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Untangling the Conceptual Issues Raised in Reydon and Scholz's Critique of Organizational Ecology and Darwinian Populations

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Abstract

Reydon and Scholz raise doubts about the Darwinian status of organizational ecology by arguing that Darwinian principles are not applicable to organizational populations. Although their critique of organizational ecology's typological essentialism is correct, they go on to reject the Darwinian status of organizational populations. This paper claims that the replicator-interactor distinction raised in modern philosophy of biology but overlooked for discussion by Reydon and Scholz provides a way forward. It is possible to conceptualize evolving Darwinian populations providing that the inheritance mechanism is appropriately specified. By this approach, adaptation and selection are no longer dichotomized, and the evolutionary significance of knowledge transmission is highlighted.

Keywords

adaptation, Darwinism, Lamarckism, organizational ecology, replicator-interactor

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1. Introduction

Inspired by population ecology and niche theory, organizational ecology was developed by Hannan and collaborators during the 1970s and 1980s to explain organizational diversity and the evolution of industry characteristics. Noted for its successful application to all manner of organizations, organizational ecology spawned an abundance of empirical research in management and strategy (Burgelman 1991), jobs and routines (Miner 1991), and industrial economics (Klepper 2002; Carroll and Hannan 2000).

Unlike Nelson and Winter (1982), who notably underplayed the Darwinian influence in their evolutionary approach, Hannan and Freeman (1989) explicitly aligned themselves with Darwin's theory. They embraced the Darwinian message that it is populations that partake in evolutionary processes, and they strongly rejected the traditional organization science approach, with its "Lamarckian" focus on organizational adaptation. The focus of their attention was on the dynamic, industry-shaping selection process.

It is this application of the selection process that has come under attack by philosophers of science Reydon and Scholz (2009).[1] In a powerful critique, they argue that organizational ecology is not a Darwinian research program and, moreover, that organizational populations do not have what it takes to participate in evolutionary processes. This paper challenges Reydon and Scholz on both counts.

The problem with organizational ecology is that it lacks an inheritance mechanism. There is no explanation for how knowledge concerning adaptive solutions to survival problems gets passed on. Pointedly, however, while its authors openly acknowledge their failure to articulate its explanatory mechanism, knowledge transmission is clearly presumed in the account. Accordingly, organizational ecology remains compatible with Darwinism and is more accurately described as an *incomplete* Darwinian account rather than a "non-Darwinian" account. Indeed this highlights a crucial aspect of the debate here where opposition between the two positions is seen as incompatible versus incomplete Darwinism.

On the key question of the Darwinian status of organizational populations, Reydon and Scholz conclude from organizational ecology's commitment to typological essentialism that organizational populations in general are not

[1]See also Scholz and Reydon (2010).

Darwinian. This author takes a different view. While abstract formulations may vary in their characterizations, scholars in philosophy of biology and elsewhere have convincingly demonstrated the generic nature of the core Darwinian principles of variation, inheritance (retention), and selection. Moreover, at a lower level of abstraction, generalized terms now exist that facilitate the conceptualization of Darwinian entities and processes in the socioeconomic domain. Through this prominent Darwinian formulation, it is now possible to speak of an inheritance mechanism in relation to knowledge transmission in the social arena and, accordingly, to speak in terms of evolving organizational populations.

Specifically, the important distinction between replicators and interactors (Hull 1988) now permits articulation of a Darwinian evolutionary selection process for organization scientists. It will be shown here how this distinction untangles the ontological and conceptual issues raised in Reydon and Scholz's critique of organizational ecology and reveals theirs to be a rather narrow formulation of Darwinism. Drawing on these conceptual advances, in an outline sketch, this paper shows how organization scientists can finally begin to construct evolutionary accounts that accommodate both selection and adaptation effects in the business world and account for the role of knowledge transmission.

The paper is organized as follows. Section 2 presents a brief overview of organizational ecology and outlines Reydon and Scholz's critique. Section 3 presents the main argument of the paper through discussion of the limitations of Reydon and Scholz's position, followed by an elucidation of the advances in the philosophy of biology they do not discuss. Section 4 considers the importance of knowledge transmission for evolutionary accounts in the socioeconomic domain, and section 5 proposes the way forward for organizational ecology via the replicator-interactor distinction. Section 6 concludes and suggests further lines of inquiry.

2. Organizational Ecology and Reydon and Scholz's critique

> The view that selection processes govern the dynamics of organizational diversity shades naturally into a Darwinian evolutionary position. (Hannan and Freeman 1989, 17)

Mindful of the deliberative behavior and adaptive potential of the firm, the evolutionary position traditionally adopted by organizational scholars from

biology is "Lamarckism"[2] (Levitt and March 1988) or, more specifically, the idea of Lamarckian inheritance. This is because Lamarckism admits the possibility of the inheritance of acquired characteristics, in other words, within-generation inheritance as opposed to intergenerational inheritance. Undeniably, the processes in the business world that involve individual organizations adjusting strategy, adapting to the prevailing conditions, changing their form, and going on to reproduce that new form are Lamarckian, as the term is generally understood by evolutionists (Mayr 1976).[3]

Note that "adaptation" here refers to adaptation of the individual organization, not the population, to its environment. In biology, adaptation and natural selection are intertwined processes, and, thus, the technical term there has a very different meaning.

For Hannan and Freeman (1977, 1989), organization theorists have been misguided in their fixation with the individual organization and traditional Lamarckian adaptation explanations of the evolution of organizational forms. This encouraged a narrow "focal organization perspective" as well as unrealistic assumptions about the flexibility of firms and the adaptive capabilities of managers. They argue that the analysis has been stymied by its lack of contextual environmental considerations and that causality has been misconstrued.

Hannan and Freeman sought to redress the balance by portraying organizations as complex systems that in reality have strong limitations on flexibility and speed of response. They constructed a theory that they believe more properly accounts for the competitive industry environment of other organizations and explains how "macro-social" forces (social, economic, political) affect their changing structures. In this view, the diversity of organizations is explained not through the strategic decision making of managers but through the recognition of these inertial pressures on organizations and the measurement of "vital rates," such as rates of founding and entry into a population,

[2]The theory is attributed to the French evolutionist Jean-Baptiste de Lamarck (1809) because of his popularization of the idea of the inheritance of acquired characteristics. In this view, changes that are acquired during the lifetime of an organism and that result from interaction with its environment are changes that can be inherited by the offspring of that organism. In other words, phenotypic changes or "adaptations" are somehow transmitted to the organism's genotype and subsequently passed on to the next generation in reproduction.

[3]Albeit that Lamarckism is discounted in biology, notwithstanding a controversial and minority view in biology to the contrary (Steel et al. 1998), which would not, in any case, affect the argument about the validity of Lamarckism in the social sphere.

the rate of change in strategy and structure, and the rate of failure or mortality (1989, 201). Since a broad social change can affect any one of these rates, it is these "macro-social" forces that shape organizational diversity and determine the characteristics of the population or industry.

