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Organisms, Life Relations, and Evolution: Inter-Dependencies after Kropotkin's *Mutual Aid*

Organismos, relaciones de vida y evolución: inter-dependencias a partir del Apoyo Mutuo *de Kropotkin*

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Abstract

We examine some implications of Kropotkin's seminal work on mutual aid as a factor of evolution to analyze how non-competitive life relations are understood in current biological theories. We distinguish two research lines deriving from

his work:; one of them studies intraspecific relations of altruism and selfishness, and the other one is focused on interspecific symbiotic relations. Furthermore, we use the example of pregnancy and viviparity is used to extend the analysis to the evolution of novel inter-organismic characters. We conclude with a conceptual review of how collaborations and inter-dependencies among organisms shape individual autonomy and sociability in organismal evolutionary biology.

Keywords: altruism; symbiosis; ontologies; sociability; individuality; viviparity; reproduction; autonomy.

Resumen

En este trabajo examinamos ciertas implicaciones de la obra seminal de Kropotkin sobre el apoyo mutuo como factor evolutivo para analizar cómo se entienden las relaciones de vida no competitivas en las teorías biológicas actuales. Distinguimos dos líneas de investigación que pueden derivarse de su obra: una sobre las relaciones intraespecíficas de altruismo y egoísmo, y otra centrada en las relaciones simbióticas interespecíficas. Además, recurrimos a ejemplos de embarazo y viviparidad para extender el análisis hacia la evolución de nuevos caracteres inter-organísmicos. Concluimos con una revisión conceptual de cómo las colaboraciones e inter-dependencias entre organismos conforman la autonomía individual y la sociabilidad desde la biología evolutiva organismal.

Palabras clave: altruismo; simbiosis; ontologías; sociabilidad; individualidad; viviparidad; reproducción; autonomía.

1. Introduction

The organism-based account of evolution develops a different perspective from the one focused at the level of genes or populations, where the organism is established as a salient level of explanation for biological phenomena (Baedke & Fábregas-Tejeda, 2023; Cortés-García & Etxeberria, 2023; Etxeberria & Umerez, 2006; Nicholson, 2014). Since organisms are organized entities, many decisive biological features are grounded on the individual organization of constitutive parts interacting with the environment, and will only appear and stand out at that level.

Moreover, in addition to being constituted in relation to their environments, organisms act on them, they are agents and as a result of that, milieus are also shaped by organic activities. The understanding of organisms as inseparable from their environments, and constituted by the relationship they establish with

them, is becoming widespread in the philosophy of biology, but we believe that this environment is often conceived of as inanimate, and more attention should be paid to organism-organism relationships and their bearing in evolution.

In the standard evolutionary theory of the Modern Synthesis, many of the traits that characterize the fitness of organisms, including both their abilities to survive and to reproduce, are already context-dependent and relational (Millstein, 2014, Okasha, 2002). Relationships involved in predator-prey interactions, mating behavior, parental care, etc. shape the individual properties of organisms and characterize the way in which they are constituted, and thus, their survival and reproductive capacities. Many of those relations have been studied within a competitive understanding of Charles Darwin's "struggle for existence", an expression he used under the influence of reading Thomas Malthus and which underlies the idea of natural selection. However, there has always been a debate as to whether it should be understood as a direct competition between organisms and how much scope it allows for cooperation between them.

It is for this reason that we turn to the work of Pyotr Kropotkin, as an author who in the beginning of the twentieth century forthrightly denounced the sheer competitive reading of Darwinian theory and encouraged the development of biological studies that included relations of life that were not necessarily competitive to explain the nature of social bonds and interspecies relations in humans and other species.

Therefore, this paper explores some views on the role of non-competitive relationships between organisms in evolution starting from some aspects implied by Kropotkin's work in his book *Mutual Aid* (1902/2018).

Our analysis combines historical research with philosophical aspects that we believe are relevant to advance organismal biology. The argument proceeds as follows: firstly, we review some of Kropotkin's fundamental ideas on mutual aid as an evolutionary factor in order to emphasize that important aspects of the ontology of relationships in evolution already appear in this book (section 2). Then, we present two major research lines or traditions of which Kropotkin's work can be considered a relevant precedent: one of them centered on intraspecific relations and the possibility of altruism, and the other one addressing strong collaborative interspecies relations articulated in terms of symbiosis and material imbrication (section 3). Next, the example of viviparous reproduction in eutherian mammals is invoked to compare conflict and entanglement models of pregnancy (section 4). Finally, we examine central notions of organismal evolutionary biology, such as individual autonomy and sociability, from the perspective elaborated in the preceding sections.

2. Kropotkin's "*mutual aid*" as an evolutionary factor

2.1 Struggle for existence

The notion of struggle for existence is an expression Darwin (and other contemporaries such as Alfred Russel Wallace) borrowed from Malthus, according to whom the growth of population is an exponential phenomenon, a lot faster than food supplies, therefore when natural populations are constant in size this means that many individuals die (Gayon, 1998). Often this framework is associated with the idea that a competitiveness underlies all relationships among living beings. However, this requirement is controversial and has been debated by scholars. The insight entails that all organisms compete to survive and reproduce "whether with other members of its species, other species, or even its environmental conditions (of drought or temperature, for instance)" (Pence, 2022). Thus, Darwinian interpretations of life and of natural relationships sometimes hold that direct competition between organisms is required for natural selection, although other authors contend that the struggle for existence is broader and encompasses more than competitions (Lennox & Wilson, 1994). In the *Origin of Species,* Darwin himself states: "I use the term Struggle for Existence in a large and metaphorical sense, *including dependence of one being on another*" (1859, 62; emphasis added).

