

## On The Topic of Species and Speciation in Biology

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**Abstract:** After a long period of static species concept, followed modern times with new technologies of investigations and wider vision of most systematists who accepted the dynamic species outlook. Adopting population thinking, it was also accepted importance of intra- and interpopulation variation due to geographical and other forms of isolation. The key words - reproductive isolation are referring to the way of a community or part of a population are becoming genetically very different from other populations; it is so called genetic incompatibility of interbreeding. Thus, appeared the meaning of biological species concept (BSC). Because deep differences arise in a long time and in a certain area, the scientists are underlining the historical, geographical, natural and objective character of the biological species. In details there are many types of speciation, but finally the species is considered as the main unit of evolution. In case of allopatric speciation, the size of population, the spread and colonization of new areas as well as potential effect of genetic drift are very important. Underground habitats, the unique ecological conditions of ocean depth, orogenetic movements (e.g. mountain rising) and glaciations, were additional factors that determined speciation and endemism phenomenon. Mutual relations or co-speciation also play an important role in opening new evolutionary lines.

**Key words:** species, speciation, reproductive isolation, genetic variability, evolution

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### I. Introduction

The term species is hotly debated among naturalists and therefore today there are more than 25 recognized definitions - all applicable to sexually reproducing species and unsuitable for asexually reproducing species, such as bacteria. The area of debates on the topic of the species concept is called microtaxonomy or microevolution.

Because in many cases, reproductive isolated living groups are not easy to identify species (e.g., cryptic species) and there is a link from total reproductive isolation (non-crossover) to panmixia - where crossings are random, without morphologically, genetically or ethologically incompatibilities between individuals, we have the explanation of the difficulty of finding a generally accepted species definition.

If after Racoviță (1929), the species is the fundamental biological unit, Mayr (1957, 1963) noted that: “Linné the fixist, underlining the specific characters and the precise delimitation of the species, came closer to the present biological opinion on the species than those transformists who denied both their relative constant and their categorical delimitation in their wish of proving the species evolution”.

Recognizing that it took some time for the evolution of species, we understand their historical character. But that evolution took place in a certain space and from here we understand that speciation is a geographical phenomenon.

Today, the problem of the species is different from what Charles Darwin (1859) and other scientists of XIX-th and early twenties century wondered how the new species appeared? Darwin was the first to best define the species, given its constant change.

The idea after which an organism reproduces, giving birth to a similar organism comes from the most distant times, since the domestication of animals and the cultivation of plants began. At the time, most were tempted to believe that speciation was a relatively stable process, but there were also beliefs that accepted change was possible. The term species was first used to refer to a particular type of organisms. John Ray (1686) introduced a biological concept, after which the species was different from whatever that species had produced, and it was fixed and permanent, although there were considerable variations within a species.

Carolus Linnaeus (1758) formulated the species taxonomic level and divided it into two - call it the binomial nomenclature system, which is still used today. However, misunderstandings about how best to identify a species have not been ruled out. It can therefore be said that the history of the definition of the term species was debated long before Darwin.

The purpose of this article is not to review methods of grouping organisms and identify species, but to suggest progress in understanding traditional definitions of the species term, with a view to unifying all concepts for the harmonization and unification of lengthy contradictory debates between biologists as well as between philosophers and the historians of sciences.

## II. Discussions

The traditional point of view, developed by Cain, Mayr and Hull at mid-century. XX-ies argued that until Darwin's work (*The Origin of Species*), both philosophy and biology regarded the species as something invariable, natural, with essential features. This "essentialist story" was adopted by many scholars, but some of them wondered "why," long after Aristotle, many other ancient naturalists wrote about the essence of the species. They refer to the essential "functions" and not to the essential "properties".

Richard (2010) wrote the book *The Species problem: A Philosophical Analysis*. Cambridge University Press, pointing out that Linnaeus (1735) saw the species as eternal, fixed, and only a few years later discovered hybridization as a way of speciation.

**From Darwin to Mayr.** Charles Darwin's famous book (1859) provided an explanation of the evolution of the species over a long period of time. Although Darwin did not give details on how one species is divided into two, he saw speciation as a gradual process.

If Darwin was correct, when an early species is formed, it takes a period of time, in which the species being separated are not different enough to be recognized as distinct species. Darwin's theory suggested that often there were no objective criteria to say whether one or two species are.