In framing their agenda, Hannan and Freeman posed the question "Does change in major features of organizations over time reflect mainly adaptation or selection and replacement?" (1989, 13) and argued unreservedly for the latter. For organizational ecologists, "there is no reason to presume that the great structural variability among organizations reflects only or even primarily adaptation" (1977, 930). Change in organizational forms is the result of selection processes operating on populations of "structurally inert" organizations. Thus, in contrast to Nelson and Winter's influential evolutionary approach,[4] Hannan and Freeman propose a "top-down" explanation of evolutionary change that does not account for firm-level "adaptive" change. In other words, whereas the former acknowledge that population-level changes are also influenced by the variety brought about through mutations (learning, imitation, random errors), Hannan and Freeman see evolutionary change explained principally through the selection and retention of new organizational forms. Indeed, this selection bias brought about a significant reorientation of theory, involving a shift in focus from the individual firm to the *population* of firms as the proper unit of analysis

Coupled with assumptions of inertia and managerial irrelevance is the limiting view that the prevailing variety for organizational ecology is traced to the variety of organizational forms at founding. Following Stinchcombe (1965) and the idea that cohorts of organizations are imprinted with social, cultural, and technical features common to the environment at founding and that these are highly resistant to change, Hannan and Freeman (1989, xiii) assert, in an extreme version of the Darwinian position, that "current characteristics of populations of organizations reflect historical conditions at the time of founding rather than recent adaptations."[5] Accordingly, in pursuance of the diversity question "Why are there so many (or so few) kinds of organizations?" (1977), organizational ecology focuses on differential rates of entry, or "births" (new founding, mergers, division of existing organizations), and exit, or "deaths" (disbanding, acquisition), for organizations, since most

[4]Which confusingly, while featuring the core Darwinian principles of variation, inheritance, and selection, is labeled "Lamarckian" by its authors (Nelson and Winter 1982, 11).
[5]Again, note that Hannan and Freeman allude here to the firm-level "Lamarckian" understanding of adaptation.

variability in the core structures of organizations comes about through the creation of new organizations and the demise of existing ones (1989, 12). Other sources of variety, such as the learning and development that occur over the lifetime of individual firms, are not accounted for in the analysis. To be sure, adaptation is effectively decoupled from selection in this approach.

2.1. Reydon and Scholz's Critique

Although presented as a Darwinian approach and widely acknowledged as such, philosophers of biology Reydon and Scholz (2009) argue that organizational ecology is not a Darwinian research program. In a paper that focuses on its flawed ontological foundations, they set out the reasons why organizational ecology's explanatory strategy does not work.

Organizational ecology, Reydon and Scholz argue, is not evolution in the proper sense; it does not include any entities that actually evolve; there is no principal causal mechanism to explain diversity; and its selection process is not "Darwinian." This ultimately means that it cannot explain organizational diversity. Significantly, as a result of their analysis, they come to the view, challenged here, that populations in general "do not have what it takes to participate in evolutionary processes" (408).

Reydon and Scholz clarify the complex and foundational ontological reasons why, strictly speaking, organizational ecology cannot be classified as Darwinian. Their critique offers an incisive account of the contrast between the typological essentialism evidenced in organizational ecology and the little-understood population thinking approach, which is indispensable for an evolutionary selection process. Accordingly, they demonstrate that the selection process portrayed in organizational ecology is not an instantiation of a Darwinian selection process and thus does not explain a Darwinian *evolutionary* process.

Other notable merits of Reydon and Scholz's critique include substantiation of the claim that variation and inheritance are necessary conditions for the existence of Darwinian populations and the related claim that inheritance cannot be separated from selection. Indeed the main conceptual issues arising for applications of the core Darwinian principles to socioeconomic phenomena are clearly identified.

In a review of these crucial aspects of evolutionary theory, it is shown below how the evolutionary dynamic in organizational ecology falls short of a Darwinian evolutionary selection process and highlights where this author is in agreement with Reydon and Scholz. This section is followed by an evaluation of the limitations of their position.

Typological Essentialism versus Population Thinking. The foundational problem for organizational ecology emerges from the theory's conceptualization of variety, the origin and replenishment of which it fails to account for in its typological view of organizational populations as "sets" or "classes," which, by definition, cannot change. While Reydon and Scholz do not deny that populations thus conceived will display variation among types, they stress the critical difference in conceptualization of populations when it comes to explaining *evolutionary* change by Darwinian natural selection. In a response to Lemos (2009), who sought to defend the Darwinian credentials of organizational ecology, they explain,

> It is a mistake to define organizational populations typologically—as sets of organizations with a shared form—because this does not allow for the variation between the members of a population that is required for evolution to occur. (Scholz and Reydon 2010, 506)

On the contrary, in their elaboration of the variation and inheritance link, they explain that populations need to be defined in terms of "structural cohesion" or "lineages." Population thinking was a profound challenge to the typological essentialism that characterized the thinking of Darwin's own era. This was committed to the notion of fixed, immutable, or ideal types and thus logically prevented the conceptualization of evolutionary change (Mayr 1959).[6] Through this approach, Darwin presented an entirely new way of thinking (Mayr 1976), creating a philosophical schism that was barely perceived at the time and that even today is underappreciated by evolutionary scholars (Hull 1990; Scholz and Reydon 2010). Darwin dismissed the prevailing analytical priority of representative types and introduced the population thinking perspective that instead privileges variety, the critical source of change in evolving systems.

For essentialists, entities are grouped according to a fixed number of typical traits that describe their essence. The typical or average type is central to the analysis. For population thinkers, however, the emphasis is on variable populations of entities in which each individual entity is *unique* and variety is paramount.[7]

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[6]See Ariew (2008) for excellent elucidations of the contributions of Mayr and Sober to our understanding of population thinking.

[7]"For the typologist the type (eidos) is real and the variety an illusion, while for the populationist the type (average) is an abstraction and only the variation is real" Mayr (1976, reprinted in Sober 2006, 327).

In organizational ecology, organizational populations are conceived of as "sets" of organizations and are defined in terms of their "structural similarities," in other words, their shared properties and behaviors. Accordingly, organizational ecology is unable to express a Darwinian evolutionary process. The problem with typological essentialism is that variations from type are perceived as deviations or noise in the system and are thus discounted in the analysis. Whereas with population thinking, variation serves as the essential fuel of evolutionary change, without which there could be no selection process. Reydon and Scholz explain the significance of this distinction (2009, 423):

> The point, then, is that defining populations in terms of structural similarities cannot allow for *evolutionarily significant variation* in populations. Typologically defined populations can change to a limited extent and new varieties of existing basic forms can come into being, but no entirely novel forms can come into being in the population. Once an entirely novel form comes into being, it falls by definition outside the population, so the population has not evolved.

What Reydon and Scholz emphasize here is the critical role of variety as the driver of change in a natural selection process. The restrictive typological view of populations as sets of immutable types that exclude novel forms does not account for the requisite sustained replenishment of variety upon which selection needs to work and thus actually prevents the conceptualization of change over time. Although in key works, Hannan and Freeman (1977, 933; 1989, 15) head up passages on population thinking, signaling its importance for evolutionary theorizing, this is not to explain it in the terms understood in biology. And while their approach does indeed accord with a tractable general selection theory (Knudsen 2004), Reydon and Scholz are right to conclude that it cannot be described as a Darwinian evolutionary selection process.