It is precisely to this last sentence by Darwin that Kropotkin seizes upon at the beginning of his book *Mutual Aid: A Factor in Evolution* (Kropotkin, 1902/2018). In this volume, he criticized the interpretation of evolution as a direct competition between organisms and emphasized the role of non-competitive relations among organisms in evolution. His contribution came immersed in what has been considered to be a tradition of Russian naturalists and biologists, who sympathized with Darwin's work and considered themselves Darwinists, yet questioned whether relations in nature can be reduced primarily to competition. In their view, no characterization of life and nature would be complete without addressing that many evolutionary phenomena are only possible as a consequence of collaborative relationships between individuals.

As Daniel Todes elaborates in his highly influential study, the term "struggle for existence" is ambiguous and has multiple potential meanings: "[Russian biologists] were especially careful to make three sets of distinctions: between indirect competition and direct struggle [...]; between intraspecific and interspecific relations; and between an organism's relations with other life forms and those with the physical environment." (Todes, 1987, 543). We consider this threefold distinction to be highly commendable and should be borne in mind when dealing with inter-organismic relations.

2.2 Nature and morality

In his book *The Descent of Man*, first published in 1871, Charles Darwin expanded on the topic of competition and distanced himself even further from a purely competitive interpretation. There, he defended the importance of cooperation in nature, arguing that social instincts, which are common in animals, endow them with "a moral sense or conscience" that lead them to feel sympathy for their fellows and to aid one another in a form of many mutual services (Darwin, 1877, 98, 101). He also had acknowledged that it is not uncommon that animals belonging to different species live together and that this impulse to aid one another is impelled by the satisfaction the individual who performs the service receives for their action (100, 104). Darwin hypothesized that these sensations of sympathy that prompt animals to live together were developed in order to induce those animals that would benefit from living in society to gather in groups (105). Moreover, Darwin importantly distinguished the emotion of sympathy from that of love. Unlike social Darwinism, which considered that competitiveness prevailed in nature and in society, Darwin makes some place for cooperative instincts, favored in particular at the level of the group.

Thomas H. Huxley also elaborated on the topic of nature and morality in his book *The Struggle for Existence in Human Society* (1888). There, he criticized the social Darwinist thesis that nature is ruled by fierce competition and has a normative value, so that struggle is the only way to reach progress in society. In contrast, he proposes a more radical separation between nature and morality: while in nature the struggle for survival prevails, human societies come about because there are principles of cooperation. Human civilized society is then a social construction in which principles different from those that dominate in nature prevail. Therefore, cooperation is only possible when the struggle for life that corresponds to nature is reduced to a minimum in society due to "unnatural" cooperative moral principles (Dugatkin, 2006; Huxley, 1888).

Kropotkin's work on *mutual aid* generally falls broadly within this network of discussions outlined above, but the elaboration of his proposal was triggered in response to Huxley's argument. He disagrees that the animal world is all about fighting, "at the same level as a gladiators' show," in Huxley's words (Huxley, 1894, 200). In response to Huxley, Kropotkin argues that nature is itself cooperative, and he appeals to science to offer a "naturalized" alternative to explaining cooperation among both humans and other animals. Although Kropotkin has been considered more of a political thinker than a scientist, some scholars contend that he was a high esteemed scientist for his contributions to Geography and Earth Sciences, whereas his theory of mutual aid was "mostly rejected or

ignored" and suggest that there was an "a priori rejection" of his thesis by the scientific community (Johnson, 2019, 5). The influence of his thinking for scientific reasoning has been overall underappreciated.

2.3 A Russian tradition

The emphasis on the role of cooperation in evolution has been judged to be a main point of disagreement between the British (and, generally the Western) evolutionary tradition and others (Oldroyd, 1986), including the Russian one (Todes, 1989). Kropotkin states that he was inspired by the Russian biologist Karl Kessler, who proposed the notion of mutual aid and defended its relevance for the evolution of species in a speech delivered in December 1879 at the St. Petersburg Society of Naturalists, under the title *On the Law of Mutual Aid*. The ideas put forward in his speech were received with enthusiasm within Russian academia and, although Kessler died before he could develop his theory, the idea of the relevance of mutual aid in nature became a common component of Russian evolutionary thought (Todes, 1989), and served as a starting point for the development of later lines of research on the collaborative nature of relationships between animals. Particularly, the Russian tradition claimed that rather than struggle between individuals belonging to the same species, it is the direct action of the environment, combined with geographic isolation, that produces new species, while mutual aid between individuals increases the likelihood that these new variants will survive and develop (Todes, 1989).

In contrast to Kessler's ideas, Kropotkin's theory is built in terms of instincts of sympathy between individuals, which would have evolved as a response to the need to adapt to the harsh conditions of living. A central idea in Kropotkin's work is that organisms fight other organisms when resources are limited, as anticipated by Malthus, but cooperate when they face adverse environmental conditions or threats posed by members of other species (e.g., predators). Subsequently, this hypothesis on the natural evolution of mutual aid served him to naturalize his political and moral theory regarding human societies.