Darwin's book sparked a crisis of biologists' uncertainties about the objectivity of the species and some wondered if the individual species could be real, objective, setting an example that is independent of human observation. Laird (1873) referred to Darwin's theory and Law of the Migration of organisms.

In the 1920s and 1930s, Mendel's theory of heredity and Darwin's theory of evolution through natural selection were united in what has been called modern synthesis. This union of theories has had a powerful impact on biologists' thinking about the term species.

Edward Poulton (1904) anticipated many ideas about the species (which are accepted today), which were later much developed by Theodosius Dobzhansky and by Ernst Mayr - two architects of modern synthesis theory.

Dobzhansky's book *Genetics and the Origin of Species* (1937) articulated the genetic processes that occur when incipient species begin to differ. Dobzhansky described in particular the critical role of the evolution of reproductive isolation in the formation of a new species.

**Mayr's concept of the biological species:** Ernst Mayr's book *Systematics and the Origin of Species* (1942) constituted a change of views on the problem of the species. He mentioned how different criteria for identifying species were, used by different researchers, and characterized their research on the concept of species. Thus, Mayr (1942) issued the Biological Species Concept (BSC), after which a species consists of populations of individuals that can reproduce with each other and are reproductively isolated from other populations.

Thus, Dobzhansky (1937) was not the first to define "species" based on reproductive compatibility. For example, Mayr (op. cit.) noted that Buffon proposed such a definition of "species" as early as 1753. Later, Buffon (1778) was, however, the first to understand the existence and meaning of "representative species." suggesting that they were based on the existence of an ancestor, launching the idea of species transformation and division.

Dobzhansky was a contemporary of Mayr and the author of the classic book on the evolutionary origin of reproductive barriers between species, published a few years before Mayr. Many biologists have trusted Dobzhansky's association with Mayr to highlight the topic of reproductive isolation.

After Mayr's book (1942), more than 20 concepts about the species emerged. Some (*e.g.*, Phylogenetic Species Concept - PSC) have been shown to be more useful than BSC for species description. Many authors have tried to better "solve" the problem of the species. Some have argued that the problem of species is too multidimensional to be "solved" by a concept. Since the 1990s, some experts have argued that all the concepts that were intended to help describe the species did not help to "solve" the species' problem. Although Mayr promoted BSC for use in systematics, some systematists criticized it as not being operational.

For others, BSC is the preferred definition over the species. Many geneticists working on speciation are preferring BSC, because it highlights the role of reproductive isolation. It has been argued that BSC is a natural consequence of the effect of sexual reproduction on the dynamics of natural selection.

**Realism, from a philosophical point of view.** It is a philosophical position, according to which the species is a real-independent entity, it is something natural. Mayr (1942) - supporter of realism, tried to prove the nominalist system that "... *the species exists naturally*", as an extra- mental category. He pointed out, for example, that the people of the tribes of New Guinea, differed from 136 species of birds, which western ornithologists came to recognize: native of New Guinea. "*I have always thought that there is no greater rejection of the nominalist system than the above-mentioned facts about the primitive natives of New Guinea, in the culture of the Stone Age. They can recognize as species, exactly the same entities that Western taxonomists recognize*"

If the species were anything but arbitrary, it would have been totally unlikely for representatives of two drastically different cultures to reach identical criteria for delimitation between species.

This argument of Mayr has been criticized, considering that independent people see the same species in nature, but this does not mean that the species are rather real than the nominal categories.

Ridley (1993), showed that, observing the same species in nature, proves that human brains are endowed with similar perceptions on statistical clusters. Under this aspect, we (humans) can make connections or "...*have different representations and that species can be represented differently by us*". Therefore, it could be said that no representation or connection of ours can be "realistic" or true.

Another position on the conception of the realism of the species claims that natural things or phenomena are separate from the world itself, having a unique property, for all members of a species and no one is outside the group. In other words, a natural thing has an essential or intrinsic trait ("an essence") that is self-individual and is not arbitrary.

This notion has been severely criticized as essentialist, but modern realists have argued that while natural things have essences or peculiarities, they do not need to be fixed and are likely to change by speciation.

