ANNEX 2 - Biological Concepts' Table

The table below describes more in details biological concepts (in the context of this research also considered as "biological solutions") summarized in section 4.3 and utilized to extract principles as per section 4.4.

(Epi)Genomics	
Basic definition	**Description**
Gene	Genes are the sequence of nucleotides in DNA or RNA that encodes the "instructions" of product such as RNA or protein. They are region of the DNA. Genes can acquire mutations in their sequence, leading to different variants, known as *alleles*, in the population. (Wikipedia – *Gene*)
Genotype	The genotype is the part of the genetic makeup of a cell, and therefore of any individual, which determines one of its characteristics, traits or phenotypes. Genotype is one of three factors that determine phenotype, along with inherited epigenetic factors and non-inherited environmental factors. (Wikipedia – *Genotype*)
Phenotype	The phenotype of an organism is the composite of the organism's observable characteristics or traits, including its morphology or physical form and structure; its developmental processes; its biochemical and physiological properties; its behavior, and the products of behavior, for example, a bird's nest. An organism's phenotype results from two basic factors: the expression of an organism's genotype, and the influence of environmental factors, which may interact, further affecting phenotype. (Wikipedia – *Phenotype*)
Gene expression	GE is the process by which information from a gene (genetic code-the nucleotide sequence) is used in the synthesis of a functional gene product contributing to the emergence of phenotypes. There are different mechanisms at play that carry out and regulate gene expression (Wikipedia – *Gene expression*)
Concepts/ Processes	**Description**
Genes variations	Modification of genes is a major avenue for generation of genetic novelties which could potentially become adapted phenotypes and therefore innovations. Genes variations can occur by: **DNA/Gene Mutations:** A mutation is the permanent alteration of the nucleotide sequence of the genome of an organism, virus, or extrachromosomal DNA or other genetic elements. Four classes of mutations are (1) mutations due to errors during replication (2) mutations due to error-prone replication bypass of naturally occurring DNA damage, (3) errors introduced during DNA repair, and (4) induced mutations caused by mutagens. (Wikipedia – *Mutation*) **Gene Duplication:** Gene duplication (or chromosomal duplication or gene amplification) can be defined as any duplication of a region of DNA that contains a gene. Gene duplications can arise as products of several types of errors in DNA replication and repair machinery. Duplication creates **genetic redundancy**, where the second copy of the gene is often free from selective pressure (so they are not deemed to be expressed during the development of the host) —that is, mutations of it have no deleterious effects to its host organism. If one copy of a gene experiences a mutation that affects its original function, the second copy can serve as a 'spare part' and continue to function correctly. Thus, duplicate genes accumulate mutations faster than a functional single-copy gene, over generations of organisms, and it is possible for one of the two copies to develop a new and different function. (Wikipedia – *Gene duplication*) During duplication the following can occur: **emergence of new function** (Neo-functionalization), **split of function** between the two new genes (sub-functionalization) or also **loss of function** in one of the duplicated genes. (True and Carroll 2002) **Genetic Recombination:** GR is the exchange of genetic material between different organisms which leads to production of genetic variations in offspring. Homologous recombination (HR) is a type of genetic recombination in which genes (nucleotides sequences) are exchanged between two similar or identical molecules of DNA. Homologous recombination is also used in horizontal gene transfer to exchange genetic material between different strains and species of bacteria and viruses. This is a major avenue of generation of novelties (more than mutations) (Wikipedia – *Genetic Recombination*)

	Horizontal Gene Transfer: HGT is the movement of genetic material between unicellular and/or multicellular organisms other than by the ("vertical") transmission of DNA from parent to offspring. It is a typical mechanism utilized by bacteria to evolve. The horizontal gene transfer contributes to the diversification and adaptation of microorganisms, thus having an impact on the genome plasticity. (Wikipedia – *Horizontal Gene Transfer*)
Genetic Co-option (Exaptation)	Co-option (or Exaptation) occurs when natural selection finds new uses (functions) for existing traits (also: a shift in the function of a trait during evolution), including genes, organs, and other body structures (and behaviors). Birds feathers are a classic example: initially they may have evolved for temperature regulation, but later were adapted for flight. Genes can be *co-opted* to generate developmental and physiological novelties by changing their patterns of regulation, by changing the functions of the proteins they encode, or both. Both structural gene and developmental genetic circuit co-option can occur and co-option may underlie major episodes of adaptive change in multicellular organisms. Comparisons among the genomes of multicellular model organisms, indicate that apparent increases in complexity, in terms of morphogenetic intricacy, cell-type diversity, and behavioral and physiological repertoires, from worms and flies to mice and humans have not involved a corresponding amount of gene invention. From this the importance of co-option as avenue for diversity. (True and Carroll 2002)