Kropotkin's views were also motivated by his observations, during his expeditions through Siberia and the Manchurian peninsula, that competition between individuals of the same species for resources was not the norm, but the exception. Kropotkin argues that the struggle for existence occurs primarily in the face of adverse environmental conditions, not as competition between individuals of the same species for the access to scarce resources:

> [...] even in those few spots where animal life teemed in abundance, I failed to find –although I was eagerly looking for it– that bitter struggle for

> the means of existence, AMONG ANIMALS BELONGING TO THE SAME SPECIES, which was considered by most Darwinists (though not always by Darwin himself) as the dominant characteristic of struggle for life, and the main factor of evolution. (Kropotkin, 1902/2018, 1; emphasis is original)

The harshness of living conditions is the main obstacle to the survival of individuals and the maintenance of species, so that mutual aid between individuals can be expected to be a valuable resource (Dugatkin, 2006; Kropotkin, 1902/2018). Kropotkin argues that mutual aid is far more frequent than competition between individuals of the same species and refers to several examples of cooperative sociability in the animal kingdom. In building his argument, he relies both on his own observations of migrations of large ruminants in the Siberian steppe and large flocks of birds for mutual protection, as on examples of cooperation and mutual aid in (almost) all major animal groups, both vertebrate and invertebrate, drawing on a copious literature in zoology and ethology.

Hence, in order to understand life and nature, we must attend to cooperation between individuals as much or more than to competition: "Kropotkin has therefore created a dichotomy within the general notion of struggle – two forms with opposite import: (1) organism against organism of the same species for limited resources, which leads to competition; and (2) organism against environment, which leads to cooperation." (Gould, 1988). In this sense, as Gould (1988,18) remarks, Kropotkin should not be read as an isolated thinker, but as representative of a "standard, well-developed Russian critique of Darwin, based on interesting reasons and coherent national traditions."

Kropotkin did not view cooperation and mutual aid as being based on reciprocity, at least not in the sense of tit-for-tat exchanges. Following Darwin, he considered mutual aid a natural instinct in humans and animals, a means of fulfilling a natural desire for social connection and community, a capacity not limited to within-species cooperation, but occurring also between different species, as observed in symbiotic relationships. He conceived of mutual aid as a fundamental principle of evolution, not based on an individualistic, self-interested calculation of benefits and costs, but on a holistic view of relationships and inter-dependencies (Azurmendi, 2016).

2.4 Life relations

A main theoretical contribution of Kessler's work that we want to underline is the introduction of the concept of "life relations" between different organisms, which operate as an evolutionary factor in nature (Todes, 1989). Kessler referred

to these "life relations" as inter-organismic dependencies occurring in relation to two types of drives: the need for food and the impulse to reproduce. Of the two, reproduction is presented as the activity in which collaborative relationships are more likely to be established:

> The 'life relations' among fish, however, were fluid and subject to two distinct influences: while the drive for food generated a harsh, individualistic struggle, the drive to reproduce often led fish to live peacefully together. (Todes, 1989, 110)

According to Kessler's observations in fish, fighting and competition are more often associated with foraging, while cooperation and sociability are connected to reproduction. We are particularly interested in the concept of "life relations" because of its positive aspects with respect to the role that cooperation plays in evolution. However, this distinction did not hold in the subsequent literature on cooperation within the mutual aid tradition (for instance, Kropotkin does not attribute cooperation to certain life functions or drives), but it does provide a basis for exploring the importance of reproductive life relations when examining biological ontologies.

In the next sections, we suggest that Kropotkin's ideas resonate with much of the later literature on social collaboration between individuals and constitute a good starting point for a conception of life which stresses mutual relations for, after all, "[s]ocial life —that is, *we*, not *I*— is the normal form of life. *It is life itself"* (Kropotkin, 1922/2009, 44-45; emphasis in the original).

From these nineteenth-century discussions, two ways of understanding and studying the relationships between organisms and their role in evolution can be distinguished in the history and philosophy of biology. They are associated with two important scientific problems of a great philosophical interest: the relative role of collaboration in evolution and the genesis of new types of individualities in the evolution of the living world. Both have been quite controversial for different reasons as we will show in the following section.

3. Collaborative relationships: two research lines

Throughout the twentieth century, two very important research lines were developed in evolutionary biology addressing the role of collaborations, and not just competition, in evolution. They both share at least a derived connection with the work of Kropotkin, or with the idea that it is important to study how collaborations evolve and influence evolution.

The first research line focuses on whether there can be altruist behavior between individuals of the same species on the basis of evolutionary dynamics (Etxeberria & Pérez Iglesias, 2020). Relationships between individuals are modeled in game theory terms, where individuals must always maximize their benefits. This way of conceiving relationships in nature is based on an idealized notion of individuality, according to which the individual organism (and sometimes the individual gene), clearly delimited and individualized in its environment, is the relevant unit in ecological interactions and hence, in evolution.