The following section explains the crucial links between variety and inheritance in the populationist's definition of an evolving population and prepares the analysis here for the role of the replicator-interactor distinction in facilitating conceptualization of the interlinked processes of natural selection.

Variation, Inheritance, and Darwinian Populations. Evidently, a key failing in organizational ecology is the underestimation of the role of variation. To understand evolutionary change, we need to pay far more attention to the processes that generate and *regenerate* variation—in other words, variation and *its* inheritance (Mayr 1982). The replenishment (replication and inheritance)

of variety and the creation and dispersion of variety (innovation, entrepreneurial activity, and "copying errors") are all critical aspects of any socioeconomic evolutionary story. And this leads here to the complex interrelationships among Darwin's core principles of variation, inheritance, and selection.

In biology, the gene is the heritable entity that explains replication and the replenishment of variety in the system. Through sexual reproduction of the organism, the gene pool recombines to provide new varieties of organisms in each successive generation. Selection then acts on this variety. As Mayr (1982, 163) explains, "New gene pools are generated in every generation, and evolution takes place because the successful individuals produced by these gene pools give rise to the next generation." The continuous restoration of variability is facilitated through the heritable replicating gene. Evidently, organizational ecology needs to incorporate a replicating heritable entity. In the following evaluation of organizational ecology, Reydon and Scholz (2009, 422; my italics) arrive at the issue of inheritance and specify how this helps define a Darwinian population:

> [The] conception of populations as sets profoundly differs from how biologists conceive of the nature of populations and species…from an evolutionary perspective, species and populations are not to be understood as sets, classes, or aggregates of organisms that belong to the same population because of shared properties. Biological populations are usually conceived of as organized systems of organisms (e.g., Hull 1980, 322-24; Ghiselin 1997, 15) *that interact with each other in various ways and are held together in the population by way of various mechanisms*, such as reproduction, gene flow, social interactions, division of labor, mutual protection, intra-and inter-population competition for mates and resources, reproductive isolation from other populations, etc.

Thus, in terms of defining the evolving entity, Reydon and Scholz rightly observe that *structural cohesion*, as opposed to shared traits, is the way to establish membership of a population in an evolutionary selection process. And this rests on the reproductive interactions within the "unit of organization" and resulting common descent. In their illustration of the Darwinian conceptualization of populations as *real* entities in nature, conceived of as "units of organization," they explain that "the members (or more accurately, parts) of a system are parts of that system only by virtue of their interactions with other parts of the system" (2009, 423). This understanding of structural cohesion is extremely important and explains why typologically defined populations cannot evolve.

It is worth repeating Reydon and Scholz's citation from the eminent philosopher of biology David Hull (1978, 341), whose notion of "lineage"

explains structural cohesion and spells out the significance of reproductive and genealogical relations for a definition of Darwinian populations:

> The relevant organismal units in evolution are not sets of organisms defined in terms of structural similarity but lineages formed by the imperfect copying processes of reproduction. Organisms can belong to the same lineage even though they are structurally different from other organisms in that lineage. What is more, continued changes in structure can take place indefinitely. If evolution is to occur, not only can such indefinite structural variation take place but also it must.

Neatly capturing Darwin's meaning of descent with modification, Hull's lineage concept illustrates the link between replication and inheritance and highlights the role of the heritable unit and knowledge transmission in the evolutionary process.

In summary, Reydon and Scholz's critique concurs with the prevailing Darwinian view regarding the non-Darwinian status of organizational ecology's selection process. Most welcome about this contribution is its forensic examination and clear articulation of the complex ontological reasons for this and how these illuminate the theory's problems. However, as will be argued, the authors go on to draw a contentious conclusion about the Darwinian status of populations in general (2009, 431):

> Our criticism . . . hinges on an ontological matter: the entities that organizational ecologists claim participate in organizational evolutionary processes (i.e., organizational populations) are not sufficiently similar to the entities that participate in biological evolutionary processes, hence the two processes are not sufficiently similar to be described by the same model or similar models.

The position here also hinges on ontological issues, not least of which is the claim that social evolution is Darwinian. There is now widespread agreement about the abstract nature of the principle of natural selection (Okasha 2006). In the formulation described as "generalized Darwinism," Hodgson and Knudsen (2010) use the term "complex population systems" to denote the kind of populations that *are* sufficiently similar to those that participate in biological evolutionary processes and thus can be described by the same Darwinian model:

> Complex population systems contain multiple (intentional or non-intentional), varied entities that interact with the environment and each other. They face immediately scarce resources and struggle to survive, whether through conflict or cooperation. They adapt and can pass on information to others, through replication

> or imitation. Complex population systems are found in both the natural and the social domains. An economic example is an industry involving cohesive organizational entities such as business firms.

In this formulation, from the highly abstract core principles of variation, inheritance, and selection, scholars derive general principles and concepts that are sufficiently general to span the common features of both domains. However, it is important to observe here that they do not claim "maximal generality" for these (Hodgson and Knudsen, 2012). Note that complex population systems are consistent with Reydon and Scholz's "units of organization" as well as with Hull and Ghiselin's notions of structural cohesion.

3. The Limitations of Reydon and Scholz's Critique

The view here is that while Reydon and Scholz make many accurate claims, their conclusion about organizational populations is contentious because it does not appear to take account of the replicator-interactor distinction raised in the philosophy of biology that facilitates their conceptualization. This is what limits their Darwinian formulation. Rather than just focusing their critique on organizational ecology's set-theoretic view of populations, they go on to reject the idea that organizational populations *in general* can be perceived as evolving Darwinian entities (2009, 408, 411).

In a defense of organizational ecology's Darwinian credentials, Lemos (2009) proffered an immediate but ultimately unpersuasive challenge to Reydon and Scholz's critique, based as it was on the resolute view that sets can be conceived as real entities.[8] This was dismissed by the authors in a rejoinder (Scholz and Reydon 2010) where they reasserted the need for a population thinking approach for Darwinian evolutionary selection processes.[9]

[8]As far as this author is aware, this has been the only other published challenge to Reydon and Scholz's paper. Although sympathetic to Lemos's (2009, 474) view regarding the moot point of "how thoroughly Darwinian a theory must be to be justly labelled a 'Darwinian' theory," this author concurs with Reydon and Scholz's insistence on the need for a population thinking approach.

[9]As Scholz and Reydon explain (2010, 506), Lemos defends a Spencerian "survival of the fittest" interpretation of evolution, which overlooks the evolutionary significance of differential reproduction: "evolution does not consist in the *survival* of the *best*, but in *more reproductive success* for the *better* adapted as compared to the less well off." Correspondingly (507), they disagree that the variation in typologically defined populations is significant from a Darwinian evolutionary perspective.

This paper presents a much more robust challenge to Reydon and Scholz that disputes their claims about the non-Darwinian status of organizational ecology and organizational populations in general. Overlooked for discussion by both papers is the extensive work on the replicator concept (Sterelny, Smith, and Dickison 1996; Godfrey-Smith 2000) and the replicator-interactor distinction (Hull 1981, 1988; Brandon, 1990, 1998; Hodgson and Knudsen, 2004, 2008, 2010). Drawing on these and other works, the argument presented here is that it *is* possible to conceptualize evolving Darwinian populations providing that they meet the requirement for structural cohesion and the inheritance mechanism is appropriately specified.

