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INDIVIDUALS AS ECOSYSTEMS: AN ESSENTIAL TENSION

*Ist es ein lebendig Wesen,  
das sich in sich selbst getrennt?  
sind es zwei, die sich erlesen,  
daß man sie als eines kennt?*  
(Goethe, 1819)

1. From individual to “individual”

The notion of individual as irreducible uniqueness has become an important epistemological device for modern evolutionary theory. At the same time different disciplinary tools, honed by constant technological innovation, have redefined in their turn the biological boundaries of what is understood as “individual”.

In examining the constitutive role of “individual” (e.g. its theory making in population genetics), as well the problematic meaning of the concept (one composed by many), we may observe epistemic transfers of entities, whose philosophical depth is here the issue.

«No one supposes that all the individuals of the same species are cast in the very same mould. These individual differences are highly important for us» states Darwin in the *Origin of Species* (1859, p. 45), focusing the individual differences as a crucial matter for natural selection.

In contrast with the essentialist approach, which looks for an invariant property across organisms in a species, the Darwinian turning-point was the recognition of the essential irreducibility of differences among individuals, overcoming the universal integrity of species. In Darwin’s theory variety is not merely a deviation from a “normal” state, but rather inter-individual differences caught by population thinking are meant as basic requirements for natural selection and species change (Sober, 1980).

Besides this “one long argument”, the Darwinian perspective entails other relevant approaches on the “individual” as an epistemologically unstable notion.

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Darwin focused his interest on single individual entities – among insects in particular – which serve as breeding-, feeding-sites and larvae niche-sites for other individual entities, in which boundaries between body and environment cannot be easily distinguished, as they fade one into one another<sup>1</sup>. After all, the nineteenth-century tradition of vegetable hybridity through grafts is also included in Darwinian evolution, pointing to the “plural-individual” rather than the “individual-niche”<sup>2</sup>.

Afterwards, in the 1940s, body-compounds (not only species-specific) as hybridism or durable relations of parasitism have no space in Modern Synthesis (MS) discussions, which are primarily inspired by the strong explicative principles of population thinking and natural selection.

The “differing-among-individuals” is in fact the backbone of one of the most challenging topics of MS: population genetics.

This discipline – the statistic measurement of allelic frequency distribution within random mating populations, *panmixia* – allows us to formalize Darwinian population thinking and to corroborate gradualist and microevolutionary explanations for speciation through mathematical and statistical modeling style (Mayr and Provine, 1980).

Nevertheless, still another conception of “individual” is preserved. Studies on form in changing and body identity over a lifetime shows how all individuals transform themselves over time, i.e. the statute of “individual” singularity changes from embryogenesis to senescence. Transformations of identity during the course of a single life are characterized by multiple realities. For this reason, non-linear (structural and functional) explanations are required<sup>3</sup>.

Far from our species’ experience, the category of individuality – that is, the meaning of “cohesion”, “identity”, “uniqueness” and “self-belonging”, “autonomy” – has changed dramatically in recent times. The definition of identity attributions is even more ambiguous when organisms – including humans – are considered along with all the micro-alterity they house and

<sup>1</sup> Ichneumonidae is one of these cases. Injected larvae of wasps feed the body-host, till it becomes their habitat. See Darwin’s letter to Asa Gray May 22 1860 (Darwin, 1887, p. 312).

<sup>2</sup> Cfr. Darwin, 1868, p. 405: «There is a considerable but insufficient body of evidence showing that the tissues of two plants may unite and form a bud having a blended character; or again, that buds inserted into a stock may affect all the buds subsequently produced by this stock. Two embryos, differing from each other and contained in the same seed, may cohere and form a single plant».

<sup>3</sup> A non-linear explanation is, for example, the explanation of the developing in arthropods focusing on larva or on adult form (Minelli, 2007), as well as periodic oscillations between stable multicellular aggregates or singular moving entities depending on ecological restrictions (*Dictyostelium discoideum*), or even the ambivalent status of a body which is, during its living state, meal or nest of another.

with which they are mutually dependent. In this line of research, the focus is on bacterial world (symbionts) according to which each organism is a real “chimera” entity (Pradeu, 2012) made up of several bacterial species combining into a single major host organism (eukaryote).