The second research line examines how relations between organisms transcend individualistic ontology: it postulates the emergence of new types of entities based on processes of symbiosis and interweaving between individuals. In this second tradition, through the development of *naturalized ontological models*, the evolutionary role of heterogeneous individuals, such as chimeras or holobionts, is considered.[1]

3.1 Intraspecific relations

The first perspective views evolution through the lens of fitness, and assumes that the traits of biological individuals reflect their individual interests; therefore, the goal of evolution is to increase the fitness of individuals. Mathematical models attempt to assess the degree to which relationships between individuals may be advantageous or disadvantageous in maximizing the organism's fitness. From this perspective, natural selection would not favor acts of biological altruism resulting in improving the fitness of other individuals while decreasing the fitness value of the individual performing the altruist behavior (Lewens, 2015). Hence, in evolutionary biology altruism seems not to be possible in view of certain theoretical assumptions.

This paradox has been addressed by mainstream evolutionary biology during the twentieth century by either denying the existence of altruism in nature or finding alternative ways of explaining the evolution of altruism. Both strategies have been explored by the elaboration of game theoretical mathematical models in terms of conflict of interests. It is within this research line that the group selection controversy takes place, which debates the feasibility and strength of natural

[1] An anonymous reviewer sensibly noted that these two traditions that we describe here are the ones that gave rise to the 'evolutionary change' and 'adaptationist' traditions, respectively, as distinguished in (Goodnight, 2015). The former, which corresponds to kin selection theory, tries to explain social traits such as altruism by identifying the adaptive forces that lead to it; in contrast, the latter tradition, which is identified with the theory of multilevel selection, focuses on measuring ongoing selective processes. This points to the relevance of our historical work for current biological practice .

selection at the level of the group, in contrast to the level of the individual. Group selection, in contrast to individual selection, could explain the evolution of collaborative behaviors. As mentioned before, Darwin had already tried to explain these phenomena by making use of group selection thinking. In *The Descent of Man* (1877, 132, 610), he discusses the idea that natural selection could act at different levels of organization, including the level of the group. Darwin argues that the advance of morality would give an evolutionary advantage to cooperative tribes over those formed by selfish individuals. This idea was also defended by Alfred Russel Wallace, who firmly believed that competition between groups could lead to the evolution of cooperative behaviors. He also proposed that group selection could help to explain the evolution of moral behavior in humans, and that the development of such instincts could help groups to compete more effectively against other groups (Durant, 1979).

This idea, however, became highly controversial during the development of evolutionary thought during the twentieth century. The precursors of the Modern Synthesis, who developed the first evolutionary mathematical models during the 1920s and 1930s (Ronald Fisher, J. B. S. Haldane and Sewall Wright) understood that group selection may allow the evolution of altruism, but they "doubted the importance of this evolutionary mechanism" (Okasha, 2020). However, Sewall Wright developed his *shifting balance theory* in 1932, where he considered inter-group selection in the evolution of natural populations (Wade & Goodnight, 1998). Later on, during the mid-twentieth century, different biologists, most notably Konrad Lorenz, began to study cooperation in animals by making use of group-based thinking, but these studies did not prosper much further, as several mathematical models discredited the idea of group selection at the time, and the hypothesis lost its prestige within the scientific community (Okasha, 2020). In the 1960s, George C. Williams and John Maynard Smith also opposed to group selection theory by questioning (mathematically) the possibility of it evolving, since, they argued, group selection was a very weak evolutionary force. Hence, it would eventually lead to altruistic strategies being exploited for the benefit of selfish individuals, and therefore, they would eventually disappear. However, by this time Michael Wade was doing both theoretical and empirical work proving the role of group selection in the evolution of social behaviors such as cooperation (Wade, 2016).

Later models tried to understand behaviors of apparent altruism among genetically related individuals, while maintaining the selfish premise. *Kin selection*, initially proposed by William Hamilton, explains altruism on the basis of *inclusive fitness*, which allows to calculate whether it is worthwhile for an individual to help relatives carrying the same genes. These are strategies to preserve certain

genes regardless of who their carriers are in the form of apparently altruist behaviors that would mask an ultimately selfish reality, as Richard Dawkins (1976) concluded.

An alternative to kin selection was offered by Robert L. Trivers (1971), who developed the theory of *reciprocal altruism* in order to explain support between individuals that do not belong to the same family, population or species. Here, the basis for explaining altruism is not shared genes but reciprocity. Altruism depends on the probability that the favor performed will be returned in the future. Hence, altruism will only evolve if this probability is high. According to this model, the disadvantages for altruistic individuals are compensated by the help that the current helper will receive in the future. This would be the basis on which cooperative behavior would evolve.

Later, by relying on the work of Wade and others who had been elaborating on the idea of group selection, Elliott Sober and David Sloan Wilson (1998) would defend the feasibility of group selection; they developed a model that demonstrated the advantage of groups where altruist individuals abound, with respect to groups where altruists are more scarce, even when selfish individuals do better than altruists within the group.

The strand of this research line that rejects group selection has been built on the premise that individuals are largely self-sufficient, and that their investments are best for themselves and not for other individuals. Hence, they conclude that altruism ought to be rare or insignificant in nature, and apparently non-existent in the most primitive organisms, so that it cannot build up evolutionarily until humans.