Gene regulation and the Gene Regulatory Network	Gene regulation is a label for the cellular processes that control the processes of gene expression. It is a complex set of interactions between genes (structural and regulatory), RNA molecules, proteins and other components of the expression system which determine *when and where specific genes are activated and the amount of protein or RNA product produced.* Gene regulation gives the cell control over structure and function, and is the basis for cellular differentiation, morphogenesis and the versatility and adaptability of any organism. Gene regulation may also serve as a substrate for evolutionary change, since control of the timing, location, and amount of gene expression can have a profound effect on the functions (actions) of the gene in a cell or in a multicellular organism. (Wikipedia – *Gene expression*)
Phenomics	
Concepts/ Processes	**Description**
(Developmental) Genetic Toolkit	Genetic toolkit is *the small subset of genes in an organism's genome whose products control the organism's embryonic development*. Toolkit genes are highly conserved among phyla (sign of robustness), meaning that they are ancient. Differences in deployment of toolkit genes affect the *body plan* and the number, identity, and pattern of body parts. The majority of toolkit genes are *components of signalling pathways*, and encode for the production of transcription factors, cell adhesion proteins, cell surface receptor proteins, and secreted morphogens, all of these participate in defining the fate of undifferentiated cells, generating spatial and temporal patterns, which in turn form the body plan of the organism. (Schneider and Amemiya 2016)
Continuous vs discontinuous variation of trait	**Continuous** variation of a trait refers to changes in a *quantifiable property* across extensive numbers of generations. More likely to reach adaptive peak than a single large discontinuous change. **Discontinuous** variation refers to a binary change between the two states of absent and present as a consequence of developmental dynamics rather than the accumulation of small variational changes (no link with ancestor). *Qualitative* change. (Peterson and Müller 2016)
Epigenetics and Epigenetic network	Epigenetics is the study of *heritable* phenotype changes that *do not involve alterations in the DNA sequence* (but activation of genes for new functions). A change in phenotype without a change in genotype — which in turn affects how cells read the genes. Epigenetic change is a regular and natural occurrence but can also be influenced by several factors including age, the environment/lifestyle, and disease state. Epigenetic modifications can manifest as commonly as the manner in which cells terminally differentiate to end up as skin cells, liver cells, brain cells, etc. (Wikipedia – *Epigenetics,* https://www.whatisepigenetics.com/fundamentals/) An epigenetically-inherited trait *can arise simultaneously in many individuals*, as opposed to a single individual with a gene mutation. Moreover, a transient epigenetically-modified phenotype can be quickly "sunsetted", with individuals reverting to the original phenotype. Thus, epigenetic phenotype switching is dynamic and temporary and can help bridge periods of environmental stress. Epigenetic inheritance likely contributes to evolution both directly and indirectly. (Burggren 2016; Mendizabal et al. 2014; Handy, Castro, and Loscalzo 2011)
Ecology	

General concepts	Description
Evolution	Evolution is the change in the heritable traits characteristic of a population over generations. These characteristics are the expressions of genes that are passed on from parent to offspring during reproduction. Different characteristics tend to exist within any given population as a result of mutation, genetic recombination and other sources of genetic variation. Evolution occurs when evolutionary processes such as natural selection (including sexual selection) act on this variation, resulting in certain characteristics becoming more common or rare within a population. It is this process of evolution that has given rise to biodiversity at every level of biological organisation, including the levels of species, individual organisms and molecules. (Wikipedia – *Evolution*)