According to Mayr (1957), reproductive isolation or crossbreeding provides an objective measure, a "*completely non-arbitrary*" criteria, and describes the presence or absence of relationships that make the notion of species not arbitrary. By BSC, the species is defined as "*a group of natural populations, which in fact (or potentially) may intersect, and which are reproductively isolated from other similar groups*". From this perspective, each species is based on a property (e.g., reproductive isolation), which is common to all organisms of the species that objectively differ from each other.

**Nominalism.** Some philosophical variants of nominalism consider that species are only names, which man has given to groups of creatures, but in which the differences between species do not reflect any fundamental biological difference.

Thus, the names given by people, to groups, in reality wouldn't reflect any difference. This would mean that the species does not exist outside our thinking, because the species would be just abstract names. Moreover, if the species are not real, it would not be correct to speak about the "origin of a species". At mid-century. XX-ies, some authors have adopted this view and have written that species are not real beings.

A different view from nominalists on species was held by Michael Ghiselin (1969), who argued that a certain species is not a type, but rather a current individual, a current entity. This idea comes from the thinking or belief that the species is considered a dynamically evolving population. If they were seen as an entity, a species would exist with or without the human being observing it and with or without giving it a name.

**Pragmatism.** In a popular alternative, supported by philosophers such as Philip Kitcher and John Dupre, it has been claimed that since the species does not exist in the sense of natural things, they are conceptually real and exist as a result of conventions and for practical applications. For example, no matter what definition of the species we use, it can be quantitatively compared to the diversity of the species in different regions or decades, as long as we refer to the same definition of the species during the study. This is of practical importance in the advancement of biodiversity science and environmental science.

**The language and role of human factors investigators.** Nominalists have criticized the view that there are certain things, increasing the consideration of the role of the human factor in the problem of the species. Haldane (1956) suggested that species are only mental abstractions. Some authors have noted the similarity between "species" as a world of ambiguous meanings, which include Wittgenstein's views on the concept of family resemblance and indeterminate language.

Jody Hey (2001) described the problem of the species as the result of two motivations on the behalf of biologists:

- 1 - categorization and identification of organisms;
- 2 - understanding the evolutionary processes that determine the appearance of species.

According to the first point, the species appears to us as a typical natural thing, but when biologists try to understand the evolution of species, they discover them as changing realities, without precise delimitations.

Hey (2001) showed that it is unrealistic to expect a definition of "species" to serve the need for categorization and to reflect the changing realities of evolved species.

**Pluralism and monism.** Many studies on the species problem have attempted to develop a common conception of what species are and how they can be identified. There is a belief that if such a monistic description of the species could be developed and agreed upon, then the species problem would be resolved.

On the contrary, some authors have advocated pluralism, invoking the fact that biologists cannot agree on a concept regarding the definition of the species and that they would accept more ideas, incompatible with the species term. However, David Hull (1973) showed that pluralistic proposals were not able to solve the species problem.

**Quotes:** According to the opinion of XIXth century scientists, in the world observed that no land is more difficult to define than a species, and no problem in zoology is more controversial than the understanding of this term.

Dobzhansky (1937) noted that: "*In the end, the futility of trying to find an universal criterion valid for the distinction of species has become very general, if it is doubtful in recognizing it*".

Haldane (1956) issued the concept, after which "... a species is a concession made to our ordinary language and neurological mechanisms".

Hey (2001) appreciated that: "*The problem of the species is an old failure of biologists to understand how we could identify species and how we could define the word species*".

According to Pigliucci (2003): "*First, the problem of the species is not at all empirical, but rather one loaded with philosophical questions that require - but cannot be determined by - empirical evidence*".

Bonde (1977) noted that: "*An important aspect of any definition of a species (either in neontology or paleontology) is that any specification or determination as characteristic of individuals (fragmentary specimens) to belong to a particular species is a hypothesis and not a fact*".

Rieseberg *et al.* (2006) stated: "*We know that although in most genera (over 80% in plants) there are discrete phenotypic connections (clusters), the correspondence of taxonomic species to these clusters is weak (below 60%) and is not different in plants and in animals. On the contrary, in conventional wisdom, the existence of independent reproductive lines is more possible in plant species than in animal species.*"

**History and research techniques for speciation.** The oldest research on speciation reflected the importance of geographical spread and therefore, those types of speciation were called geographical, semi-geographical and non-geographical. The geographical speciation corresponds to the current use of the term allopatric speciation.