In sum, within this research line, questions of cooperation and competition are discussed in the framework of an understanding of evolution in which organisms must maximize their fitness. In general, with the exception of Trivers, models are restricted to cases of intraspecific relationships. Kinship, reciprocity, or group cohesion are the features that make it possible to transcend selfishness in certain special cases. When relations between organisms are considered beyond a strict individualistic framework, evolution can be compatible with altruistic manifestations, even in the framework of population genetics. This is precisely the aim of group selection scientists and the motivation of multi-level selection theories.

With respect to the theses defended by kin selection advocates, we can note that Kropotkin already criticized in his writings the fact that cooperation is conceived at the level of the family, since he considers that family relationships between individuals were formed later in evolution than those occurring in the wider group or tribe. Therefore, relatedness cannot be the foundation of social

organization. Kropotkin is convinced that cooperation is the norm rather than the exception in nature, and present in all forms of life, microbes included. Consequently, he argued that altruistic principles of cooperation constitute an instinct, a basic drive of life, instead of a social construct as Huxley proposed. The contribution of Kropotkin and the proponents of mutual aid to the research agenda of the group selection theory is the realization that fitness can also be increased by cooperation. For instance, Mark Borrello (2004) finds a parallelism between group selection and Kropotkin's mutual aid, in contrast to the view of nature where struggle of each against all prevails, such as Huxley's.

3.2 Interspecific relations

The second biological research line for which Kropotkin's cooperative thinking is relevant is the one centered on symbiosis and, more importantly, the theory of endosymbiosis, which gave rise to the notion of the holobiont. Kropotkin makes a brief mention of the possibility of cooperation even among microbes, when he states that "Mutual aid is met with even amidst the lowest animals, and we must be prepared to learn some day, from the students of microscopical pond-life, facts of unconscious mutual support, even from the life of micro-organisms" (Kropotkin, 1902/2018, 13–14). Indeed, Kropotkin appears as a precedent for work on evolution by association of individuals (Sapp, 1994), holobionts (Baedke et al., 2020) and symbiosis (Toepfer, 2011, Carrapiço, 2015, Suárez, 2018).

On her part, Lynn Margulis often acknowledged debts in her ideas of evolution by symbiosis or association of individuals to her Russian precedents (such as Brandt), who originated in the same research line stemming from Kessler's seminal speech (Lazcano & Peretó, 2021). Also, Margulis noted that Kropotkin's work on mutual aid had "inextricably permeated discussions regarding the participants in symbiosis" (Margulis, 1997, 298). Margulis developed a collaborative view of life, according to which evolution occurs on the basis of the relationships established between organisms. This was called the theory of symbiogenesis, a phenomenon that constitutes a major factor in evolution (Sagan, 1967). In general terms, within this research line, collaborations between individuals of different species in the co-constitution of individuals is studied. Also, the importance of microbes on Earth is stressed, something that until a few decades before was not so evident, since studies of both life and evolution were mostly limited on animals and plants. Margulis, in contrast, focused on the microcosm of the smallest organisms on the planet and was interested in how they relate to each other. In particular, she elaborated the endosymbiotic theory of the origin of eukaryotic cells, which emphasizes the origin of eukaryotic cells as the most remarkable discontinuity in the evolution of life on Earth, an evolutionary

transition that is not due to the slow and progressive accumulation of mutations under the scrutiny of natural selection, but by the *collaboration* between two prokaryotic cells that previously had independent lives and that, after the association, give rise to a new kind of individual: the eukaryotic cell.

The collaboration envisaged in the theory of symbiogenesis is substantially different from other accounts which also consider that there can be cases of interspecific cooperation in the form of mutual aid (such as Trivers' proposal of section 3.1.), as it suggests a tighter form of collaboration involving the generation of new ontologies in the living world.

The fundamental difference between symbiogenesis and the use of the term symbiosis in ecology is that while the latter is a relation between separate individuals, often understood in game theoretical terms, in the former a partnership is established at the organizational level, which alters both the topological configuration and the functional dimension of the new system, from which arises an entangled inter-being between the two parties that are associated. The distinction between the strongest cases (i.e., endosymbiosis) and the weakest (i.e., temporal association) is not sharp, as nicely shown by Javier Suárez and Vanesa Triviño, who argue that cases of symbiosis apart from endosymbiosis, such as holobionts, also entail a fundamental reorganization of the interacting individuals to the point of altering their individuality and identity (Suárez & Triviño, 2020).

The two main avenues or research lines that since Kropotkin have explored collaborations as relations between organisms propose very different ways of approaching the nature of such relations. More importantly than whether they focus on intra- or interspecific relations, we have stressed some of the most remarkable differences in the models that are proposed: while the first approach elaborates game theoretical models that try to reflect the evolution of natural populations in terms of fitness values and differing interests, the second research line focuses on the material dimension of the relations between organisms and the entanglements that give rise to new systems and individualities.[2]

[2] The second research line has recently extended towards different kinds of models for the evolution of holobionts. Notably Huitzil et al. (2018) model the host and the microbiota as Boolean networks, Roughgarden (2020) compares vertical and horizontal transmission of microbiota within a multilevel selection framework and Lloyd & Wade (2019) discuss holobionts using community genetics and population genetics models.