Within this context, the notion of individual seems to be constitutively redefined (Casiraghi, 2013; Baptiste and Dupré, 2013), thus entailing two possible, but unusual, explanations: 1) it is a “niche” inhabited by others; 2) it is a composite and “heterogeneous whole”. Apparatuses, cells and even our eukaryotic DNA include a huge prokaryotic world (bacteria) inhabiting them, which modulates their chemistry, and governs their metabolism. The eukaryotic genomes themselves, originated from remote puzzles, are composed also of bacterial insertions (Gilbert and Epel, 2009). This implies an epistemological shift that will account for systems made up of multiple genomes which are still interfered by such hosts.

“Symbiome” (Lederberg, cit. in: Sapp, 2003, p. 333, n. 5), “con-dividui” (Gagliasso, 2009), “integrated systems” (Symbionts and host), “hologenome” (Rosenberg and Zilber-Rosenberg, 2011), “chimeras” (Pradeu, 2012), “holobiont/holobiome” (Guerrero, Margulis and Berlanga, 2013) are some of the metaphorical terms that are given birth (to decay or to successfully colonize the field) in order to name or redefine unusual entities embedded in the traditional and species-specific concept of individual. These composite entities which are characterized by different identity features – even from an immunological standpoint – as discussed hereafter – may still be studied from the perspective of population genetics.

However, within this context, many statement in evolutionary terms seems to lose univocal meaning, unfolding different theoretical perspectives and methodological paths. How can we identify an individual constitution? At which level does selection operate? What methodological instruments should be used to investigate the above-mentioned coherence and this sort of micro-ecologies? Last but not least: what happens to population genetics in the context of symbiontology?

## *2. Same equations with conflicting interpretations*

Since the 1930s-40s Modern Synthesis has explained both the uniqueness and differing of each organism among others in genetic terms. The strategic expansion of mathematical patterns derived from the Hardy-Weinberg Law<sup>4</sup>, has made it possible to use computational analysis of

<sup>4</sup> Within constant conditions – i.e. when evolutionary forces of mutation, selection, drift

allelic frequencies to measure evolutionary changes in a population.

Using a unifying but non homogeneous focus, MS created a new meeting ground for different disciplines. The naturalist and ornithologist Ernst Mayr focused on the role of naturalism in non-essentialistic review of systematics<sup>5</sup>. For the geneticist William B. Provine, instead, the focus was on his own field: the new discipline of population genetic (Mayr and Provine, 1980).

The difference was subtle but it does have some theoretical relevance for the scientific status of MS (Continenza, 2010). One side gave priority to computational protocols based on axiomatic standard in relation to population genetics; naturalists, on the other hand, gave priority to systematic investigations of the role of drift, isolation or behavior.

As a result, an essential epistemological tension emerged and still persists between a reductionist and a pluralist approach.

Despite this polarization, population genetics became a common testing ground for evolutionism in those years. In the joint project of the 1930s, the “differing-among-individuals” was at the basis of the mathematical modeling strategies adopted. Nevertheless, the pioneers of population genetics, Sewall Wright, John S. Haldane and Roland Fisher had their disagreements, as shown by the controversy between Fisher and Wright (Provine, 1986, p. 232). Although using the same equations, while neither of them called into question the operative role of mathematical and statistical analysis, they radically differed in terms of theoretical premises of living nature. The controversy had to do with the identity of the object on which natural selection operates, the role of natural selection itself and the nature of evolutionary change (Winther and Wade, 2013). According to the mathematician Fisher, revealing gene interactions for quantitative traits in great and uniform populations random inbreeding was at the heart of statistical analysis. The physiologist Wright, instead, pointed to the problematic underdetermination of inbreeding in non-uniform natural population, thus developing a different concept of population, called “structured population”. Fisher argued that:

the whole investigation may be compared to the analytical treatment of the the-

and migration are not at work – the Hardy-Weinberg principle affirms that frequencies remain constant from one generation to another and the dominant allele does not eliminate the recessive one. This balanced state is a landmark of population genetics. In fact, if one knows the balance point, the statistical study of interferences that alter this balance can provide a reasonable estimate of allele frequencies in the future generation.