Moritz Wagner (1868) was the first to propose the concept, for which he used the term Separationstheorie. His idea was later interpreted by Ernst Mayr (1942) as a form of the founding effect of speciation, initially focusing on small populations, geographically isolated (see peripatric speciation).

Edward Bagnall Poulton (1904) - an evolutionary biologist and a strong supporter of natural selection, clarified the role of geographical isolation in promoting speciation and coined the term "*sympatric speciation*".

There is controversy if Charles Darwin (1859) recognized in his publication "*The Origin of Species*", a true model of speciation on a geographical basis. In Chapter 11 - "*Geographical Distribution*", Darwin discusses the geographical barriers to migration and gave as an example that "*any kind of barriers or obstacles to free migration are in a close and important relation with the differences between the productions of the different regions (from the planet)*".

F. J. Sulloway (1979) stated that Darwin's position on speciation was "*misleading*" or ultimately misleading. He later misinformed Wagner (1868) and David Starr Jordan (1905) into believing that Darwin saw sympatric speciation as the most important way of speciation. However, Darwin never fully accepted Wagner's (1868) concept of geographical speciation.

In the early 20ies century, David Starr Jordan (1905) played a significant role in promoting the concept of allopatric speciation, providing natural examples to support this theory. Much later, biologist Ernst Mayr (1942) was the first to synthesize his contemporary literature, both in the book *Systematics and the Origin of Species*, from the viewpoint of a zoologist, and in his forthcoming 1963 publication - *Animal Species and Evolution*. Like Jordan's work, he referred to direct observations in nature, documenting the emergence of the allopatric species, which is widely accepted today. We have already mentioned that before this research, Theodosius Dobzhansky (1937) had published *Genetics and the Origin of Species*, in which he based the genetic framework on how speciation could have appeared.

Other researchers have mentioned the existence of allopatric distribution of species pairs in the wild. Joel Asaph Allen (1905), coined the term "*Jordan's Law*," after which geographically isolated species, closely related to one another, are often divided by physical barriers. This view was also shared by Robert Greenlaf Leavitt (1912).

However, it is estimated that Wagner (1868), Karl Jordan (1903) and David Starr Jordan (1905) played an important role in forming the concept of allopatric speciation. This concept is evolutionary and based on it, Mayr and Dobzhansky contributed substantially to the formation of the theory of modern evolutionary synthesis. At the end of the century 20ies mathematical models have been developed on allopatric speciation, leading to a clear theory on the plausibility of geographical isolation, which may eventually lead to the reproductive isolation of two populations.

After 1940, allopatric speciation was generally accepted. Today it is unanimously regarded as the most common form of speciation that occurs in nature. However, allopatric speciation is not without challenges, although both parapatric and sympatric speciation are reconsidered as real modes of speciation, which occur in nature. Some researchers even believe that they can influence events favorable to the allopatric species. Thus,

in a 2009 study, with revision of 73 published papers on speciation, only 30% suggested allopatric speciation according to the observed models, considering other modes of speciation possible.

Contemporary research links the multiple lines of evidence that determine the events of speciation. Thus, patterns of geographic distribution in relation to phylogenetic relationships, based on molecular biology techniques, are determined. This method was introduced by John D. Lynch in 1986 and has been used by many researchers. The correlation of geographical distribution with phylogeny data gave birth to a subdomain of biogeography - called biogeographic vicariance. This new field was developed by Joel Cracraft (2011), Lomolino (2000), James Brown and Mark V. Lomolino (1998), Lomolino *et al.* (2016) among other biologists, specializing in ecology and biogeography.

Similarly, by analyzing and deepening the different types of scientific, analytical and applied research (- phylogenies at the species level; - areal overlaps; - areal symmetry of some sibling-species pairs; - species movements in their geographical area) determine which mode of speciation has suffered one species or another in the past.

Two or more species (but also larger monophyletic taxa) can be considered vicarious if they have allopatric distribution. In the case of sister-species (sibling-species), their vicariousness is proven by the proximity of each other more than with any other species or were derived by geographical isolation, from a common ancestor or from a mother-species.