4. "Life relations" in viviparous reproduction

In the process of reproduction, various forms of relationships can occur between organisms, including those that reproduce sexually and those that reproduce asexually. However, in sexual reproductive relations we observe a greater diversity of inter-organismic relational dependencies: between sexual partners during mating and/or fertilization, between the gestating individual and the developing embryos for incubation and food provision, between parents and their offspring during parental care, and even care relationships between individuals without direct kinship (alloparenting).

In this section, we illustrate the female-fetus inter-dependence in viviparous reproduction to compare the contrasting interpretations of pregnancy from the two research lines in the previous section. The former suggests a conflict between the mother and embryo that needs resolution, while the latter proposes collaborative mechanisms that sustain gestation duration.

4.1 Modeling eutherian pregnancy as a conflict

Mother-offspring relations have been modeled in standard biology during the twentieth century as conflict between the interests of the gestating organism *versus* those of the conceptus, or embryo, both conceived as discrete individuals according to the first research line of section 3. The way in which individuality and evolution are conceptualized within the standard framework of the Modern Synthesis has led to this depiction of the mother-offspring relationship. Individuals are considered to be distinct, cohesive entities with traits that can exhibit some degree of heritable variation. Such variation can influence the likelihood of successful reproduction and may, therefore, be subject to natural selection. Then, ecological interactions between individuals, including those that occur during reproduction, are typically analyzed in terms of their impact on the fitness of the parties involved. As a result, the prevailing narrative often portrays these interactions as a struggle between individuals with competing interests. This perspective is also applied to reproductive relationships during gestation in viviparous species.

The conflict hypothesis of mammalian pregnancy can be traced back to the work of Peter Medawar, who in 1953 defined the immunological paradox of pregnancy: "how does the pregnant mother manage to nourish within herself, for many weeks or months, a fetus which, antigenetically, is a foreign body?" (Medawar, 1953, quoted in Schjenken et al., 2012, 212). Medawar arrived at this paradoxical situation by drawing a comparison between the immunological circumstances of the embryo during gestation and a semi-allogenic graft.

The latter refers to a foreign organ or tissue that possesses allogenic antibodies, which should typically trigger the immune system to recognize it as non-self and prompt rejection by the organism.

However, this analogy is inappropriate because, in contrast to what occurs in the case of a transplant, during pregnancy the circulatory systems of mother and embryo do not mix, as the placenta acts as an anatomical and immunological barrier (Male, 2021). Victoria Male argues that the immune situation of pregnancy is more akin to that of the gut in presence of the microbiome, which enjoys an *immune privilege*. This situation allows the uterus to establish and maintain some lack of response to external elements at the mother-embryo interface, which includes the placenta and the uterine wall (Male, 2021). This form of immunological tolerance should be understood as an active and collaborative immunoregulation carried out by the systems of the mother and the embryo, not as a phenomenon of immunosuppression or a "sabotage" of the passive mother's immunology by the developing embryo[3]. Hence, this shows how studies on reproductive immunology are flawed insofar as they are based on a false assumption that misleads a proper understanding of reproductive ontology. This conflict-oriented mode of reasoning, which is built upon a bias in scientific practice, has shaped a whole research line that tries to identify immune regulatory mechanisms to aid embryo tolerance (see Schjenken et al., 2012 for a review).

This conception of reproductive immunology as a conflict between mother and embryo has been very influential in the evolutionary conceptualization of pregnancy, leading to the formulation of the so-called "mother-offspring conflict hypothesis" (Haig, 1993, 1996). In his work, David Haig argues that, because mother and fetus possess an unequal genetic makeup, they may have misaligned "interests" in nutrient supply. From an evolutionary point of view, fetal genes would have been selected to increase investment, while maternal genes would be selected to limit nutrient transfer. Thus, because half of the fetal genome is of paternal origin, the optimal amount of investment for the fetus is always higher than that of the mother, so that mother and fetus are predetermined to compete for resources. This model, formulated in economic terms of investment, competition for available resources and conflict of interests, clearly reflects the mode of reasoning characteristic of the standard framework of the Modern Synthesis and to the theory of kin selection explained in section 3. This account, in which war-like terminology abounds, seems but an extension of the interpretation of nature as fierce competition for survival, conceptualizing the mother-fetus interface as

[3] This form of collaborative immunoregulation is clearly illustrated by the fact that components of both maternal and embryonic origin participate in the immunoregulation that allows implantation and maintenance of the embryo in the maternal uterus in pregnancies with invasive implantation, as in the case of primates and rodents (Male, 2021).

a "battlefield" (Haig, 2003, 500), where the mother tries to contain the "fetal invasion" (Haig, 2003, 502). However, this interpretation of the relationships established during gestation, which supports the pregnancy conflict hypothesis, is not the only possible one: models of maternal-fetal coadaptation have been formulated, which predict the evolution of genetic factors that favor the integration of maternal and fetal traits (Wolf & Hager, 2006, 2009). Furthermore, the prevalence of matrigenetic control (i.e., dependent on maternally derived genes) in placental development and embryo selection at implantation indicates that the depiction of the embryo manipulating maternal physiology toward increased investment is flawed.