<sup>5</sup> Despite direct observation, in Linnean systematics the taxonomic method is still dominated by scholastic logic, i.e. individuation criteria based on morphological differences and similarities. Modern systematics is based instead on differential reproduction, as opposed to static and timeless categories (Mayr, 1942).

ory of gases, in which it is possible to make the most varied assumptions as to the accidental circumstances, and even the essential nature of the individual molecules, and yet to develop the general laws as to the behaviour of gases, leaving but a few fundamental constants to be determined by experiment (Fisher, 1922, pp. 321-322).

Instead, based on his observation of variability in nature, Wright started from different assumptions, which led him «to use statistics interpretatively rather than for description and prediction» (Crow, 1994, p. 445).

In other words, Fisher assumed that random gene-frequency fluctuations and gene interactions in a population are similar to noise in uniform systems (e.g. physical systems). Wright, instead, considered these fluctuations an opportunity for evolutionary change and believed that selection usually operates on a «large species which is subdivided into many small local races, each breeding largely within itself but occasionally crossbreeding» (Wright, 1932, p. 166)<sup>6</sup>. Sharing the same equations, population genetics has conflicting interpretations based on its qualitative research object seen as “structured population” or “uniform population”.

Whereas the effects of selection have been adequately formalized in population genetics, the object of selection is still problematic, due to the fact that research usually focuses on the interaction between organism and environment.

Richard Lewontin, Wright's most influential student and theoretical forerunner of present Darwinism, can be considered the joining link between MS and current extended theories of evolution. Since the 1970s, as a population geneticist, Lewontin focused on ecological action, that is, the integration between the genetic dimension of organisms and their role as a whole and as builders/destroyers within the environment. The individual is seen by Lewontin not only as a unity of selection, but as a “subject in action”<sup>7</sup>, thanks to a double level of explanation: evolutive and eco-evolutive. Thus, a genealogical level (i.e. the individual in population genetics) and an ecological level (i.e. the individual whose action transforms environments and *vice versa*) are simultaneously taken into account (Eldredge, 2002).

As a result, the notion of individual is located in a circular relationship, extending the thematic field of inter-individual differences: from the gene pool to living conditions. A circularity between active and passive role is the result of emerging loops between what organisms do and their genetic

<sup>6</sup> According to the “shifting balance theory”, the evolutionary adaptation in sub-populations with limited gene-flow is faster. This theoretical formulation is topologically expressed by its images of “fitness landscape” (Caianiello, 2009).

<sup>7</sup> This is even better accounted by Lewontin-inspired theory of “niche construction” (Odling-Smee, Laland and Feldman, 2003).

drift.

This active and passive roles have theoretical and practical implications for theory and this undermining and redefining of what is nowadays meant by “individual” is reinforced by exploring of bacterial worlds that both are hosted and modulate it.

### 3. Plurality “of” individuals and plurality “within” individuals: symbiotic universes

Only in the twentieth century, have microbes been truly integrated in evolutionary biology<sup>8</sup>. Since the 1970s, Lynn Sagan Margulis has been investigating the history of ancestral DNA and each linear phylogeny following the theory of bacterial and viral intersections in primordial DNA. This theory was later defined as Horizontal Genome Transfer (HGT) (Jain *et al.*, 1999). Her approach ratifies the leading role of bacterial worlds and their aggregative rather than selective properties (Sagan, 1967; Margulis and Fester, 1991).