Bănărescu (1996) mentioned that sibling-species firstly were vicariants, but their next evolution were accompanied by barriers disappearance, extension and superposition of their areal. This is why genera, groups of species etc., frequently became totally or partly sympatric.

There is a long debate between biogeographers as to whether the detachment of these new species is "vicariousness" or "vicariism". It is appreciated that vicariism term expresses the phenomenon or fact itself and that it should be more widely accepted. Moreover, the same biogeographic specialists argue that a distinction must be made between primary and secondary vicariism.

Primary vicariousness refers to the pair of sibling-species that resulted directly from a parental-species. Usually, their range covers the entire range of their common ancestor, but one or both of them have exceeded that range. In most cases they are closely related species, they have close ranges, but they are nonetheless allopatric.

Secondary vicariousness is in case of new today taxons are totally allopatric, but in the past they were at least partially sympatric. According to Thenius (1970), their current allopatry is not after the division of a common ancestor, but through the disappearance of one or both members from a part of their former, common areal. It is given as an example - the family of elephants, with two monospecific genera: *Elephas* - from tropical Asia and *Loxodonta* - from Africa. While for *Loxodonta* genus there are fossils only from Africa, the fossils for *Elephas* were discovered both from Eurasia and Africa; the fossils of this second genus are of older age.

The two genera are sisters, later separated, by the fragmentation of their old areal. That fragmentation or vicarious event took place in Africa and does not correspond to the edges of the current areal of the two recent genera.

Then, vicariousness should not be confused with disjunction. There are vicariate freshwater species, separated by a very narrow strip of land. It is case of freshwater pools, very close to each other. On the other hand, both in the case of sister-genera, and of other closely related overspecific taxa (which today have disjoint areals), their vicarious relations can be determined only when their sister-taxon relationships can be established.

Molecular clock dating methods are often used to explain or clarify the time divergence reflected by fossils or geological data. It has become a classic example of shrimp that have been separated by the closure of the Panama Canal and the separation of populations in the Pacific Ocean from the Atlantic Ocean.

Another example of vicarious relationships is the species of the genus *Cyclamen* among Primulaceae plants. One of its species arrived in Somalia, which caused the botanists to reclassify it into the Myrsinaceae family. Only after 2009 could it be established with the help of modern methods of investigation that, in fact it was about the subfamily Myrsinoideae of the family Primulaceae. Other techniques used today have evaluated gene flow between populations, modeling ecological niches. This is the case of myrtuses of the genus *Myrtus*. Another example is of all the chickadees of the species *Setophaga auduboni*.

By testing the monophyletic groups, it was found that in the case of amphibians in the family Dendrobatidae (from Ecuador) there was environmental speciation. Advanced biotechnologies have allowed large-scale comparisons of the multi-locus genome, with the possibility of allopatric speciation occurring between human ancestors and chimpanzees. Thus, the connection of the evolutionary history of the species with the ecology was discovered and the phylogenetic models could be clarified.

**Allopatric speciation** - from ancient Greek *allos* = "other", and homeland with a sense of country - native country or native land. It is about geographical speciation, vicariant speciation or the "dumb model" (after its old name), as a mode of speciation, which appears when biological populations are becoming isolated from

one another, until the avoidance of interference by genetic exchanges.

Different geographical changes may occur, such as the movement of continents, when mountains, islands, water basins or glacial lakes can be formed. Human activities (*e.g.*, agriculture) or economic and infrastructure development can also change the distribution of some species' populations.

These factors can substantially alter the geography of a Kingdom, resulting in the separation or isolation of a population of a species, in isolated subpopulations. Vicarious populations are subject to genetic changes and become subject to different selective pressures, the genetic drift experiences and accumulate different mutations in separate populations, but with the same genetic background.

Barriers prevent the exchange of genetic information between two populations, leading to reproductive isolation. If the individuals of the two populations are coming later in contact, they will not be able to reproduce and then we are dealing with the actual or real speciation.

Other isolation factors, such as dispersal of populations, cause emigration and may produce speciation (*e.g.*, dispersal and isolation of a species on an oceanic island). This is considered a special case of speciation, called peripatric speciation. Thus, allopatric speciation is typically subdivided into two major models: vicariant and peripatric. Both models are differing from each other, by the virtue and the size of their populations as well as by the mechanisms of geographical isolation.

