusing on one entity’s impact upon the other, as banks and markets evolve in tandem with each influencing the other. Developments in the credit screening strategies used by banks enhance the credit quality of borrowers going into the market, therefore increasing confidence and capital market investor participation. This allows the market to evolve, which in turn benefits banks by reducing the cost of bank equity capital and providing incentives for banks to hold more capital. “Bank evolution is thus stimulated as banks consequently serve previously unserved high-risk borrowers” [38, p. 1021].

Fatas-villafranca et al. [12] propose a co-evolutionary model to describe the simultaneous development of companies in science-based industries and their national university system. The success of technology companies on the international market often has impact on their domestic institutional environments, including the creation of research universities, the establishment of new disciplines of study, and the formation of publicly funded agencies with a technological or industrial focus. The authors suggest that the development of electricity, developments in organic chemistry and biotechnology, and the computer and IT revolution all have produced such impacts. The competence of universities and the resources available to them for research and innovation in these fields have a reciprocal impact on the development of the science-based companies, thus the institutional performance of both sectors – academic and industry – coevolves. The combination of scientific competence and institutional responsiveness is also central to Sæthera et al. [36] explanation of why Norway has benefited from its rich natural resources in comparison to other resource-based economies which have experienced a less positive path of development. The authors argue that Norway has formed a well-functioning national innovation system through the co-evolution of industry, knowledge organisations and national policy in the petroleum and aluminium sectors.

Mitleton-Kelly [27,28] developed the notion of *co-evolutionary integration*, when discussing mergers and acquisitions (M&A). She describes two cases with two different enabling environments, a successful and a dysfunctional environment; the former facilitated co-evolutionary integration post-M&A between the acquiring partner and the acquired, while the latter inhibited it. The paper analyses the factors that contribute to successful co-evolutionary integration, placing emphasis on the co-evolutionary dynamics.

Increased use of agent-based models in investigating co-evolution, (rather than the traditional biological examples) have uncovered some additional factors that must be taken into account when assessing the way that human organisational processes evolve [20]. For example, the knowledge and skills of older people can be passed down to younger people, or that of outgoing or long-term employees to newer employees, affecting the change and adaptation process. Human agents within a system may change their intentions, goals and strategies, in turn changing the way the system co-evolves in line with these goals and as a response to these strategies.

4 Co-evolution within Socio-technical Systems

The concept of co-evolution has also been used to inform analysis of information systems development. In fact, much of the research on co-evolution within socio-technical systems has focused on the development of effective information management systems within organisations and corporations. Literature in this area focuses on the "mutually constitutive role of Information Systems in shaping organisations and of organisations in shaping Information Systems" [20, p. 37]. This research emphasises that continual change is a fundamental factor in the co-evolution of socio-technical systems [7, 8, 29].

According to Kim and Kaplan [20], previous literature on information systems development has focused on implementation processes, technological resistance on the part of employees, and misalignment between the technological product or solution and the needs of the organisation. This focus, while generally useful, fails to take into account "the contextual and mutually constitutive nature of systems and organisations during Information Systems engagement, thereby ignoring the co-evolutionary phenomena that drive both in new, and largely unanticipated, directions" [20, p. 36]. On the contrary, implementing an information system is a co-evolutionary process in which the software system, the information technology provider or specialist, the organisation itself and its constitutive employees are all forced to continually adapt to a context that changes by the various actions of one another [20].

Other studies that approach information systems development from a co-evolutionary perspective agree with the central thrust of these findings. Benbya and McKelvey[7]) state that more effective information system design and operation can be achieved through a combination of top-down 'official' systems design and bottom-up 'emergent' co-evolutionary adaptations to user requirements. Information systems are emergent by nature, and need to respond to rapidly changing organisational demands and user requirements [8]. Traditional top-down, engineered approaches will be inadequately static, the authors argue. Managers should see information system design projects as 'complex adaptive systems' in order to deal with evolutionary complexity. To deal with unexpected contingencies, emergent goals and imperfect knowledge of current and future requirements, information system design should be seen as an ongoing, co-evolutionary process: "Information system alignment is not an event but a process of continuous adaptation and change" [7, p. 20].