In addition to the evolutionary history at macroscopic species level, an “underground” history thus unfolds starting from remote eras (O’Malley and Dupré, 2009). Starting from macromolecular prebiotic aggregates, the archaeobacteria developed becoming capable of self-reproduction and cooperation by adopting a border-membrane that isolated them from the outside, through which they exchanged energy with the environment. By colonizing of the Earth, archaeobacteria mass induced a chemical transformation of the primordial atmosphere, making life possible for other living beings.

These cooperative co-optations and mixed symbiotic genomes priority do not seem compatible with classic MS, namely the idea of DNA informational species-specific code and selective competition as the main drives of evolution.

This invisible bacterial world, made up of viruses and nucleus-lacking prokariota with floating DNA, accounts for 90% of our planet’s biodiversity. Only in the last 30 years, these life forms, so remote from our anthropocentric projections, have been explored in detail thanks to powerful new technology and *ad hoc* modeling<sup>9</sup>. Data has revealed many different rates of

<sup>8</sup> After the works of Pasteur and Koch, the world of “bacilli” and “microbes”, whose existence, in 1676, had been guessed by Leeuwenhoek thanks to the use of the first microscopes, became the object of a real discipline: microbiology. Since the mid-nineteenth century viral and bacterial microcosm (with the exception of the microorganisms responsible for fermentation) were considered as a world of pathogenic and contagious entities.

<sup>9</sup> New advanced technologies such as culture in isolation, observations by transmission

evolution, unusual morphologies, unexpected reproductive processes, specific motility towards chemical stimuli (Berg, 2004), peculiar nutrition-absorption strategies along with planet wide presence even where life is seemingly absent. The rate of symbiotic genes within human population has turned out to be about six times that of human genes<sup>10</sup>. From the bacterium side – the biologist S.J. Gould has commented – the human body appears as a huge mountain widely extended, virtually eternal, suitable for all kinds of exploitation and not very dangerous, unless you stumble into penicillin (Gould, 1997). In such world of bacteria over 70% of the analyzed gene sequences belongs to previously unknown bacterial species. On a theoretical and explanatory level, the bacterial universe puts consolidated theories and models to the test and engenders new ones (Ramellini, 2013).

It also challenges some among the classic principles of the philosophy of biology, as illustrated by two recent special monographic issues of *Philosophy and Biology* (O'Malley, 2013a) and *Biological Theory* (Van Baalen and Huneman, 2014), devoted to symbiontology. Bacterial universe highlights the limitations of the trophic definition of life based on oxygen consumption and carbon cycle<sup>11</sup>, the modern systematics of differential reproduction – since prokaryotes reproduce themselves asexually (Cleland, 2013) – and the linearity of phylogenetic descent, due to the phenomenon of genetic transfer from bacteria to the other species's genomes. Finally, and of paramount interest from a philosophical perspective, the bacterial universe calls into question the notion of individual itself.

Work in progress in the philosophy of biology presently includes high differences among bacterial species, the possible revision of the notion of species, and the identification of adequate theoretical and pragmatic criteria to do that.

When we take into account genetic insertions as sources of continuous genetic variation what becomes increasingly evident is that viruses and bacteria are very important factors for the uninterrupted “evolvability” of the living world as well as its extraordinary biodiversity (O'Malley, 2013a). HGT phenomena as encapsulated traces of ancestral evolution, already identified in the 1970s, seem to be common, pervasive and constantly occurring (de la Cruz, Davies, 2000).

electron microscope (observing thin sections of cells and internal structures) or scanning (for three-dimensional images of the cells), as well as strategies for staining bacterial necessary to view entities that otherwise couldn't differ from the surrounding.

<sup>10</sup> In every individual there are from  $10^{13}$  to  $10^{14}$  microorganisms that contain genes 100 times more than the human genome (McFall-Ngai, 2008; Hattori and Taylor, 2009).

<sup>11</sup> In the case of extremophile bacteria that earthly life works synthesizing other substances such as sulfur, methane, chloride salts (Cleland, 2013).