The terms allopatric and vicarious are often used in biogeography to describe the relationships between organisms whose areals do not overlap significantly, but are immediately adjacent to each other. They do not appear together in the same place or appear in contact only on a very narrow area.

From a historical point of view, the language used refers to the speciation directly reflected in the biogeographic distribution. Thus, allopatry is a geographical spread, opposite to the sympatry or is speciation that occurs within the same areal.

Further, the terms allopatric, vicariant, geographical speciation are often interchangeable in the literature. In this article we use them in the same sense, except in special cases - peripatric, centrifugal speciation, among others.

Nature observations create difficulties in proving the allopatric speciation "from A to Z" (from beginning to the end) in which the speciation operates as a dynamic process.

**From here a series of difficulties arise in defining the term species**, in defining the isolation barriers and in measuring the reproductive isolation. Mathematical modeling of the genetic basis of reproductive isolation supports the plausibility of allopatric speciation. Laboratory experiments on *Drosophila melanogaster* and on other animal and plant species confirmed that reproductive isolation acted or evolved as a product of natural selection.

Reproductive isolation acts as a primary mechanism in genetic divergence in allopatry and can be amplified by divergent selection. Prezygotic and postzygotic isolation are the most common mechanisms in allopatric speciation and thus it is difficult to determine which form evolved first, in the phenomenon of allopatric speciation.

The simple **prezygotic isolation** suppose the presence of a barrier before any act of fertilization. This is the case of an environmental barrier, which divides or shares two populations.

**Postzygotic isolation** involves avoiding any success of interpopulation crossing after fertilization, as it is the case with infertile hybrids.

Because pairs of species that are separated by allopatry often have pre- and post-zygotic isolation mechanisms, investigating the earliest stages of the species life cycle can indicate whether or not divergences are due to the prezygotic or postzygotic factors.

However, the establishment of the specific mechanism may not be very clear, if the pairs of species continue to move away from each other, over time. For example, if a plant suffers from a chromosomal duplication phenomenon, reproduction will be possible, but sterile hybrids will result - functioning as a form of postzygotic isolation.

Consequently, new pairs of formed species may encounter prezygotic reproduction barriers, as selection acts independently on each species. Eventually it will lead to genetic changes, which will make it impossible for hybrids to appear. From the point of view of researchers, current, common isolation mechanisms may not reflect past isolation mechanisms.

**The most common form of speciation is the allopatric speciation model.** Vicariance is a process by which the geographical area of a particular taxon or an entire biota is divided into discontinuous populations (disjoint distribution), by forming an extrinsic barrier in exchange for genera. In this way, the process of speciation was due to the appearance of a barrier from the outside. These extrinsic barriers often occur due to geological causes, topographic changes (*e.g.*, formation of mountains or orogenic movements), formation of rivers or water basins, glaciers; the formation or elimination of continental decks, the displacement of continents

or tectonic plates in time, the formation of islands, etc., which may cause changes in the areal or distribution of species populations.

The appearance or configuration of a favorable or unfavorable habitat can lead to similar changes and may be due to climate change or large-scale anthropic activities: extension of agricultural techniques, development of civil engineering, fragmentation of habitats, etc.

Among other things, these many factors can alter a geographical region so profoundly that it results in the division of the population of a species into completely separate geographically and reproductive subpopulations.

Vicariant populations then suffer from genotypic or phenotypic divergence:

a - are subjected to different selective pressures; b - suffers independently from genetic drift;

c - different mutations appear in the genetic background of the populations.

Extrinsic barriers make it impossible to exchange genetic information between two populations and inevitably lead to differentiation due to the action of ecologically different habitats. Then, selective pressure inevitably leads to complete reproductive isolation.

Furthermore, the propensity or tendency of a species to remain in its ecological niche (see the phylogenetic conservatism of the niche) by changing environmental conditions, may also play a role in isolating populations from each other, resulting in new evolutionary lines.

Allopatric speciation can be represented as a continuum of genetic flow. Thus, the level of gene flow between populations in allopatry would be equal to the rate of gene exchanges.

In sympatric, as in parapatric speciation, there is also a total continuum.

Thus, not all researchers accept the scheme of geographical classification, which does not necessarily reflect the complexity of the species. Allopatry is often seen as a lack or "null" method of speciation, but this view is also debatable.