The mother-offspring conflict hypothesis is in agreement with a conception of pregnancy that regards the mother's body as a mere container of the developing embryo: the so-called *container model* of pregnancy, according to which the female uterus is nothing but a vessel that contains the embryo who, purportedly, has by itself all the necessary tools for developing. This model is as well aligned with the way in which individuality and evolution are understood within the standard framework of the Modern Synthesis, which neglects the causal importance of developmental processes and material entanglements, and, correspondingly, does not pay attention to the relationships between mother and embryo in the generation of the progeny. The container model of pregnancy has been recently criticized from many different perspectives (Gilbert, 2022; Kingma, 2018, 2019; Nuño de la Rosa et al., 2021).

The issue is that the pregnant female-embryo relationship is often modeled in the same terms as inter-organismic relationships in kin selection models, which assume that individuals must maximize their own fitness to evolve. This is problematic for reproductive relationships where both parties aim to achieve a shared goal and perform functions that are not solely individualistic.

4.2 Modeling eutherian pregnancy as an emerging symbiotic unit

Alternative models to the conflict account of pregnancy appear to be closer in inspiration to interspecific models of entanglement and symbiosis (than to the intraspecific ones). For example, a recent proposal consists in overcoming the mother-embryo conflict view to embrace a cooperative perspective of the relations that are established during pregnancy in eutherian mammals. In Nuño de la Rosa et al. (2021) an ontological view of relations of inter-dependency in eutherian pregnancy involves the emergence of a new form of joint individuality based on the physiological entanglement constituted by the gestating mother and the developing embryo.

While emphasizing the historical dimension of the evolution of pregnancy, in this model viviparous gestation implies the emergence of a new type of biological individual: the pregnant female as a *historical individual* (Nuño de la Rosa et al., 2021). This gestating individual, composed of the integrated physiology of female and embryo, has a transitory character, this being one of the fundamental aspects of its ontology. Eutherian pregnancy, as well as the historical individual of the pregnant female, is a stationary stage, which is temporally delimited by two inflammatory events: the implantation of the embryo and the delivery. Hence, this model offers a strikingly different view of the role of the immune system in pregnancy from that proposed in the conflict model. Here, the immune system is not a limiter of mother-embryo interaction or an element of conflict, but a facilitator of the incubation relationship and the exchange of substances. The evolution of eutherian viviparity involves the evolution of a new cell type that is fundamental for the establishment and maintenance of mother-embryo relations during gestation: the decidual cells. This new cell type, involved in the exchange of nutrients and waste substances between mother and embryo, arises as a consequence of the recruitment of the inflammatory mechanisms of the innate immune system, which allow the implantation of the embryo in the endometrium (Erkenbrack et al., 2018; Stadtmauer & Wagner, 2020; Wagner et al., 2014).

According to this model, the development of the embryo occurs from a stage of quasi-non-differentiation in this emergent and transient individual that constitutes the *pregnant* gestating female, to a stage of birth, after which the individual constituted by the gestating female would cease to exist and gives way to female and offspring as separate beings; although the connection remains close after birth, the interacting entities no longer consist of a single individual (Nuño de la Rosa et al., 2021). Therefore, according to this model, the mother-embryo relationship is the result of a form of *collaboration* in evolution, where the mother's physiological systems are reorganized and accommodated to incorporate the developing embryo; therefore, both mother and embryo collaborate in reproduction through the establishment of the transient individual of the pregnant female.

Thus, as illustrated throughout this section, the ideas initially proposed by Kessler in the context of Russian biology, and importantly developed by Kropotkin, are of great relevance when discussing ontological problems about life relations in reproduction. The notion of mutual aid, extended to genetic and physiological collaboration between individuals for reproduction, offers a compelling alternative to accounts restricted to competition and conflict in biology.

5. On collaborations and inter-dependencies

The inter-organismic dependencies which we discussed in the previous sections can be seen as a special class of life relations in that they exert a form of top-down influence in the *relata*, which is a fundamental and unavoidable feature of life as an Earthly phenomenon. The concept of *inter-dependence*, which involves a form of top-down causation, refers to the collaborative relationships that have been stabilized through evolution between (two or more) organisms of the same or different species. These relationships can have an impact on the development and evolution of the involved organisms. These supra-organismal phenomena can occur at the social level within an organism's ecological environment, and they have the potential to modify the interactions in which individuals participate, thereby influencing their adaptability.

The form of collaborative relationality as dependence on the others that we propose in this paper endows significant consequences for organismal autonomy. Autonomy is often associated with views in which autonomous individuals appear to be self-contained to a large extent (in the sense that their identity depends only on internal conditions), and whose goals are related to self-development and self-maintenance (Moreno et al., 2008; Moreno & Mossio, 2015). Such internal organization secures the system from being altered by the external environment by maintaining their internal stability (Bich et al, 2016; Rosslenbroich, 2014). This conception of autonomy, which overemphasizes individuality, has been the target of many criticisms, especially in domains related to care, such as healthcare, or political and economic scenarios defending collectively regulated settings (Armstrong et al., 2019; Mackenzie & Stoljar, 2000). In this paper, we have shown a perspective that opposes to this conception within the biological domain: in Pyotr Kropotkin's "mutual aid" scenario not only cooperation is enhanced instead of competition, but also it is based on a different notion of individuality, which is stronger in the sense of being more comprehensive and richer because it conceives of multiple biological inter-dependencies. Hence we can identify two different understandings of autonomy in biology: one of them relates to isolation in the sense of independence from the effects the environment and focuses on the inner workings and processes of the organisms, and the other one has to do with the interactions of a system with the environment and others and how those relationships shape the identity and individuality of the organism.