In the light of these rapid HGT, macromutation – a crucial question of philosophy of biology – needs to be reconsidered, leading to a radical revision of phylogenetic trees and systematics.

The metaphorical image of the tree constantly branching out into more and more separate species is becoming inadequate to represent the continuous genetic intersections among species (Woese, 2004, p. 184). A new type of tree with anastomosed branches is proposed by Cleland (2013) and O'Malley (2013b) to highlight lateral transfers of bacterial groups: a sort of “webbed- tree”<sup>12</sup>.

Genetic transfer is a break in the species-specific linearity of DNA descendants. The cohabitation between the hosting body and its hosts, previously considered as a temporary exception, is now conceived as a lasting phenomenon, making major organisms and bacteria mutually dependent.

In addition to bacterial intersections in other genomes, the presence of bacteria “assists” embryonic development and guarantees its regularity in many eukaryotic species (McFall-Ngai, 2002). In practice, we are dealing with mutually dependent cooperating systems and functional metabolisms which break genetic and cellular linearity and undermine the notion of self-identity, driving it into an undefined and uncertain area.

While iconic metaphors of webbed-tree are used to take into account HGT, there is also a proliferation of linguistic metaphors used to redefine the notion of “individual”, both in a genetic and organic sense (Frezza and Gagliasso, 2014).

“Genome” even though currently in use, is not accurate enough. In its place, “hologenome” is used to designate this integrated *bricolage* between bacteria and eukaryote DNA. The “holobiont” is no longer an “individual” but, as a functional system of plurality, is becoming a “biotic system”. The “microbiome” is an entire ecological world inhabiting a major organism, more precisely «the ecological community of commensal, symbiotic, and pathogenic microorganisms that literally share our body space and have been all but ignored as determinants of health and disease» (Lederberg, 2001, p. 1).

<sup>12</sup> In the light of this new representation of evolution (webbed-trees), the studies on more classical metaphorical images in the history of nature, such as the ladder, the map and the tree, could be further updated (Barsanti, 2010).

#### 4. Epistemological shifts and essential tensions at work

The above situation can be described in two ways: as a) an organism “composed” of multiple species (a major organism and its symbionts) or as b) different types of “cohabiting Symbionts” for whom the major organism is the habitat. Which should be the unit of selection, or on what level does natural selection act, has recently become an intriguing question. From the side of “hosted” entities (symbionts) bacterial strains are selected by internal habitat changes (e.g. the interference of antibiotics), so that the major body is the context (*milieu*) where plural micro-diversity evolves. In this case the individual is replaced by nested systems of various different entities, a micro-ecology where what matters are the boundaries between parties, membranes, trophic exchanges (i.e. “microbiota”). From the major organism’s perspective (holobiont/hologenome), instead, the “dividual” is selected as a cohesive unit. However, the differences between such composite entities are still captured by population genetics analysis, even if the major organism and hosts entities are connected in a co-evolutionary history<sup>13</sup>.

More precisely, when we inspect holobionts (i.e. the organisms with their accompanying microbial communities) we realize that population thinking is applied to bacterial strains housed by major organism, and these strains are selected on the basis of their differences. What is more, in this network of mutual dependence, every single bacterium has its own immune system to defend itself against its “predators”: the bacteriophages<sup>14</sup>. Thus, the notion of population is even more extended to include the phages which prey on bacteria while using them.

In other words, on the one hand, even bacteria – singular entities or population groups – are “individuals” and they are selected on the basis of their differences. On the other hand, bacteria are also builders/destroyers of their habitat (the body-host). Thus, it is possible to apply to bacteria both perspectives: “population thinking” and the “eco-evolutive key”, two perspectives which are already combined by population genetics’s critical scientists.

Thus, the multi-level application of population thinking does not exclude the approach of organism/environment as integrated whole. For example, a lack of some bacteria in embryonic cells can distort embryonic

<sup>13</sup> A recent example is provided by a comparative study between Italian population and the Hazda, a clan of Tanzania population. In this case two populations, living in very different cultural conditions, are considered together with their own, context-dependent, different gut symbiotic balance (Schnorr *et al.*, 2014).