As will be elaborated, the generalized replicator and interactor concepts together present an important conceptual tool that untangles the conceptual issues raised in Reydon and Scholz's critique. Through its adoption, adaptation and selection processes are no longer dichotomized, and the evolutionary significance of knowledge transmission in the social realm is highlighted.

3.1. Beyond Reydon and Scholz's Narrow View of Darwinism

From a modern Darwinian perspective, organizational ecology is best described as an incomplete or partial evolutionary account (Levinthal 1991; Bruderer and Singh 1996) that nonetheless remains compatible with Darwinism.[10] The main problem with organizational ecology, which derives from its downplaying of adaptation in favor of selection, is its lack of an inheritance mechanism. Although an important knowledge transmission role for routines is acknowledged, this remains undeveloped, and the theory's architects admit that they do not attempt to explain adaptation or "inheritance" (Hannan and Freeman 1989, 20). This omission renders organizational ecology an incomplete Darwinian account rather than a non-Darwinian account as claimed by Reydon and Scholz in their narrow view of Darwinism.

[10]For most critics, it is the heavy emphasis on selection that leaves the theory wanting. While acknowledging its success as a research program, it is argued that by accentuating one particular strand of evolutionary theory, organizational ecology ends up presenting a distorted view of organizational phenomena (Baum and Singh 1994a).

Relatedly, although it could be argued that, in accordance with general selection theory (Price 1995), organizational ecology *does* present an evolutionary selection process, it is important to observe that this is not the same as a Darwinian natural selection process, which notably includes a mechanism to explain the replenishment of variety in the system.[11] But again, while this also admits a failure to include an inheritance mechanism, it does not suggest incompatibility with Darwinism, only an incomplete Darwinian account in need of further development.

To be sure, with the decoupling of adaptation and selection, Hannan and Freeman's own narrow reading of Darwinism not only causes problems for their theory but also misleadingly sets up Lamarckism and Darwinism as false rivals. Indeed, with the evident polarization of evolutionary accounts into either "adaptationist" or "selectionist" camps, this view exacerbates what has become known as the "adaptation versus selection debate" in organization science (Levinthal 1991). The ultimate consequence of this false dichotomy is that it precludes a complete causal account for organization scholars that would permit the integration of deliberation and selection.

We now consider these issues through the adjusted lens of a modern generalized Darwinism approach where it will be shown how the replicator-interactor distinction provides a way forward for organizational ecologists to bring "evolution proper" back into the analysis. Accordingly, it will be shown how Reydon and Scholz's claims turn out to be less decisive.

Overview of Modern Darwinism. Modern Darwinism found its authority and formal articulation during the last three decades of the twentieth century,[12] and, as Reydon and Scholz acknowledge, this development began with exploration of the theory's generic nature. By purposefully adopting a general approach for analysis of these evolutionary processes, in other words separating them from their biological origins, scholars sought to determine

[11]See Hodgson and Knudsen (2010) on the difference between "subset" selection and "successor" selection, where the former removes variation over time and thus eventually grinds to a halt.

[12]These developments relate to the established Darwinism, which has long since embraced Mendelian genetics and which biologists often call "neo-Darwinism"—specifically to signal its synthesis in the 1950s with Mendelian genetics. It is important here to distinguish this meaning of "neo-Darwinism" from another that tends to occur in the social sciences literature where neo-Darwinism has sometimes been used pejoratively to refer to genetic determinism or "ultra-Darwinism."

the general principles of natural selection and resolve the enduring unit-of-selection debate (Lewontin 1970; Hull 1980, 1981).[13]

While the unit-of-selection debate has notably shifted in focus since the 1980s and continues unresolved (Okasha 2006), from these earlier developments in the philosophy of biology emerged Hull's (1988) influential "replicator" and "interactor" concepts: used to denote the gene and the organism in biology and the routine and organization in the socioeconomic realm. Seemingly discounted by Reydon and Scholz, these concepts have helped clarify the complex processes involved in natural selection and indeed have now become "generalized terms" (Brandon, 1990). As previously indicated, however, it is important to stress that the replicator and interactor concepts, as originally conceived and recently developed, are of more limited generality than the core principles of inheritance and selection. There is no attempt, for example, to use the replicator concept as a basis for a wholly general theory of evolution (Hodgson and Knudsen 2012).[14]

The Replicator-Interactor Distinction. Evolutionists were divided over the true *unit* of selection. However, Hull (1981) eventually discerned that units and levels had become conflated in the debate and, following Mayr (1978), determined that selection was in fact a "two-step" process that involved a replicating entity and an interacting entity. In other words, he determined that there was a functional *distinction* between these entities. Illustrating the nature of the debate and the import of his generalized replicator and interactor terminology, Hull (2001, 61) explains the linguistic confusion:

[13]Hull (1981) reflects on the approach of geneticist Richard Lewontin (1970), observing how the latter first characterizes the evolutionary process and then considers evidence for and against selection at various levels of organization. Hull then explains his own distinctive approach, which, in contrast, begins by focusing on the evolutionary process itself, investigating its *general* characteristics, and only then considering which entities have the requisite characteristics to function in the evolutionary process.

[14]Hodgson and Knudsen (2012, 609) state, "In making the claim (which we share with Gers and Godfrey-Smith) that social evolution is Darwinian, we are interested in establishing principles and concepts of sufficient but not maximal generality. The principles and concepts must be sufficiently general to span the key common features of biological and social evolution, but they need not encompass any conceivable definition of evolutionary processes (and implied phenomena) in these domains."

> When Dawkins says that genes are the units of selection, he means replication. Genes are the primary units of replication and "hence" selection. When others such as Mayr say that organisms are the primary focus of selection, they mean environmental interaction. In gene-based biological evolution, organisms are the primary units of environmental interaction and "hence" selection.

The conceptual clarification of this "indirect selection" of genes provides understanding of the apportioned location of causality in the natural selection process. This was a major development in the philosophy of biology, for as well as demonstrating that selection is a two-step process[15] and clarifying what happens at each level of the organizational hierarchy, it established the important distinction, or "dual aspect" nature, of the primary unit of selection (Mayr 1988), otherwise known as the organism or "primary interactor" (Hull 1988). Furthermore, this replictor-interactor distinction presents an invaluable conceptual tool for organizational ecologists. Premised on the population thinking perspective and providing expression of a replicating heritable unit for knowledge transmission, it also asserts structural cohesion, as defined earlier, for membership of an evolutionary population.

The replicator is defined by Hull (1988, 408) as "an entity that passes on its structure largely intact in successive replications," and it is hosted by an interactor. The interactor is defined as "an entity that directly interacts as a cohesive whole with its environment in such a way that this interaction *causes* replication to be differential." These are the entities that function within the selection process and their combination (in terms of an interactor composed of replicators) amounts to what we generally think of as the primary interactor or unit of selection. In biology, this is the organism, and in the business world, this is the organization or the firm.