Evolutionary Novelty/Innovation	The concept has different definitions still open to debate. Ernst Mayr defined novelty as ‘‘*any newly acquired structure or property that permits the assumption of a new function’’. The notion of equating novel traits with novel functions”*. Linking novel traits to novel functions often carries with it the implication that the new trait evolved because of the new function that it carries out, *that selection somehow favored the origin of the new trait because its new function was advantageous.* However, for selection to play a role, there must have been heritable variation for both trait and function, but if that were the case the trait under consideration could no longer be considered a novelty. In another way, *selection cannot act on traits that do not yet exist, and therefore cannot directly cause novelty*. Muller, who defined novelty as ‘‘*a qualitatively new structure with a discontinuous origin, marking a relatively abrupt deviation from the ancestral condition*’’. No need of new function. However, this definition does not determine where quantitative variation ends and qualitative distinctness begins. How much deviation from the ancestral condition is enough? How different is novel? A *morphological novelty* is a structure that is neither homologous (“the same organ in different animals under every variety of form and function’’) to any structure in the ancestral species or homonomous (“the same organ in different places of the same organism “) to any other structure in the same organism’’. (Moczek 2008) According to Pigliucci*, evolutionary novelties are a necessarily fuzzy concept* and proposes an amended definition of evolutionary novelties*: Evolutionary novelties are new traits or behaviors, or novel combinations of previously existing traits or behaviors, arising during the evolution of a lineage, and that perform a new function within the ecology of that lineage.* This definition makes explicit the fact that (1) often novelties are not absolute discontinuities but can be built on previously existing parts, (2) indicates that they are a phenomenon that affects the evolution of certain lineages without implying that all derived characters are in fact novelties, and (3) requires some kind of ecological function to eventually be coupled with the novelty (Pigliucci 2008; Pigliucci, Müller, and Konrad Lorenz 2010)
Fitness	Fitness is the quantitative representation of natural and sexual selection within evolutionary biology. It can be defined either with respect to a genotype or to a phenotype in a given environment. In either case, it describes individual reproductive success and is equal to the average contribution to the gene pool of the next generation that is made by individuals of the specified genotype or phenotype. The fitness of a genotype is manifested through its phenotype, which is also affected by the developmental environment. The fitness of a given phenotype can also be different in different selective environments. The term "Darwinian fitness" can be used to make clear the distinction with physical fitness. Fitness does not include a measure of survival or life-span; Herbert Spencer's well-known phrase "survival of the fittest" should be interpreted as: "Survival of the form (phenotypic or genotypic) that will leave the most copies of itself in successive generations." (Wikipedia – *Fitness (biology)*)
Ecological niche	Ecological niche is a term for *the position of a species within an ecosystem, describing both the range of conditions necessary for persistence of the species and its ecological role in the ecosystem*. Ecological niche subsumes all of the interactions between a species and the biotic and abiotic environment, and thus represents a very basic and fundamental ecological concept. The tentative definition presented above indicates that the concept of niche has two sides which are not so tightly related: one concerns *the effects environment has on a species*, the other *the effects a species has on the environment*. In most of ecological thinking, however, both meanings are implicitly or explicitly mixed. The reason is that ecology is about interactions between organisms, and if persistence of a species is determined by the presence of other species (food sources, competitors, predators, etc.), all species are naturally both affected by environment, and at the same time affect the environment for other species. If we want to treat both of these aspects of ecological niche within one framework, we can define it more formally as *the part of ecological space (defined by all combinations of biotic and abiotic environmental conditions) where the species population can persist and thus utilize resources and impact on its environment.* It is useful, however, to distinguish three main approaches to the niche. The first approach (*Grinnellian*)

	emphasizes environmental conditions necessary for a species presence and maintenance of its population, the second approach (*Eltonian*) stresses the functional role of species within ecosystems, and the third one (*Hutchinsonian*) sees a dynamic position of species within a local community, shaped by species' biotic and abiotic requirements and by coexistence with other species. In the Eltonian concept of niche, each species has a particular role in an ecosystem. For instance, according to Elton, there are detritivorous, dispersal or pollination niches (Elton 1927). Therefore, this functional niche refers to a species position in ecological networks, and is often used in functional ecology and ecosystem ecology. This definition is also closely related to the concept of 'guild' or 'functional groups' which aggregates species according to their trophic relationships with the biotic environment (e.g. scavengers, grazers and seed eaters). Therefore, the Eltonian specialization refers to the functional position of species in its environment and is measured as the species *breadth* of functional roles (that is considered a synonym of impact) instead of resource used. Elton historically assimilated the niche of a species to its 'place in the biotic environment, its relations to food and enemies' *so that the functional role of the focal species most usually refers to its impacts on other species* (e.g. pollination, predation and herbivory). However, abiotic changes generated by the focal species can also be considered (e.g. oxygen generation, carbon dioxide acquisition and mineralization) as they indirectly impact on other species in the ecosystem. (Polechová and Storch 2008; Dehling and Stouffer 2018)