<sup>14</sup> Bacteria also have a sort of immune system which recognizes and defends them from foreign genetic material such as the one brought by phages (Seed *et al.*, 2013).

development in many animals. For this reason, bacteria populations are inherited on a maternal basis, parallel to a genetic one (Jablonka and Lamb, 2006). Far from being an aseptic growth in a sterile container, development in the womb gives rise to lifelong bacterial companions. Within 4-36 months of life, the bacteria-based (microbiota) human immune system develops through maternal intimate contact.

In the light of these facts, the connection between hologenome (the combined genetic information of the diverse microbiota) and holobiont (body-host and microbiota) establishes a common field for symbiontology and epigenetic research (Love and Travisano, 2013; Stazi and Toccaceli, 2014).

Furthermore, the extension of the concept of “individual” to include different sets of species-specific entities, outlines a new subject: a plural and coordinated construct. Thus, in symbiontology a sort of biased way of thinking is reiterated: as a matter of fact, the population thinking, *lato sensu*, is corroborated and enlarged, whereas population genetics, *stricto sensu*, based on formalization of allelic frequencies reduces its centrality and has to renounce some of its previous gene-centered hegemony.

As much as population thinking enlarges himself, population genetic narrows its previous gene-centered hegemony. The individual, formerly described as a passive object of selection (the “vector” of genes), becomes instead actively involved of the selection processes thanks to its behavioral and ecological activity, as emphasized by Lewontin, Gould, Eldredge, Laland, Pigliucci. This active-passive dynamic is found also in the transactional relations between symbionts and their host. Once again, the alternative is between gene-centered *vs.* eco-evolutive criteria. This implies a transformation of the classical notion of individual, in which the polarities are neither mutually exclusive nor summable.

From an epistemic standpoint, this means that it is necessary to switch back and forth between the two perspectives. In nature, instead, polarities operate in the same “complex set” of regulations and selections. Thus, from a cognitive viewpoint, interpreting research data on symbiosis in an evolutionary framework requires a non-trivial “and-and” approach, rather than an “either-or” one, adequate to the ambivalence of the categories.

In the 1970s, the Pandora’s box of microbiology (Woese, 2004) was opened, but only in the last twenty years an ubiquitous symbiotic bacteria world has emerged, with all of us in the role of major host organisms.

This is why it is only recently that discoveries have had a feed-back on genetics and on contemporary evolutionism, including a significant influence on theoretical and categorical issues. The cooperation of different embedded strains raises the question of species-specific identity. Genetic and

epigenetic inheritance – inclusive inheritance – juxtaposes with the linearity of classic population genetics and the natural selection acts on multilevel units. Thus, an “entity” can be grasped as our perceptual-cognitive simplification of this process, a kind of “still image”<sup>15</sup>. As a result, boundary renegotiations and connections within and between organisms are no longer only species-specific.

Important epistemic challenges to disciplinary borders (Woese, 2004), and re-definitions of the ontological entities involved, are now being debated in philosophy of biology and philosophy *tout court* (Gagliasso, 2009).

Lexical innovations which try to grasp new portions of reality – interactive metaphors such as the above-mentioned hologenome, holobiont, microbiome, chimeras, etc – are being circulated. At the epistemic level there is a sort of fluctuation between a reductionist approach (in population genetics) and a transactional interpretation of processes (in theories of development and in symbiontology).

Yet, as we have already argued, the two different approaches do not seem mutually exclusive. Rather they are in a relation of “essential tension”, which is characteristic of evolutionary theory itself. Indeed, similar tensions seem present even inside the discipline of symbiontology.

On the one hand, there is a project of human hologenome sequencing. It is interesting to note that, in this project, the complex of bacterial hosts is called *Second Genome*<sup>16</sup>. The research project is in line with the vision (or pre-vision) of the *Human Genome Project* (Fox Keller, 2000): it has the same predictive ends as a goal, along with a promise of benefits for our species, such as innovative drug therapies.