As indicated, these terms were inspired by the replicating function of the genotype and the interacting function of the phenotype. In biology, the genotype is understood as the genetic composition of an organism, and the phenotype is its developed characteristics or capacities. For social scientists, habits, rules, and organizational routines are the paradigmatic ("social") replicators, in other words, the encoding entity (Aldrich 1999; Hodgson and Knudsen

[15]Mayr (1988, 98) explains, "Natural selection proper is only the second stage of a two-step process. The first step consists of the production of variation in every generation, that is, of suitable genetic or phenotypic variants that can serve as the material of selection, and this will then be exposed to the process of selection. This first step of variation is completely independent of the actual selection process, and yet selection would not be possible without the continuous restoration of variability."

2004, 2006a), while groups or organizations are the paradigmatic ("social") interactors, characterized and developed by the replicators of which they are composed, which interact with their respective environments and compete for scarce resources.

With the replicator-interactor distinction, Hull (1988, 409) defines the selection process as "a process in which the differential extinction and proliferation of interactors *cause* the differential perpetuation of the relevant replicators." Accordingly, in the socioeconomic domain, there will be fitness differences among the various heritable organizational routines. The differential proliferation of the most successful firms will in turn *cause* the perpetuation of their organizational routines. Through the "knowledge retaining" replicating routines, the knowledge concerning adaptive solutions to survival problems are thereby retained and passed on.

Thus, as suggested, with this conceptual apparatus, it is now possible for organization ecologists to develop a framework to model an evolving Darwinian population. These conceptual advances established the functional difference between units and levels, properly situated the heritable unit, and clearly defined the evolving entity. From this perspective, it is shown that Reydon and Scholz's dismissal of Darwinian populations in the social realm is unfounded.

To be sure, following Hull (1978) and Gannett (2003) whom Reydon and Scholz notably cite as authorities on this issue, the replicator-interactor distinction clearly enables conceptualization of an evolving population, for example, in relation to inheritance, through what Hull describes as structural cohesion (defined in terms of common descent or lineages)[16] or what Gannett describes as the binding factor of reproductive cohesion.[17] Again, following Hull (1988), whom Reydon and Scholz notably do not consult on this particular issue, we have a clear definition of an evolutionary selection process that concurs with their own Darwinian interpretation but decisively incorporates the replicator-interactor distinction that facilitates conceptualization of an inheritance mechanism.

In their critique of organizational ecology's selection process, Reydon and Scholz argue that "another mechanism would be required to ensure that later-generation organizations resemble successful earlier-generation organizations"

[16]Indeed, it satisfies their own requirements regarding "membership of a system" (Reydon and Schulz 2009, 423).

[17]"Ultimately, relations among organisms . . . provide the glue, the spatial and temporal cohesion, to bind individual organisms together into population wholes" (Gannett 2003, cited in Reydon and Scholz 2009, 425).

(2009, 428). The heritability of traits, they observe, "is a necessary requirement for evolution to occur." It is argued here that these calls for due attention to be paid to the inheritance mechanism and the reproductive and genealogical relations that determine membership of a Darwinian population are convincingly addressed through adoption of the replicator-interactor conceptual apparatus. This is underlined in a recent definition of the Darwinian selection process offered by Hodgson and Knudsen (2010, 92):

> *Selection* involves an anterior set of entities that is somehow being transformed into a posterior set, where all members of the posterior set are sufficiently similar to some members of the anterior set, and where the resulting frequencies of posterior entities are correlated positively and causally with their fitness in the environmental context. The transformation from the anterior to the posterior set is caused by the entities' interaction within a particular environment.

Modern Darwinism is clear on what it defines as a dynamic evolutionary selection process. In this scientific usage of selection, population thinking is assumed; structural or reproductive cohesiveness is required; and selection involves an interacting entity that embodies a replicating entity. This is quite different from and not to be confused with the common understanding of selection that simply refers to *choice.* An important body of literature that explores the technical definition of selection is usefully summarized by Hodgson and Knudsen, who, in their discussion of the principle of selection, highlight the important difference between general "subset" selection (Price 1995) and evolutionary "successor selection."[18]

Now established in biology, the idea of social replicators and interactors has since been variously deployed by scholars in organization sciences (Baum 2002), evolutionary economics (Hodgson and Knudsen 2004, 2006a, 2006b), evolutionary anthropology (Hull, Langham, and Glenn 2001), and memetics (Aunger 2000). While a rich body of work has emerged on general definitions of replication (Sterelny et al. 1996; Godfrey-Smith 2000; Sperber 2000), scholars continue to explore the viability of candidate social replicators (e.g., habits, routines, and rules) and social interactors (e.g., groups, organizations, and institutions).[19]

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[18]The term *successor selection* is their own: "subset selection is very different from the concept of successor selection—which was part of Darwin's great achievement—where offspring are not subsets of parents. Successor selection involves replication, whereas subset selection is a simple elimination process" (2010, 94).

[19]See Brandon (1998), Godfrey-Smith (2006, 2009), and Hodgson and Knudsen (2010).

Significantly, the replicator-interactor distinction is implicit in Nelson and Winter's (1982) highly influential evolutionary economics, where they equate routines with genes and firms with organisms; it is also present in the prominent evolutionary approach of Howard Aldrich (1999) in *Organizations Evolving*. Moreover, as will be discussed in section 5, the distinction is present in Hannan and Freeman's (1989) *Organizational Ecology*—if only in embryonic form. While these authors do not use the replicator-interactor terms in these works and their evolutionary interpretations suffer their own particular problems of intractability or incompleteness (Dollimore 2006), it is nevertheless apparent in their respective accounts that at some level they are aware of this important distinction and its causal role in the evolutionary process.

Lamarckism and Darwinism. Indeed, for these and all evolutionary scholars in business economics and organization sciences, the challenge remains to construct a more complete evolutionary account that comprises Darwinian selection but also somehow accounts for the "Lamarckian" deliberative or intentional behavior that characterizes the social world. This very real possibility brings the present discussion to other conceptual advances in evolutionary theory especially relevant to organizational ecology and its resurrection as a viable Darwinian evolutionary model—that is, reconciliation of Darwinism with Lamarckism and consequent resolution of the adaptation-versus-selection debate in organization science.[20] It will be seen here how the replicator-interactor tool addresses the conceptual problem at the center of this controversy.

It has been established, contrary to a widespread belief, that Lamarckism and Darwinism are *not* rival or mutually exclusive theories (Mayr 1978; Hull 1982; Dawkins 1986). The notion of acquired character inheritance, long since dismissed in biology, though notably not denied by Darwin (Mayr 1976), is now shown to be theoretically possible. Indeed, the same genotype-phenotype distinction necessary to explain Darwinian inheritance in the biotic world also facilitates conceptualization of a Lamarckian inheritance process in the social domain through the replicator-interactor distinction. This permits articulation of same-generational change for organizational ecology.

[20]Recall that in organization science, the interlinked processes of adaptation and selection have become separated partly due to the misapprehension that they denoted Lamarckian *or* Darwinian evolution.