This theory about the evolutionary relevance of mutual aid in nature certainly makes sense in the framework of an agential theory of evolution, which understands evolutionary change as the product of interactions between the agent organism with its environment, including other agents.

It is generally understood that the agential behavior of organisms emerges from the individual's struggle for existence in their environment (Jaeger, 2021). From the lens of our reading of Kropotkin, this "struggle for existence" can be viewed in a wider way which includes organisms collaborating for survival in a co-dependent way. Hence, life relations (both inter- and intraspecific) would have an enormous evolutionary value, because, through agential evolution, they would importantly construct and shape the environment in which organism-agents dwell, which have important effects on the evolution of new characteristics, be they social or morphological. For example, the complex intraspecific relations observed in some social insects can be interpreted as an emergent organizational level facilitated by cooperative sociability in a framework of reciprocal causality between the organismic level and the colony, including top-down influences of the social relations between organisms in the wider framework of the colony upon the individual insects (cf. Canciani et al., 2019). Correspondingly, interspecific cooperation undoubtedly plays a fundamental role in the evolution of many species.

Some of the most important discussions about the evolution of sociability have revolved around kinship (*does it facilitate prosocial and cooperative behavior?)* and reciprocity (*does the evolution of prosocial behavior require a basis for reciprocity?).* A recent collection on the topic (Swain et al., 2021) criticizes the idea of associating solidarity with reciprocity as this scheme does not ensure the advance of a collaborative social organization.

One issue where Kropotkin's position seems to challenge some intuitions about the evolution of sociability is the need for helping others to be compensated by reciprocity. Although throughout his book Kropotkin seems to compel the idea that reciprocity at a social level is what sustains mutual aid, it does not occur necessarily in one-to-one instances of cooperation. Thus, not every single case of mutual aid between any two individuals needs to be reciprocal in the sense of rendering a net positive balance for each of the participants in any particular relation. It is in the wider frame of social inter-dependence in which mutual aid is sustained and the top-down influence of life relations upon organisms is exerted.

Therefore, when it comes to the evolution of prosocial behavior, the greater difficulty is to account for the dynamics of commitment between collaborative sociability and autonomy. In doing so, we would have to explore what types of behaviors and inter-dependencies favor the evolution of a form of sociability that guarantees autonomy, while being based on dependencies and relationships between individuals.

Among the cooperative relations discussed in section 3, reciprocal altruism has received a great deal of attention. An important contribution of Trivers'

model of reciprocal altruism (reviewed in section 3) is that it can explain altruistic behavior between individuals belonging to different species. Trivers presents the examples of cleaning symbioses between fish of different species and warning calls between birds belonging to the same species. The basic thesis is that natural selection may favor altruistic behaviors of this type because they are beneficial to the altruistic organism in the medium/long term, as well as to the organism receiving the help in the short term.

Since it does not benefit the fitness of the altruistic individual even in the medium/long term, non-reciprocal altruism is difficult to integrate into evolutionary theory. And yet, it seems clear that, at least in the case of human beings, some individuals behave in non-reciprocal altruistic ways toward strangers that are difficult to be explained by kin selection and reciprocal altruism (Singer, 2011).

Michael Tomasello (2016) relates altruism, reciprocal or not, to inter-dependence: individuals of socially complex species depend on each other in many ways and, if an organism's fitness depends on the group (as, for example, to defend against predators, to make alarm calls, as coalition partners, etc.), then it is in the organism's interest that group mates do well. In these cases, cooperating or helping is not a sacrifice, but an investment at the group level. Altruism, then, would be an essential part of the social lives of organisms living in inter-dependent relationships with other organisms.

One of the aims of this paper has been to examine the role of collaborative relations within an organismal framework concerned with the notion of autonomy in biological explanations. The notion of autonomy as individuality has to be questioned to emphasize inter-organismic relations in charge of many of the features of organisms. Accordingly, the challenge in biology is how to understand autonomy in a way that it does not restrict the identity of an individual to its internal organization and addresses the relevance of interactions with the environment (including other living beings), while it allows us to understand individuality as a true self-determination that emerges from a set of inter-dependencies.

6. Conclusions

The goal of this paper was to explore the evolutionary significance of collaborative relationships among organisms, whether they belong to the same species or different ones. We accomplished this by drawing on Kropotkin's ideas as well as various biological research lines that have been inspired by them: the first debate concerning altruism and the second concerning symbiotic ontology. The former has led to several research projects on pro-social behavior from various biological disciplines such as ethology and behavioral ecology. These projects fall under the

paradigm of evolutionary biology, which views organism-environment fit as optimizing adaptations. The second topic under consideration pertains to the way in which individualities are merged or interwoven during evolution, whether the individuals belong to the same species or different ones. Apart from symbiosis, we also examined the development of transient individualities during eutherian viviparous reproduction. In this scenario, collaborating individuals not only assist each other, but also become integrated or fused with each other, resulting in the emergence of novel ontologies that vary in terms of their stability. This provides the basis for our investigation of inter-dependence as an evolutionary factor in organism-centered evolutionary biology. By taking inter-dependence into account, our perspective on individuality, agency, and sociability is transformed.

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