On the other hand special attention is paid to epigenetic and circular modulations of ecological microcosms “within” the organisms, that is, the microbiome as a complex system that co-evolves and interacts with the host organism. From archeobacteria co-optations in eukaryote cell structures in remote eras (Sagan, 1967; Margulis and Fester, 1991; Ramellini, 2013), to current epigenetics interactions among individuals, this research can be well integrated within the methodological framework governing the studies of the interconnected dynamics of living networks (Buiatti, 2013) and of the multiple forms of cooperation between plant species and fungi (Giovannetti, 2013).

<sup>15</sup> In supporting this kind of “Heraclitean” biology, Waddington (1940) emphasized “moving equilibria” dynamics, as a “pause” more or less extended in the flow of development process.

<sup>16</sup> The *Second Genome Project* is a huge project consisting in the sequencing of the genome of over 100 trillion microorganisms on interior and surface human apparatus. See <http://www.secondgenome.com/vvhat-is-the-microbiome/>.

Summarizing, population genetics and its axiomatic trend – a pillar of population thinking – has allowed us to reformulate systematics without falling into essentialism. Going beyond and connecting biometric and mutationist theories, population genetics has been able to explain gradual speciation, placing evolutionary biology among predictive sciences. This formalization can be useful also for hologenomes and “mixed” genetics, as shown by the *Second Genome Project*.

However, if explanations is made by interactive dynamics, in and out organisms, and symbiogenesis is in connection with embryonic development studies (Minelli and Pradeu, 2014) this frame constitute the other epistemic side, whereas studies of the individual as “body-niche” do not seem to use tools from traditional population genetics.

Thus, from an epistemic viewpoint, what is meant by “individual” is changing. At the same time, the notion of natural selection, the main explanatory principle of evolution, has become even more problematic.

The subject of selection has shifted in population genetics from the organism, as in Darwin’s perspective, to the cellular level. The constructive interaction between organism and environment highlighted by population genetics evidences the co-evolutive interaction and the active role played by the whole organism. In this context, the “individual” corresponds to the species-level (Gould, 2003), or the cluster-level on which selection acts. Moreover, “sorting selection” in groups (Gould and Vrba, 1986) calls into question the classical notion of natural selection. Within a symbiotic universe, the selected unit is a plural entity such as the holobiont.

These level transitions have a role in the meta-critique of old and new priorities in a philosophy of biology that questions classical philosophical categories like “individual”. In order to recognize the so-called individual entity and to follow its development over the course of time, the philosophical criteria are neither only “identifiers” nor “individuative”, since identifying means pointing to an identity, and the issue we are dealing with concerns, precisely, plural and dividual, entities.

Nevertheless, there are coherences among heterogeneous components (i.e. different species nested in one). What matters is the fact that an entity changing over time is both an organism and a habitat for others entities. The ubiquity of symbionts’s populations across species-specific differences and their pervasiveness affects plants, insects, and other animals, including human beings.

This requires revising pre-existing categories based on ontological criteria of homogeneity and “thingness”.

Current evolutionary theory also needs to reset its notions. New metaphors and trends, competing or corroborating each other, raise new ques-

tions about what are the main drives of evolution and consequently what kind of Evolutionary Synthesis we should expect.

Since new names are indicators of chosen priorities, even renaming is a meaningful operation. Thus, the name “Modern Synthesis” is at the heart of a heated conflict between those who still consider it as valid and those who consider it obsolete, downgrading the MS of the twentieth century to “Standard Synthesis” (Laland *et al.*, 2014).

More weight is given to disciplinary fields previously overshadowed by gene-centered causality, such as developmental biases, plasticity, niche construction and inclusive inheritance. Thus, “Post-modern Synthesis” (Koonin, 2009), “Extended Evolutionary Theory” (Pigliucci and Müller, 2010), “Hierarchical Synthesis” (Eldredge, 2002), and “Eco-Evo-Devo” (Ecological, Evolutionary and Developmental theory) (Gilbert and Epel, 2009) are some indicators of an epistemic effort claiming for re-orienting research protocols through a recognition of their alternative evolutionary approach by the scientific community.