Guild	A guild (or ecological guild) is any group of species that exploit the same resources, or that exploit different resources in related ways. It is not necessary that the species within a guild occupy the same, or even similar, ecological niches. Ex nectar eating, seed eating birds. *Guilds are defined according to the locations, attributes, or activities of their component species.* For example, the mode of acquiring nutrients, the mobility, and the habitat zones that the species occupy or exploit can be used to define a guild. The number of guilds occupying an ecosystem is termed its *disparity* (different specializations/function). Members of a guild within a given ecosystem could be *competing for resources*, such as space or light*, while cooperating* in resisting wind stresses, attracting pollinators, or detecting predators. Although studies of species linked by a common resource (i.e. ecological guilds) have so far mainly focused on competition and predation, guilds are also good places to find mutualism. (Wikipedia – *Guild (ecology)*) (Blondel 2003; Simberloff and Dayan 1991; Wilson 1999)
(Evolutionary) Adaptation	In biology, adaptation has three related meanings. Firstly, it is the dynamic evolutionary process that fits organisms to their environment, enhancing their evolutionary fitness. Secondly, it is a state reached by the population during that process. Thirdly, it is a phenotypic or adaptive trait, with a functional role in each individual organism that is maintained and has evolved through natural selection. (Wikipedia – *Adaptation*) Adaptation differs from *flexibility*, *acclimatization*, and *learning*. Which are all processes of *phenotypic plasticity*. Flexibility deals with the relative capacity of an organism to maintain itself in different habitats: its degree of specialization. Acclimatization describes automatic physiological adjustments during life; learning means improvement in behavioural performance during life. (Burraco et al. 2017)

Processes	Description
Co-evolution **Guild or Diffuse co-evolution**	Each party in a co-evolutionary relationship exerts selective pressures on the other, thereby affecting each other's evolution. Coevolution includes many forms of mutualism, host-parasite, and predator-prey relationships between species, as well as competition within or between species. In many cases, the selective pressures drive an evolutionary arms race between the species involved. *Pairwise* or specific coevolution, between exactly two species, is not the only possibility; **in guild or diffuse coevolution,** several species may evolve a trait in reciprocity with a trait in another species. For instance long-tongued bees and long-tubed flowers coevolved, whether pairwise or "diffusely" in groups known as guilds. The evolution is still reciprocal, but is among a group of species rather than exactly two. More generally, flowering plants are pollinated by insects from different families including bees, flies, and beetles, all of which form a broad guild of pollinators which respond to the nectar or pollen produced by flowers. (Wikipedia – *Coevolution*) (Thompson 1994)
Co-Adaptation	In co-evolution, where the existence of one species is tightly bound up with the life of another species, new or 'improved' adaptations which occur in one species are often followed by the appearance and spread of corresponding features in the other species. These co-adaptational relationships are intrinsically dynamic, and may continue on a trajectory for millions of years, as has occurred in the relationship between flowering plants and pollinating insects. Co-adaptation and co-evolution, although similar in process, are not the same; *co-adaptation* refers to the interactions between two units, whereas *co-evolution* refers to their evolutionary history. (Wikipedia – *Adaptation* and *Co-adaptation*)
Niche differentiation/ Partitioning	The term niche differentiation (synonymous with niche segregation, niche separation and niche partitioning), refers to the process by which *competing species use the environment differently in a way that helps them to coexist.* The *competitive exclusion principle* states that if two species with identical niches (i.e., ecological

	roles) compete, then one will inevitably drive the other to extinction. When two species differentiate their niches, they tend to compete less strongly, and are thus more likely to coexist. Species can differentiate their niches in many ways, such as by consuming different foods, or using different parts of the environment. (Wikipedia – *Niche differentiation*)