An earlier paper [25] had anticipated these findings. The paper focuses on the enabling environment or infrastructure that facilitates co-evolution, and by so doing, helps to reduce the problem of IT legacy systems. The paper argues that 'legacy' is not solely a technical issue (p. 164) but a socio-technical one; legacy is a gap between the business needs and the organisation's technical capabilities (p. 168). It concludes that by "encouraging co-evolution (as opposed to the pursuit of separate evolutionary paths) between the domains [i.e. the information systems (IS) and business domains] requires an enabling infrastructure which provides the conditions for self-organisation, emergence and exploration of the space of possibilities". This insight highlights that co-evolutionary dynamics involve other principles of complex systems, such as self-organisation, emergence and the exploration of the space of possibilities. These dynamics have not been adequately explored in the literature.

The paper studies a specific case and looks at "reciprocal interactions among agents at all levels of analysis" both at "the micro level of interaction between individuals and between individuals and artefacts (IT systems) and the macro level of interaction between the business and IS domains as well as between the organisation and its environment" (p. 165).

Interactions are based on relationships between the interacting entities and the paper emphasises that these relationships are not simple. "In human systems, co-evolution in the sense of the evolution of interactions places emphasis on the relationship between the co-evolving entities. The study, therefore, focused on the relationship between the business and IS domains, and explored the assumption that the degree, intensity and density of interaction between the two entities affect the rate of co-evolution between the two domains." (p. 178) The conclusion is therefore that an enabling environment not only facilitates co-evolution but can also influence its rate.

Other research has taken a more birds-eye view of technological-social co-evolution. D'Hondt et al. [9] have applied the idea of co-evolution to their analysis of the relationship between computer hardware and software, web browsers and web applications, and computer operating systems and applications. Changes in the first entity in any of these three pairs creates new possibilities and features which are reflected in the second, often then creating new demand for further development. Evolution in one is accompanied necessarily by corresponding evolution in the other.

Other studies have looked at the influence of government policy on the evolution of socio-technical systems. Aarden et al. [1], for example, focus on the co-evolution between genetic diagnosis technologies and government policy that deals with its implementation. They show that co-evolution between pre-implantation genetic diagnoses (PGD) technologies and policy has led to specific technological arrangements in three countries: a very specific, technical version of PGD to deal with restrictive legislation in Germany, well-funded PGD with insecure indications in the Netherlands, and PGD with secure indications but uncertain funding in Britain.

Axtell [5] uses co-evolution as a framework to illustrate how increasing IT capabilities are reshaping the social sciences and vice versa. He proposes that one IT development in particular – multi-agent systems – could fundamentally alter the ways in which social science models are built, explored and evaluated. Ideas from fields of social science such as economics, sociology and game theory, particularly insights about strategic behaviour and networks, are also shaping the multi-agent systems models of computational science: "the rapid development of information technology has sparked concomitant developments in social science methodology, and obversely, computer science is being invigorated today by major research areas in the social sciences—e.g., market processes, auction design, social networks" [5, p. 3].

In another paper Axtell [6] describes a similar co-evolutionary dynamic between engineering systems and the social sciences. In the past the role of the social sciences in new engineering development and invention may have been limited to the design of user interfaces, bringing new products into the market, and enabling more sophisticated and large scale methodologies for investigation of the social world. However, increasingly engineering systems are designed and built using explicit social ideas and conceptions from the social sciences in a much needed 'science of interaction'. [6, p. 2] states: "Instead of having sharply demarcated domains of inquiry—technology on the one hand, its use by humans on the other—we are now confronted by the deep interconnectedness of the technological and the social, a phenomenon that is sure to become ever more important in the foreseeable future".

5 Co-evolution in Human Culture and Cognition

The interaction between the evolution of human cognition and cultural evolution has been long established in anthropological literature [30], however, not until recently using the specific terminology of co-evolution as an analytical frame. The human mind, cognition and perception have evolved influenced by the cultural context in which they are embedded within [18], and human culture has also been shaped by shifts in cognitive and perceptive capacity. A small number of researchers from the fields of cultural and cognitive anthropology, cognitive science and cultural psychology have all utilised the concept of co-evolution to analyse this complex dynamic to good effect.

Beat and Wettstein [39] use the concept of co-evolution in cultural psychology to analyse the relationship between the individual and culture, and the person and their environment. The authors identify three different types of human system – biotic, psychic and social – each of which are linked to particular operational processes. They suggest that culture should be conceptualized as the enduring social patterns of behaviour that are produced by a process of co-evolution of the individual psychic and social communicative systems.