Epistemology is being affected by the transitions in the above models. These can be the starting point, for instance, for a genealogical approach, starting from a re-examination of a number of heterodox theoreticians (mostly dealing with development studies, like Baldwin, Goldschmidt, Waddington) contrasted with the representatives of orthodox neo-darwinism. In other cases, consistently with a neo-lakatosian approach, evolutionary theory is seen as the enduring core, alongside which however other interpretations can be usefully employed (Pievani, 2012).

Focusing on different interpretations, instead, a deliberative act may be invoked as an account of which what matters is a temporary “partial framing”, and not a general one.

Thus, the choice between different approaches, associated with the research perspectives of different groups, is context-dependent. It is a collegial and common choice operated by those who decide that certain data or theory corroboration are sufficient to have a “new field” or a further unification of an old field.

Similarly, beyond the identification of research fields, a fruitful essential tension (using Kuhn’s expression) seems to be emerging, even though when one is in the midst of it, it is never clear whether one is navigating in the calm waters of linear cumulative research, or in the troubled ones of innovative and discordant ideas.

Certainly, as a counterpoint to the rigorous training in “convergent thought” intrinsic to scientific research (present even in the new trends), a “divergent thought” is needed, as Kuhn pointed out many years ago:

I shall therefore suggest below that something like “convergent thinking” is just as essential to scientific advances as is divergent. Since these two modes of thought are inevitably in conflict, it will follow that the ability to support a tension that can occasionally become almost unbearable is one of the prime requisites for the very best sort of scientific research (Kuhn, 1959, p. 22).

### 5. Conclusions

We started with a question: what happens when the category of individual is examined using the theoretical and experimental apparatus of a specific new perspective that have emerged in biology? Our survey shows that “individual” as a specific philosophical concept, on both a theoretical and an empirical level, is necessarily affected by what is happening in the field of biology.

In this sense, the concept of individual can be used to pursue a theoretically appealing path. The notion of individual seems to become almost an oxymoron: it is no longer a condition of self-identity but a usually discontinuous transition-phase that goes beyond a simple and homogenous ontological entity (Minelli and Pradeu, 2014). Furthermore, the individual is constituted by phases integrating a plurality of different cooperating species in a unit.

In scientific lexica it is cognitively and linguistically difficult to replace entities with processes, names with verbs. But exploring the dynamics of these concepts modifies the concepts themselves and their epistemic depth.

“Individual” is a basic category. It is a founding category of modern philosophy and of bio-evolutionary thinking, as well. It presents meaningful shifts due to theoretical and experimental upheavals whose importance is the real issue at stake for philosophy.

From this observational viewpoint, we can notice essential conceptual tensions at work (Kuhn, 1959), typical of the discipline of biology, in order to understand them through a fruitful methodological oscillation.

A critical examination of the philosophy of biology, and of philosophy in general, reveals how – even in this case – we are dealing with mobile theoretical frameworks that encapsulate categories. These frameworks are not filters that distort the relationship between us and the world, but tools offering us a conscious “looking-through” never drawing from the medium, in which we are placed exactly like insects encapsulated in amber (Garroni, 1992).

A critical reasoning in philosophy of biology, as in philosophy in general, reveals how – even in this case – we have to do with mobile theoretic-

Commentato [AG1]: Perché sottolineato?

cal frames that encapsulate categories. Frames that are not filters by which the relationship between us and the world is distorted, but tools for a conscious “looking-through” never drawing from the medium in which we are placed exactly like insects encapsulated in amber (Garroni, 1992). Every theory is a medium without which it is impossible to look-through and its vision becomes stratified “inside” conceptual categories themselves: a concept may change its internal connotations, while preserving its name. Just in this sense, the meaning of individual can come to intercept what we known to be a chimeric plurality.

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