Niche construction	Niche construction' refers to the process whereby the metabolism, activities and choices of organisms modify or stabilize environmental states, and thereby affect selection acting on themselves and other species. Niche construction frequently scales up, across individuals in a population, and over time*, to generate stable and directional changes in environmental conditions.* Niche construction also influences development and constitutes an important way in which environmental factors are incorporated into normal development, sometimes to become as dependable as genomic factors. Through their activities, organisms may also change the niches of other species in an ecosystem and in so doing lead to direct or guild-or diffuse coevolution, including via intermediate abiota, with potentially profound impacts on the stability and dynamics of ecosystems on both micro- and macro-evolutionary timescales. (Laland and Boogert 2010; Laland et al. 2015)
Micro/Macroevolution	**Microevolution** is the change in frequencies of gene variants that occurs over time within a population. This change is due to four different processes: mutation, selection (natural and artificial), gene flow and genetic drift. This change happens over a relatively short (in evolutionary terms) amount of time compared to the changes termed macroevolution which is where greater differences in the population occur. **Macroevolution** is evolution on a scale at or above the level of species, in contrast with microevolution, which refers to smaller evolutionary changes of allele frequencies within a species or population. Macroevolution and microevolution describe fundamentally identical processes on different time scales. (Wikipedia – *Microevolution*)
Adaptive radiation	In evolutionary biology, **adaptive radiation** is a process in which organisms diversify rapidly from an ancestral species into a multitude of new forms, particularly when a change in the environment makes new resources available, creates new challenges, or opens new environmental niches. (Soulebeau et al. 2015)
Key Innovation	In evolutionary biology, a **key Innovation**, also known as an adaptive breakthrough or key adaptation, is a novel phenotypic trait that allows subsequent radiation and success of a taxonomic group. Typically they bring new abilities that allows the taxa to rapidly diversify and invade niches that were not previously available (ex: the appearance of orb-weaving within a *clade* of spiders which increases the efficiency of prey capture). The phenomenon helps to explain how some taxa are much more diverse and have many more species than their sister taxa. (Muller 2002)
Novelty and Innovation in Nature	Most morphological novelties are not directly tied to adaptive radiations. Indeed in some cases the molecular and developmental origin of new phenotypic characters may often be independent of ecological opportunities, with novelty arising long before a species diversification -radiation. The processes generating phenotypic novelty is <u>separated</u> from the ecological and evolutionary processes that regulate their success. Studies of adaptive radiation and evolutionary innovation have invoked 'empty ecospace', or search through a 'space of the adjacent possible'. These approaches assume that the opportunities exploited by evolutionary innovation exist a priori, independent of the organisms, rather than being constructed by them during evolution. Discovering novelties is viewed as a search through the space of possibilities. Instead, other theories propose that novelty and innovation in nature require a *constructional metaphor* in which the possibility of new novelties and new innovations emerge through time *as a consequence of prior evolutionary changes*. Thus, new developmental processes and environmental changes may not represent gaining access to existing but inaccessible regions of evolutionary space, but the *de novo construction of new evolutionary possibilities*. Exploring the relative importance of search and construction is a critical important but largely unexplored theme within novelty and innovation. This conceptual framework for evolutionary novelty and innovation encompasses four aspects: • *evolutionary potentiation* through environmental, genetic and ecological changes; • *evolutionary novelty* involving the individuation of new phenotypic parts or attributes; • subsequent *adaptive refinement* encompassing initial accommodations to the evolutionary novelty in other characters of the organism; and • *realization via ecological establishment*, which may involve the construction of new niches. **1.Potentiation:** Classic models of adaptive radiation assume that opportunities exist, awaiting lucky clades to exploit them. But several studies of genetic and developmental changes have shown that *potentiating mutations* are often required before novelties can appear. As this may seem an rather vacuous category, with almost anything qualifying as a potentiating event, potentiating changes must be tightly restricted to those that can be directly associated with the success of a novelty. Although such potentiating mutations can be identified in experimental evolution studies, new methods will be needed to rigorously identify them in development and