In other words, in contrast to the biological domain where phenotypic change (like a broken limb or cosmetic surgery) cannot affect the genotype, same-generation knowledge transmission from organizations to their organizational routines (as firms learn and adapt to changing business environments) is now conceptually as well as empirically viable. For Lamarckian acquired character inheritance to work, it requires a mechanism that permits the encoding of acquired traits in a replicator that is passed on to the next generation. Conceptualization of this kind of knowledge transmission is *only* possible with the replicator-interactor distinction.[21]

But it is also clear that Lamarckism, in common with self-organization theory, cannot stand alone as an evolutionary theory, because ultimately it needs a Darwinian selection process to work (Dawkins 1986; Hodgson 2001, Knudsen 2001). There are important gaps in the Lamarckism explanation. For example, it fails to explain why only advantageous adaptations are inherited and not disadvantageous ones: something that can only be explained through a Darwinian selection process. Relatedly, at a more fundamental level, it fails to explain *why* organisms try to adapt to their environments. In other words, how is intentionality explained in the social arena? It is suggested that such gaps need to be filled by a Darwinian or other explanation (Dawkins 1983, 1986).

An important body of work that builds on the aforementioned advances in philosophy of biology demonstrates how these conceptual gaps are addressed within modern Darwinism (Hodgson and Knudsen 2006b; Stoelhorst 2008; Aldrich et al. 2008). In the "generalized Darwinism" formulation, proponents demonstrate how the metatheoretical framework of an abstract generalized Darwinism accommodates auxiliary, domain-specific explanations, such as the Lamarckian inheritance required in socioeconomic accounts where both deliberation and selection need to be explained for a complete causal story. Following a long but neglected intellectual tradition and grounded in the population thinking approach, generalized Darwinism upholds that the core principles of variation, inheritance, and selection are general principles that govern the evolution of all complex open systems that share fundamental ontological similarities.

We are reminded that Darwin (1859, 1871, 1874) himself predicted the general application of natural selection, for example, in relation to customs,

[21]This is different to the kind of replication involved in infection or contagion, where properties such as germs or fleas (or ideas in social world) are "passed on" from one interactor to another but do not affect the replicators of the second interactor. See Hodgson and Knudsen (2010) for elaboration.

language, and morals; that his contemporaries endorsed it (Bagehot 1872; Ritchie 1889, 1896); and that a host of others across a range of disciplines have since reinforced its application beyond the realms of biology (Veblen 1898; Campbell 1965; Toulmin 1972; Dennett 1995; Wilson 2002).

The wider relevance of these theoretical developments for the social domain is apparent in many studies where it has been demonstrated unequivocally that social evolution is both Lamarckian and Darwinian (Boyd and Richerson 1985; Metcalfe 1998; Hodgson and Knudsen 2006b). Ironically, even the polarization of the socioeconomic literature into Lamarckian or Darwinian accounts testifies to this, with some scholars perceiving a Lamarckian evolutionary story in the social realm while their colleagues perceive a Darwinian one. Undoubtedly, the theoretical accommodation of Lamarckian inheritance is a key aspect of generalized Darwinism that should not be overlooked by organizational ecologists. Indeed, it is poised to considerably improve their analytical approach. If organizational ecology is to articulate an inheritance mechanism, which it evidently needs to do to express an evolutionary selection process, it needs both Lamarckism and the metatheoretical framework of generalized Darwinism.[22]

The Question of Ontology and Darwinian Populations. It is evident that "evolutionary theory is no longer dogmatically committed to the view that there can only be individual or gene selection" (Vromen 2001) or that it is only relevant to the biotic world (Winter 1987).[23] This realization, together with the newly acquired conceptual apparatus, has informed an exciting raft of work in evolutionary economics and organization studies where scholars have revived efforts in this direction by their evolutionary forebears. As indicated in the previous section, the question of ontology and Darwinian populations has not been overlooked here.

Drawing on the advances in philosophy of biology outlined so far, it has been shown by evolutionary economists how generalized Darwinism shifts the theoretical approach beyond mere analogy and metaphor toward the more

[22]Note that generalized Darwinism does not claim to be a complete theory of everything and is not to be confused with "Universal Darwinism" (Dawkins 1983), which suggests universal validity for the theory.

[23]Ziman (2002) reflects the views of many in organization science: "The key factor in widening the field of application of evolutionary reasoning is the realization (Campbell 1974) that this is a general mode of historical change, of which the evolution of biological organisms is only one example."

analytically tractable platform of a Darwinian social ontology (Hodgson 2002). Most important for skeptical social scientists, with the realization that Darwinism is not domain specific, that it has moved beyond analogy and is a general abstract theory, it becomes apparent that social phenomena are *not* being analyzed in terms of biological phenomena, *nor* is biology determining the social research agenda.[24] In a passage from *Darwin's Conjecture* (2010, 21), Hodgson and Knudsen elaborate on the meaning of ontological communality:

> Generalized Darwinism relies on the claim of common abstract features in both the social and the biological world; it is essentially a contention of a degree of *ontological communality*, at a high level of abstraction and not at the level of detail. This communality is captured by concepts such as replication and selection, which are defined as precisely and meaningfully as possible but in a highly general and abstract sense.

Responding to critics (Witt 2004; Cordes 2006), proponents of generalized Darwinism stress that the detail about entities and their particular mechanisms will inevitably vary from one domain to another, since what happens in the social domain is clearly quite different from what happens in the biological domain. It is argued that this structural feature underlines the point that Darwinism does not mean that the analysis of social evolution will be dictated or skewed by a biological perspective or agenda.[25]

The important point to observe here is that there *are* fundamental ontological similarities among all complex evolving systems, and, from the generalized Darwinian perspective, it is possible to conceive of Darwinian entities and processes operating in the social domain. Consider the complex evolving industries studied by organizational ecologists. These industry

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[24]Correspondingly, generalized Darwinism makes absolutely clear that there are no allusions to eugenics, genetic-determinism, or, indeed, any of the racist, imperialist, or sexist ideologies that have misleadingly become associated with name of Darwin (Hodgson 2004). Darwinism is about the application of general principles, an approach that assumes a Darwinian ontology and has no need for a reductionist methodology.

[25]Many social scientists already acknowledge this point, as noted by Baum and Singh (1994b, 10): "fortunately, Darwin's idea of evolution—descent with modification—*is not* tied to particular features of biological inheritance (Boyd and Richerson 1985; Campbell 1965; Hannan and Freeman 1989; Hull 1988). Natural selection is a very general mechanism."

populations will typically comprise a variety of new and existing firms that will in turn comprise a host of enduring, developing, and novel routines. The economic selection process acts on successive generations of this variety and results in the differential survival of firms competing within that industry. The resulting pool of heritable replicating routines are those that come to characterize or define the industry in each period.

Evidently grounded on the core principles of variation, inheritance, and selection and notably incorporating the replicator-interactor distinction, Hodgson and Knudsen offer a definition of generalized Darwinism that captures the nature of these Darwinian populations (2010, 238):

> Darwinism is a general theoretical framework for understanding evolution in *complex population systems*, involving the inheritance of *replicator* instructions by individual units, a variation of replicators and *interactors*, and a process of selection of the consequent interactors in a population.