Murray [30] describes how games have had an important role in shaping the human mind and in turn cultural forms, by preserving and expanding adaptive cultural patterns, and developing symbolic thinking. Games are intrinsically social, and are a foundational element of human culture, that allow individuals to engage in purposive, focused play, learn from others, and explore symbolic action and meaning. From a cognitive development perspective, games contribute to infants' development of language and recognition of others as agents with their own goals and purposes. Through a dual dynamic of presentation of the self and expression of social cohesion in games, games have contributed to human social organisation and developments in causal thinking, which in turn leads to more complicated games. Murray argues that digital games should be understood as extending these same roles and functions, using the new and developed technologies of the computer and

Internet. Games are instruments of cognitive evolution, which in turn evolve and become more complex and demanding as cognitive skills and technologies develop.

Jefarres [15] also discusses the co-evolutionary dynamic between the human mind and the tools and technologies that people create. He warns against interpreting archaeological evidence of cultural products such as tools as simply the product of human cognition: the human mind is as much a product of the tools used by humans as these tools are products of human intelligence. He states that "we should view archaeological evidence as one half of a feedback loop between the world and the cognition of our evolutionary ancestors. Tools and minds co-evolve..." [15, p. 504]. Tools can also be the cause or trigger of cognitive development, and furthermore, the use of tools and technology changes the environment which will trigger adaptive changes in human cognition – often to create new tools and technology.

Kallis and Norgaard [18] state that another major field in which co-evolutionary analysis has been applied is gene-culture co-evolution. They make reference to a number of examples of particular aspects of the mutual evolutionary impacts that human culture and genetic make-up have had on each other, including the co-evolution of lactose-tolerance with dairy farming, incest taboos with brother to sister mating and sickle-cell anaemia with forest clearing practices. "Cultural learning, imitation and experimentation shape human behaviors; they are conditioned by human biology, and in turn change it" [18, p. 691].

6 Human Ecology and Ecological Economics

As the term co-evolution was first coined within the scientific discipline of biology, it has been widely applied in studies of ecology. Social or human ecology and ecological economics are fields that necessarily straddle both the natural and social sciences, and there is a growing body of literature applying co-evolutionary analysis to the issues of ecological sustainability and the relationship between society and the natural environment [41]. The importance of co-evolution for these fields is summed up by Kallis and Norgaard: "At an epistemological level coevolution offers a powerful logic for transcending environmental and social determinisms and developing a cross-disciplinary approach in the study of socio-ecological systems" [18, p. 690]. Evolution in the human social system affects the natural bio-physical environment, which in turn affects evolution in the social system [18]. Examples include the development of fossil fuel resources, methods of generating power, and energy-intensive cultural practices.

Ecological economics is an interdisciplinary field of research that focuses on the co-evolution of human economies and natural ecosystems. A Springer Volume from 1994 titled *Coevolutionary Economics: The Economy, Society and the Environment* explored the human economy and its co-evolutionary relationship with the natural world and the impact of human actions on the biosphere. It states "The new fields of ecological economics and evolutionary economics can help us understand the relationship between the economy, society and the environment and may help us to formulate effective policies to manage these changes" [13].

A key theorist in this field, Norgaard has developed a co-evolutionary framework in a number of papers to explain the reciprocal evolution of sociosystems and ecosystems, driven by processes of mutual selection [32,33]. Gual and Norgaard [14, p. 710] state that ecological economists can use co-evolutionary thinking "to explore how the evolution of cultural systems affects and is affected by the overall biophysical system and, in particular, how it is literally modifying evolutionary processes (as conceived in the biosciences) guiding all living species". The evolutionary processes of the social and biotic systems are interdependent and interlinked, and require a common co-evolutionary framework of analysis to enable full understanding [14]. Evolving sociocultural systems are increasingly affecting their biophysical environment and evolving ecological environments increasingly also affect socio-cultural change. Biologists have traditionally focused on piecing together the process of evolution in environments undisturbed by human interaction, which "blinds evolutionary biology to the increasingly relevant processes of evolution in the context of human action" [14, p. 708].