	morphology. Potentiation can also include environmental and ecological changes necessary for the success of a novelty. **2. Generation of novel phenotypes:** The generation of novelty is characterized by the formation of new, individuated characters. In the cases, where the developmental basis of such characters has been studied in detail, these often involve recursively wired gene regulatory networks which are highly refractory to modification. **3. Adaptive refinement** The integration of a novel aspect of the phenotype will often require some adaptive refinement. These change are often not specifically part of the novelty, but may be upstream or downstream of the kernels involved, or may be functionally related to the novelty in other parts of the body. **4. Exploitation** *The conversion of an evolutionary novelty to an innovation depends upon a suite of environmental, ecological and evolutionary conditions that may be wholly distinct from those factors associated with the formation of the novelty*. When the conditions for ecological success occur much later, there may be a long lag between the novelty associated with the initial establishment of a clade and its ecological impact. Such exploitation may occur as the result of new opportunities arising, such as after an extinction event or geographic dispersal, through a change in the environment, or via the ecosystem-modifying effects of the novelty itself. *Novelty at one level (e.g., a new gene) should not be used to determine novelty at another level (e.g., a new morphological structure). This is due to the loose causal connections between levels of organization.* Novel traits are level-dependent: As new combinations of existing genes can elicit threshold effects, novel structures may appear without the introduction of novel genes. Similarly, the introduction of a novel gene does not guarantee a novel tissue or morphological structure. Continuous change can trigger a threshold when discontinuous novelty appears. (Muller 2002; Erwin 2015; Moczek 2008)
Evolvability	Evolvability is defined as the capacity of a system for adaptive evolution. Evolvability is the ability of a population of organisms to not merely generate genetic diversity, but to generate adaptive genetic diversity, and thereby evolve through natural selection. Andreas Wagner describes two definitions of evolvability. According to the first definition, a biological system is evolvable: if its properties show heritable genetic variation, and if natural selection can thus change these properties. According to the second definition, a biological system is evolvable: if it can acquire novel functions through genetic change, functions that help the organism survive and reproduce. (Wagner 2014)
Competition	Competition is an interaction between organisms or species in which both the organisms or species are harmed. Limited supply of at least one resource (such as food, water, and territory) used by both can be a factor. Competition among members of the same species is known as intraspecific competition, while competition between individuals of different species is known as interspecific competition. Species compete when they have overlapping niches, that is, overlapping ecological roles and requirements for survival and reproduction. Competition can be minimized if two species with overlapping niches evolve by natural selection to utilize less similar resources, resulting in *resources partitioning*. In ecology, *scramble competition* (or complete symmetric competition) refers to a situation in which a resource is accessible to all competitors (that is, it is not monopolizable by an individual or group). However, since the particular resource is usually finite, scramble competition may lead to decreased survival rates for all competitors if the resource is used to its carrying capacity. Scramble competition is also defined as "[a] finite resource [that] is shared equally amongst the competitors so that the quantity of food per individual declines with increasing population density" *Contest competition* is a form of competition where there is a winner and a loser and where resources can be attained completely or not at all. Contest competition sets up a situation where "each successful competitor obtains all resources it requires for survival or reproduction". (Wikipedia – *Competition*) (Biernaskie 2011a; Weiner 1993)
Cooperation	Co-operation is the process where groups of organisms work or act together for common or mutual benefits. It is commonly defined as any adaptation that has evolved, at least in part, to increase the reproductive success of the actor's social partners. For example, territorial choruses by male lions discourage intruders and are likely to benefit all contributors. One specific form of cooperation in animals is *kin selection*, which involves animals promoting the reproductive success of their kin, thereby promoting their own fitness. (Wikipedia – *Cooperation* (evolution)) The *inclusive fitness theory* provides a good overview of possible solutions to the fundamental problem of cooperation. The theory is based on the hypothesis that cooperation helps in transmitting underlying genes to future generations either through increasing the reproductive successes of the individual (direct fitness) or of other individuals who carry the same genes (indirect fitness). Direct benefits can result from simple by-product