Contrary to Reydon and Scholz, as illustrated above and in preceding sections, it evidently *is* possible to conceptualize evolving Darwinian populations in the socioeconomic domain, providing that the inheritance mechanism is appropriately specified. Furthermore, through the same replicator-interactor distinction, adaptation and selection are shown to be reconciled in the socioeconomic sphere. Before elaborating on how the conceptual apparatus might be applied to rescue organizational ecology, the analysis briefly considers the importance of replication (inheritance) and knowledge transmission for the socioeconomic realm.

4. Darwinian Selection and Knowledge Transmission

In both the natural world and the social world, all agree that it is not possible to have an evolutionary selection process without an inheritance mechanism. Any adequate understanding of selection in the social world requires specification of the mechanisms that bring about correlations in cultural traits in successive generations (Hull 2000, 54). As Metcalfe (1987, 57) observes, it is a crude error to interpret the evolutionary argument solely in terms of selection. Relating this to the socioeconomic domain, he explains elsewhere (2004) the importance of also accounting for what he calls "upward causation," and he cautions that in separating selection from firm-level developmental processes,[26] theorists risk missing a major element of understanding.

Underlining the point that it is (a) variety that drives economic evolution and (b) technological innovation that feeds variety, Metcalfe (1987, 64) points instructively to the more complete evolutionary account offered by Nelson and Winter. In praise of their models of "search" behavior, he observes that their theory usefully accounts for the behaviors that generate the variety on which selection operates, and applauds what he calls their insightful micro-to-macro-style Darwinian selection account,[27] which appropriately embraces Lamarckian inheritance:[28]

> One of the central lessons of the Nelson and Winter world view is the need to build a theory of growth in a bottom up fashion with due attention paid to the emergence of constraints at higher levels of aggregation.

Also underlining this point, organization scholars Baum and Singh (1994a, 5) cite a host of studies demonstrating that organizations can and do change, and they stress that these changes are important to understanding what organizations do as individuals and as populations. Indeed, they too lament the one-sided selectionist perspective of organizational ecology and see this as a major area of research for evolutionary theorists in the socioeconomic domain (6):

> By and large, organizational ecologists have not attempted to link ecological processes of interaction and genealogical processes of replication. Consequently we still know very little about the other side of the evolutionary process—the structures of organizational inheritance and transmission (Baum 1989). How are organizational structures and practices perpetuated through time? What is inherited and how?

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[26]What organization scholars refer to as "adaptive" processes. Metcalfe is calling for the proper (Darwinian) marrying of selection and adaptation in evolutionary accounts.

[27]In an account where routines are portrayed as genes, Nelson and Winter (1982, 400) posit an organization-level search process that involves higher-level routines evaluating, modifying, or replacing current routines. For Metcalfe, this takes appropriate account of "bottom-up" causality within an evolutionary selection process.

[28]Nelson and Winter's account (which they insist on describing as Lamarckian) is not without its problems. Close reading reveals confusion between levels and units of selection in articulation of the search process. However, as with organizational ecology, it is suggested here that these conceptual issues can be reconciled through the application of generalized Darwinism and adoption of the replicator-interactor distinction in a multilevel selection process.

The view here is that in the absence of an adequate evolutionary framework that takes proper account of knowledge transmission and the adaptive imperative of organizations, our ignorance of the evolution of socioeconomic populations is destined to remain the same. While generalized Darwinism is not without its critics[29] and proponents acknowledge conceptual and empirical work yet to be accomplished for a scientific approach still in its infancy,[30] embracing as it does, the foremost theoretical and conceptual advances in philosophy of biology, it nevertheless offers for the socioeconomic domain the promise of a more complete evolutionary approach with greater explanatory potential. In the following section, rather than follow Reydon and Scholz's preemptive dismissal, we now consider what organizational ecology might look like from a modern, generalized Darwinian perspective.

5. The Way Forward for Organizational Ecologists

For Reydon and Scholz (2009, 409), "it must be shown that the entities under consideration in a particular research program actually meet the requirements of Darwinian evolution to occur." This paper argues that it is possible to achieve this and suggests a way forward for organizational ecologists.

In the overview of pertinent developments in the philosophy of biology and elsewhere, the preceding sections have made the argument that it is possible to conceptualize Darwinian entities and processes in the social arena. Furthermore, it is claimed that the conceptual apparatus, in the form of the replicator-interactor distinction, now exists to enable organizational ecologists to develop a more complete Darwinian program. Supporting the view here that organizational ecology is an incomplete Darwinian approach is the observation that its selection process is not incompatible with Darwinism and, furthermore, that an unexpressed inheritance mechanism resides in the theory. Elaborating on this claim, the following analysis shows how this primes organizational ecology for the necessary theoretical development, and it sketches out how, by using the replicator-interactor distinction, organizational ecology can account for adaptation and selection effects and thereby then claim to be a complete Darwinian research program.

It is agreed here that organizational ecology lacks an adequate explanation of diversity. There is a failure, for example, to identify an "organizational

[29]See Witt (2004, 2008) and Cordes (2006).
[30]See Aldrich et al. (2008).

generation" or a "social vehicle" for transmitting or inheriting traits (McKelvey 1982). Yet, a close review of its explananda reveals that Darwinian inheritance is nonetheless assumed in the theory.

Although Hannan and Freeman rejected the notion of Lamarckian inheritance, it is important to note that their work represents an empirical rather than a theoretical rejection of Lamarckism. Indeed, there is nothing in their theory that suggests that Lamarckian inheritance is impossible in principle. Moreover, they do not deny that organizations change, only that the change cannot account for the evolutionary change manifested at the population level. Also, they do not deny this gap in their theory but declare their inability to specify a transmission process, and, indeed, they signal this as an area for future research. The point is that there is clearly scope for the productive development of their theory.

This includes evidence of the core Darwinian principles lying dormant in the theory as well as an embryonic replicator. While selection unquestionably dominates, an inheritance mechanism is suggested in the concept of "structural inertia" and in Hannan and Freeman's treatment of their central interacting entity, the "relatively inert" organizational form that is described as responding relatively slowly to threats and opportunities in the environment (Hannan and Freeman 1989, 70). Continuity and replication of form are thus evidently assumed in organizational ecology. Also, in Hannan and Freeman's description of organizations as having "high inertia both in the sets of routines employed and in the set of rules used to switch between routines" (76), a replicator and interactor relationship can be discerned that is not inconsistent with Hull's distinction.[31] Organizations here are evidently composed of routines that affect organizational form. The inertial principle and recognition of "faithfully reproducing structures that resist transformation" (Hannan 2005, 59) imply replication, though *not*, of course, transformation. There is no heritability of traits, or "lineage," with preceding forms. As previously noted, the selection process here is subset selection, not "successor" selection.