Gual and Norgaard argue that a knowledge gap exists in how human action is affecting evolutionary processes and the links between cultural and ecological evolution that needs to be urgently addressed in order to incorporate greater understanding to human social and technological organisation. They identify three embedded systems: the biophysical, the biotic and the cultural, all of which evolve inter-connectedly and inter-dependently. The focus of co-evolutionary theory is the study of both what the basic units, characteristics and modes of this process of mutual evolution are, and how these processes relate to one another creating "the systemic coevolution that seems to be shaping life on our planet" [14, p. 711].

Specific examples of ecological co-evolution include: (1) co-evolution through systemic influence such as pollution of the biosphere; (2) co-evolution through consciously designed cultural products and processes, such as reciprocal changes in the genetic composition of pest populations and in agricultural practices and technologies, and the mutual adaptation of drug treatments and mutations of the HIV virus; and (3) forced co-evolution through genetic manipulation, such as the engineering of crops with higher production rates [14]. They make a distinction between more 'natural' forms of co-evolution and forms in which people have intentionally manipulated the biological evolution of other species, for example in the cases of domestication of animals or the genetic engineering of food crops. These cases still involve co-evolutionary dynamics, however must be analysed distinctively because of the element of intentional control.

The reciprocal influences between social evolution and biological evolution in the wider non-human environment are also highlighted by Kallis and Norgaard [18]. They cite co-evolution between pest populations and regulative strategies for the pesticide industry, fishing practices and fish populations, and viruses and medical practices as examples that have previously been explored in the literature. Their first example of pest populations is explored by Noailly [31], who looks at the co-evolutionary dynamic between agricultural pest management practices and changes in pest populations due to evolved pesticide resistance. As pesticide use has increased, an increasing number of pest species have developed resistance to these chemicals. The pesticide operates as a heightened form of natural selection, where genes that carry resistant traits are the ones that survive. The pest population eventually recovers as more individuals become resistant. The aim of Noailly’s paper is to calculate, using a co-evolution model, the optimum level of pesticide to use when taking into account adaptive economic and agricultural practices as well as adaptive pest population genetic evolution.

Social or human ecology is another interdisciplinary field related to ecological economics, that examines the relationship between humans and their natural, social, and built environments. Research from this field tends to focus on the ways that humans have negatively influenced the natural environment by triggering unsustainable evolutionary pathways. Sustainability research from this field has used the concept of co-evolution as an analytical frame in order to study “the dynamic mutual interactions between human societies and their natural environment” [41, p. 281] and identify sustainable pathways for co-evolution in the future. For example, Schellnhuber’s [37] ‘theatre world’ is a heuristic analytical model that represents possible pathways of sustainable development. It is presented as a diagram with a gradient of possible physical or ecological states of the globe on the one axis and a gradient of possible socio-economic conditions of human civilization on the other axis. Represented in the diagram between the two axes are all the nature/society co-evolutionary states possible. Global human society can be theoretically plotted at some point in this space, a point from which a certain number of co-evolutionary pathways are accessible. However, the space within which humans can subsist sustainably on this diagram is more limited than the possible pathways that are represented, as these include catastrophic possible worlds in which human socio-economic regimes have pushed global biosphere fertility rates to zero, an unsustainable situation for human society.

7 Additional Issues

McKelvey [24] stipulates a number of conditions which must be met for co-evolution to occur. Firstly, there must be **heterogeneous agents** within the system, as this provides the variation necessary for the adaptive selection crucial to evolution to occur. Agents in this sense can mean many entities, including people, groups, species, concepts, organisational processes, populations, companies, etc. Secondly, these agents must be capable of **learning** and adapting to circumstances in order to allow change, innovation, and therefore evolution to occur. Thirdly, these agents need to be **interacting and influencing each other** in order that mutual adaptation to one another’s behaviour occurs, as this dynamic is central to co-evolution as opposed to just evolution. Additionally, there is usually some higher constraint in place that the agents must adapt to, as well as an initiating event or stimulus that triggers the co-evolutionary process [24].