	of cooperation or enforcement mechanisms, while indirect benefits can result from cooperation with genetically similar individuals. (LEIGH Jr 2010; Crowley and Cox 2011; Doebeli and Knowlton 1998; Bever 1999; Weber and Agrawal 2014; Zhang 2003) *Direct fitness benefits*: This is also called *mutually beneficial cooperation* as both actor and recipient depend on direct fitness benefits, which are broken down into two different types: *by-product benefit* and *enforcement*. By-product benefit arises as a consequence of social partners having a shared interest in cooperation. For example, in meerkats, larger group size provides a benefit to all the members of that group by increasing survival rates, foraging success and conflict wins. Cooperation is maintained in situations where free-riding is a problem through enforcement, which is the mechanism where the actor is rewarded for cooperating or punished for not cooperating. *Indirect fitness benefits:* The second class of explanations for cooperation is indirect fitness benefits, or *altruistic cooperation*. There are three major mechanisms that generate this type of fitness benefit: *limited dispersal*, *kin discrimination* (kin discrimination, when an individual can distinguish relatives from non-relatives and preferentially direct aid towards them (nepotism))and *the green-beard effect*. A green-beard effect occurs when a genetic variant (an allele), or a set of linked alleles, produce three expressed (or phenotypic) effects: • a perceptible trait—the hypothetical "green beard" • recognition of this trait by others; and • preferential treatment of individuals with the trait The carrier of the gene (or a specific allele) is essentially recognizing copies of the same gene (or a specific allele) in other individuals. Whereas kin selection involves altruism to related individuals who share genes in a non-specific way, green-beard alleles promote altruism toward individuals who share a gene that is expressed by a specific phenotypic trait. (Wikipedia – *Cooperation* (evolution)) *Symbiosis* refers to two or more biological species that interact closely, often over a long period of time. Symbiosis includes three types of interactions—mutualism, commensalism, and parasitism—of which only mutualism can sometimes qualify as cooperation. *Prisoners Dilemma:* Situations in nature that are subject to the same dynamics (rewards and penalties) as the PDG define cooperative behaviour: it is never in the individual's fitness interests to cooperate, even though mutual cooperation rewards the two contestants (together) more highly than any other strategy. Many organisms compete better by cooperating with members of the same, or other, species. Most cooperation and mutualism involves exchange of goods and services, or tokens enabling their procurement. (Axelrod 2006; Aktipis and Maley 2017; Biernaskie 2011b; West, Griffin, and Gardner 2007; LEIGH Jr 2010)
Mutualism	Like altruism, mutualism, cooperation between species, evolves only by enhancing all participants' inclusive fitness. Mutualism evolves most readily between members of different kingdoms, which pool complementary abilities for mutual benefit: some of these mutualisms represent major evolutionary innovations. Mutualism cannot persist if cheating annihilates its benefit. Both *symbioses* and *brief exchange mutualisms* have transformed whole ecosystems. These mutualisms may be steps towards ecosystems which, like Adam Smith's ideal economy, serve their members' common good. Classification of Mutualisms: I. *By-product mutualisms*: co-operation among animals, including those of different species, as a collateral effect of selfishness, in which each derives a fitness benefit of increased survival. (For example, when an elephant defecates, this is beneficial to the elephant as a way to empty waste, and it is also beneficial to a dung beetle that uses the elephant's dung) II. Mutualisms where each partner has behaviours selected to benefit the other: A. Mutualisms without division of labour: 1. Mutualisms of mutual benefit with no possibility of cheating: each participant benefits itself and others by sharing in a common action [gregarious fruiting in dipterocarps to satiate seed predators: 2. Mutualisms whose participants share in a common action offering scope for cheating [Mullerian mimicry among butterflies to simplify education of predators, parasitized by palatable Batesian mimics] B. Mutualisms with division of labour: 1. Long-term mutualisms (symbioses) a. Mutualisms enforced by transmission of symbionts from a host to its offspring [organelles in eukaryote cells b. Mutualisms enforced by partner fidelity [sponges that fuse to pool capacities to resist different hazards for their common good]