While Hannan and Freeman stress that they shift the analysis to the level of the population, it is clear that the unit of selection is the organization and that the *effects* of selection processes are manifested at the population level. This is

[31]Moreover, a multilevel selection process might be suggested with Hannan and Freeman's "set of rules" being conceived of as a higher-level set of routines within a nested hierarchy of interactors. In other words, this "group" could comprise another interactor—providing that the group acts as a cohesive whole, as specified in Hull's (1988) definition of an interactor.

where the interactor resides in the theory, in the shape of the organization. Furthermore, while their selectionist account is rooted in typological essentialism, it is evident that there is an appreciation in the theory of the importance of variation for an evolutionary explanation; variety is assumed to be preexisting, for example, in the births and foundings of new businesses.

Organizational ecology is more compatible with Darwinism than first appearances might suggest. However, for a more complete and realistic account of organizational change and diversity, it is suggested here that it needs a reorientation back to the organization as the focus of analysis and conceived of as the primary interactor. This would not render the theory "adaptationist" but, with the adoption of the replicator-interactor distinction, would instead enable the conceptualization of a selection process that accounts for inheritance. Of course, in the socioeconomic domain, this would be a Lamarckian inheritance mechanism, since it is the notion of acquired character inheritance that best describes the intentional behavior and same-generational change observed in this domain. As described earlier, a Lamarckian inheritance mechanism is "nested" in the metatheoretical framework of generalized Darwinism.

Thus, in addition to the exploration of "vital rates" (i.e., births, deaths, exits), attempts should be made by researchers to gather data at the organizational level. Attempts should be made, for example, to identify the characteristics in individual firms that contribute to fitness in the population under study and assess the relative importance of these as selection criteria. Attention should be paid to the nature and quality of the firm's routines; to their emergence, stabilization, and disruption; and to their effects on the organization's development and growth.

The crucial point here is that organizational ecologists need to recognize that adaptation and selection are intertwined, not separate, evolutionary processes. It is correct that adaptation at the population level is the outcome of a selection process, but for an evolutionary explanation of diversity, we must include explanation of the production and replenishment of the variety upon which selection operates. In short, we need to include a replicating heritable entity, and the theory must be grounded in the Darwinian population thinking perspective. The organizational routine is the candidate encoding entity in the socioeconomic arena.

By constructing a theory that explicitly models replication and inheritance processes, organizational ecologists will be able to claim a proper Darwinian evolutionary selection process. The "peculiar duality" (Mayr 1988) of Darwinian selection that explains the all-important continuous restoration of

variety is perfectly captured in the replicator-interactor distinction where differential selection of interactors leads to the selection of heritable replicators. Adoption of this conceptual tool provides organizational ecologists with the mechanism that it needs to explain diversity.

Returning to Reydon and Scholz's central criticism, in facilitating the aforementioned, organizational ecology clearly needs to rethink its conception of variety and *its* inheritance and shift to a population thinking approach. Population thinking has direct relevance for the analysis of all open-ended socioeconomic systems where scholars need to make sense of the prevailing variety and where ultimately there are policy implications.[32] Metcalfe (1987, 56), who highlighted its significance for economics, explains that the "the shift from analyzing ideal cases to examining frequencies and their distribution is central to the elaboration of an evolutionary perspective." As demonstrated earlier, evolutionary selection processes simply cannot be articulated in a schema constructed around typological essentialism, and researchers must account for the processes that generate and regenerate variation—in other words, the replication and inheritance of innovation, entrepreneurial activity, and "copying errors." The evolutionary significance of knowledge transmission cannot be underestimated.

The aforementioned sketch of the formulation of a revised theoretical framework for organizational ecology is just that, with insufficient space here for elaboration. It does not underestimate the vast methodological challenges confronting researchers contemplating its possible integration into their research design. However, it does at least point toward the kind of theoretical framework that needs to be considered by social scientists seeking to develop a more complete Darwinian evolutionary research program, one that accounts for changes in organizational form that result from the intertwined processes of adaptation (including learning and the intentional decision making of organizational leaders) and evolutionary selection. And so, in response to Lemos's (2009) final musings where he ponders the Darwinian research program and a perceived problem with the accommodation of intentionality, the view here is that Darwinism is assuredly *not* an "unnecessary extravagance."

[32]For example, in economics, how much variety is desirable or sustainable in a particular industry? Is limited variety an indicator of competition or monopolistic practices? And, relatedly, should variety be encouraged or prevented for the health of the general economy?

6. Conclusion

The contention here is that Reydon and Scholz's assertion about the non-Darwinian status of organizational populations is unfortunate and misleading. Although this may be true of the organizational populations discussed by Hannan and collaborators in organizational ecology, it is important to stress that Reydon and Scholz cannot make this claim about organizational populations in general. Significantly, while Reydon and Scholz (2009, 411) acknowledge the possibility of the broader application of Darwin's theory and indeed discuss the required conditions, they do not discuss the replicator-interactor distinction that facilitates developments in this direction.

Misunderstandings about the explanatory scope of Darwin's theory are rife among social scientists where biophobia has led to the trained incompetence of social scientists (Ellis 1996) and where many scholars remain ignorant about modern Darwinian theory (Jablonka and Ziman 2000). As highlighted here in discussions on population thinking and the replicator-interactor distinction, foundational aspects of Darwinian theory are still not generally understood and the modern generalized terms not widely known. It is therefore very important, if we are to move forward with the development of a viable evolutionary theory for the socioeconomic realm, to be clear about what is and what is not possible in this regard. Accordingly, this paper has attempted to untangle some of the conceptual issues that have thwarted its realization.

Space does not permit adequate coverage here of the numerous quality contributions to this topic in the evolutionary economics and organization science literature.[33] Suffice to state that productive exchanges continue to progress the agenda among evolutionary scholars who continue to debate theoretical applications[34] and work on the elucidation of general principles and definitions of terms.[35] While considerable work remains to be done for the establishment of a viable and refutable evolutionary model,[36] there is

[33]See Baum and Singh (1994a, 1994b) and Laurent and Nightingale (2001). See also Dobrev, van Witteloostuijn, and Baum (2006), who explore the development of theory and empirical evidence at the interface of strategy management and organizational ecology, at what they call the "inertia-flexibility nexus."

[34]See Witt (2004, 2008), Vromen (2004), and Hodgson and Knudsen (2008, 2012).

[35]Working, for example, on the refinement of the replicator and interactor definitions and on the identification of what entities in the living world meet these definitions (Hodgson and Knudsen 2004, 2006b, 2010).

[36]Collaborators acknowledge that generalized Darwinism is still in its infancy as a research program (Aldrich et al. 2008).

widespread agreement on the need for researchers to undertake more empirical studies to aid this process.

It is now thirty years since organizational ecologists spearheaded the vast research program on selection dynamics, and it is high time that researchers took account of the evolutionary significance of knowledge transmission. Adaptation and selection need no longer be dichotomized. It is argued here and elsewhere (Dobrev, van Witteloostuijn, and Baum 2006; Hodgson and Knudsen 2010) that researchers have much to gain in merging the rich body of work in organizational ecology with the complementary stream of empirical studies focused on strategic management and the role of organizational routines in business organizations (Becker 2008). Given that the conceptual apparatus now exists to construct the necessary theoretical models, researchers are evidently well placed to exploit these complementary theoretical and empirical advances for the productive development of a tractable and complete Darwinian research program.

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