The events or stimuli that initiate co-evolution may be random and insignificant [23], such as the butterfly effect example famous to chaos theory [22]. The butterfly effect is a theoretical example of a hurricane's formation being dependent and contingent upon a butterfly flapping its wings weeks before in another part of the atmosphere. The butterfly's wing flapping represents a small change in the initial conditions at one point in a non-linear system that causes a chain of subsequent events that can result in large differences at another point of the system. Co-evolutionary systems are dynamic, and highly sensitive to initial triggers and conditions. Small fluctuations in these initial conditions can cause widespread divergent outcomes that are often difficult or impossible to predict. In complexity theory, a distinction is often drawn between complex systems and complicated systems: "Complicated systems, although composed of many intricate parts, can be understood as the sum of these parts. Complex systems, on the other hand, are comprised of populations of interacting entities where the overall system behaviour is not predefined but rather emerges through the interactions of its entities" [20, p. 37]. The entities within a co-evolutionary relationship are constantly adapting to one another's adaptations in a manner that makes any form of accurate prediction highly speculative, as spontaneous events and stimuli will continue to occur and shape the nature of co-evolution. As McKelvey states, "small behavioral effects can lead to informal group formations of considerable significance" [24, p. 4].

As a result of the dynamism and unpredictability of co-evolution, McKelvey [24] states that one of the key challenges facing complexity theorists is the factor of knowledge limitation. Co-evolution is unpredictable and non-linear, because evolutionary dynamics are reactive rather than predictive. However, contextual constraints can narrow or expand the range of outcomes produced through self-organisation [16]. These constraints can be managed, in theory, to speed or slow down the process of co-evolution as required. McKelvey calls these 'damping mechanisms', methods of "controlling the rate of coevolution, or shutting it down altogether" [24, p. 7].

Loss of agent heterogeneity is an important factor that can work as a barrier to co-evolution. Biologically, it has been shown that as species lose variety in their gene pool they lose their adaptive capability and can go extinct [24]. Likewise, in an organisational 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. According to Allen [2] managers should in fact ensure a level of 'excess' variety, because they cannot predict in advance what varieties of skills will be adaptively relevant. Diversity can however be difficult to maintain because of firstly, the tendency for individuals to form strong cliques that lead to groupthink rather than variety, and secondly, strong command and control systems in traditionally structured organisations or systems that reduce individual variations in behaviours [24].

Despite the increasing number of social theorists drawing on the concept of co-evolution in their research, its application in the social sciences has been both more ad hoc and more contested than in the natural sciences. As Gual and Norgaard state: "There is a well-developed, cohesive biological literature on the coevolution of species within ecological systems. . .The social science literature on the coevolution of components of social systems is noticeably less developed and far less cohesive than the biological literature. The social sciences have struggled with multiple, incompatible constructs" [14, p. 707].

In terms of generating policy recommendations, co-evolutionary theory is often ambiguous. Very little co-evolutionary theory has been used by social science researchers to make explicit policy recommendations, with the exception of sustainability researchers advocating that greater attention be paid to human impact on the biosphere and organisational management theorists providing recommendations to corporations. Yet many articles tend to assume that co-evolution is necessarily positive, and policies should support diversity and experimentation as these drive co-evolution forward [18]. For McKelvey, an ability to speed up co-evolutionary processes is a significant and sustained competitive advantage for groups, organisations and companies in the contemporary world. Changing environments themselves necessitate speedy evolution to keep up with dynamic contexts and demands. Co-evolution can be "the source of novelty, adaptation, and survival in a competitive, changing world" [24, p. 7]. However, as Cairns [43] states, co-evolutionary relationships can be either mutualistic or hostile to one or both parties. McKelvey [24] also warns that too much evolution can be disruptive or dysfunctional. Kallis and Norgaard state that, "coevolutionary outcomes are not necessarily beneficial in any particular sense and diversity or innovation may come at the expense of other social goals" [18, p. 697].

It may be more useful to see co-evolution as a neutral analytical frame that can determine what dynamics are at play in particular pathways of development. How to evaluate these pathways or future possibilities can then be explored depending on the goals of the particular piece of research at hand. Kallis and Norgaard [18]), for instance, specify that co-evolution is emphatically not a normative concept. Other authors [41] have pointed out that equating co-evolution with progress in social systems can imply dangerous forms of Social Darwinism. Co-evolution should be seen as a way of analysing a particular dynamic of pathways of development, rather than being associated with progress or a notion of 'survival of the fittest'. Co-evolution is "a value-free process of change" [18, p. 691].

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