	c. Mutualisms enforced by partner choice [bobtail squid that test bioluminescent bacteria before admitting them as symbionts] d. Mutualisms enforced by partner sanctions [legumes and their nitrogen-fixing bacteria] 2. Mutualisms of brief exchange a. Mutualisms enforced by partner sanctions [cleaner fish and their clients] b. Mutualisms with a limited degree of partner choice [seeds and their dispersers] *Defence mutualisms* facilitate speciation (species diversity): Plants that provide food and housing to animals in return for defense against enemies are classic examples of mutualistic partnerships in nature. The evolution of such plant–animal mutualisms also can lead to a trajectory of accelerated accumulation of plant species (speciation, increased in diversity/disparity) in the lineages that participate in these cooperative interactions. We found that the evolution of plant organs (extrafloral nectaries) that facilitate mutualisms with animal defenders was repeatedly followed by increased rates of diversification across distantly related plant lineages. These results suggest that by enabling ecological interactions with animals, the convergent evolution of relatively simple glands changed the course of plant evolution toward greater protection from pests and accelerated the generation of biodiversity. *Defense mutualisms enhance plant diversification* *Symbiotic relationships* in an ecosystem can guide the course of subsequent genetic variation. This phenomenon can be described as two phases: First, symbiotic groups find solutions where individual organisms cannot, simply because lifetime interaction produces new combinations of abilities (at phenotype level) more rapidly than the relatively slow genetic variation of individuals. Second, these symbiotic groups subsequently change the shape of the reward landscape for evolution, providing a gradient that guides genetic variation to the same solution ("constructional" rather than "search for"). Ultimately, an individual organism exhibits the capabilities formerly exhibited by the group. This process enables the combination of characteristics from organisms of distinct species without direct transfer of genetic information. (LEIGH Jr 2010; Crowley and Cox 2011; Doebeli and Knowlton 1998; Weber and Agrawal 2014; Zhang 2003; Toby Kiers et al. 2010)
Ecological mutualistic Network	Biological interaction between species and/or across space can be described via *ecological networks*. An ecological network is a representation of the biotic interactions in an ecosystem, in which species (nodes) are connected by pairwise interactions (links). They are used to describe and compare the structures of real ecosystems, while network models are used to investigate the effects of network structure on properties such as ecosystem stability. They are classified according to their type of ecological interaction, for example, host-parasite networks, trophic networks or mutualistic networks. In particular *Mutualistic networks* describing inter-guild plant-animal mutualisms (e.g. plant-pollinator) or plant-mycorrhizal interactions have structures characterized by some properties such as: 1. *Nestedness:* It describes a non-random pattern of species interactions where specialist species interact with proper subsets of more generalist species. In highly nested networks, guilds of species that share an ecological niche contain both generalists (species with many links) and specialists (species with few links, all shared with the generalists). Nestedness is often asymmetrical, with specialists of one guild linked to the generalists of the partner guild. 2. *Modularity*: Networks can have regions of nodes that are more densely connected than others. These regions are called modules or compartments, while less connected regions set the boundaries of the modules. Organisms are generally organized into modules where different subsets of units have a specific functionality. An example is provided by modules of genes involved in development. Modularity reveals the underlying structure in the network, which is relevant to detect groups of significant importance. In ecological networks we can find modules of species that are highly interacting among them but weakly between modules. Increasing the complexity of a mutualistic networks has been reported to increase the resilience of the network to environmental changes (ex: climate change). (Bastolla et al. 2009; Encinas Viso 2013; Nagaishi and Takemoto 2018)
Biodiversity related niche differentiation Theory	we can formulate the BNDT as follows: in natural conditions of immigration and emigration, with every environmental condition, species tend – directly or indirectly, thanks to their simple presence and life roles – to increase the number of potentially available niches for the colonization of other species (niche construction) until the reach of the carrying capacity of the ecosystem. At same time, niches and mutualistic networks of the ecosystem allow, through circular and feedback mechanisms, the rise of the number of species, generating a non-linear autopoietic (self-generating) system. In other words, we can argue that the species themselves, creating favourable conditions for the colonization of other species, allow the concurrent presence. This is nothing more than coexistence and the fundamental mechanism that supports the coexistence of species is the creation of diversity-related niches. The higher the number of species is, the more likely the possibilities that other species can colonize that environment are. (Cazzola Gatti 2011)

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