**Reinforcement as a speciation factor.** Most often the reinforcement has been invoked in sympatric speciation studies, because it involves the exchange of genes between two populations. Although often challenged, however, reinforcement may play a role in allopatric speciation, where reproductive barriers are removed, allowing the two populations that were previously isolated to be reunited. Through a secondary contact, individuals can reproduce and form hybrids poorly adapted to ecological conditions. Their features determine individual discrimination in the chances of mating, and this increases the prezygotic isolation between populations. Some arguments were strong because they suggested that hybrids themselves could

become species - the well-known **hybrid speciation**.

As long as the exchange or flow of genes from which viable hybrids can result is possible, reinforcement can play an important role, both in the geographical modes of speciation and in the non-geographical modes of speciation. The production of nonviable (sterile) hybrids is a form of replacement of the reproductive character, from which most definitions are only additions to the speciation event.

Research has established that interspecific cross-discrimination appears to be wider distributed among sympatric populations than it is in purely allopatric populations. However, other factors have been proposed for the observation of speciation models.

Reinforcement in allopatry has been shown to occur in nature, albeit with a much lower frequency than in the phenomenon of classical, allopatric speciation. A major difficulty arises when interpreting the role of reinforcement in allopatric speciation, as current phylogenetic models may suggest a past gene flow. It can "cover" the initial divergence in allopatry and can indicate a "mode-mixed" or "mixed-mode" of the speciation phenomenon - presenting both allopatric and sympatric speciation processes.

**Mathematical modeling:** This modeling is considered to have been highly developed in the context of the genetic basis of reproductive isolation. Through mathematical modeling, resulted scenarios, both in prezygotic and in postzygotic isolations, regarding the effects of genetic drift, sexual selection, or different combinations of these three factors.

Masatoshi Nei (1972) were the first to develop a neutral, stochastic model of speciation only through genetic drift. Both selection and drift can lead to postzygotic isolation, assuming that two geographically separated populations can evolve into reproductive isolation - which sometimes occurs rapidly.

Fisherian sexual selection can also lead to reproductive isolation if there are small variations in selective pressure (e.g., predation risk or habitat differences) within each population.

Mathematical modeling of reproductive isolation distance has shown that populations can manifest a firm reproductive isolation, which is directly correlated with physical, geographical distance. This has been exemplified in the models of **ring species** or by the existence of links in a number of neighboring populations. Each of them can be reproduced with individuals from geographically and related populations, but there are at least two "heads" of populations in this series. Those heads are really removed as a degree of kinship, so that their individuals can cross. This means that there is a potential genetic flow between all populations in the ring.

Although genetically related, such "heads" of populations do not reproduce with each other, but can coexist in the same region (sympatry) and thus close a "ring".

However, it has been argued that ring species are a special case, representing reproductive isolation because of distance, and the existence of parapatric speciation, which is a speciation along a line, has been demonstrated.

**Other models.** Within the allopatric speciation, different alternative models have been developed. Special cases of vicarious species have been studied in detail, one of them being **peripatric speciation**, while a small part of the population of a species becomes geographically isolated (*e.g.*, in the oceanic islands); **centrifugal speciation** is an alternative model of peripatric speciation that concerns the extension and contraction or restriction of the species' areals. There are other models, called secondary, of allopatric speciation, among which we already mentioned

- peripatric speciation.

It is a mode of speciation in which a new species is formed from the isolation of a peripheral population. If a small population of a species becomes isolated (*e.g.*, a bird population on an oceanic island), the selection may act on that population, regardless of the parent or parent population. Given that, there are both geographical isolation and sufficient time, and peripatric speciation can occur.

Three important factors can be distinguished from the allopatric speciation:

- 1 - the size of the isolated population;
- 2 - strong selection, imposed by dispersion and colonization in the new environment;
- 3 - the potential effects of genetic drift on the small population.

However, it is often very difficult for researchers to determine, if peripatric speciation has emerged as an explanation for vicariousness, which can be invoked because both models involve the absence of gene flow between populations.

The size of the isolated population is important, as individuals colonizing a new habitat may contain only a small portion of the genetic variation of the original population. This supports the divergence, due to the strong, selective pressure, leading to the rapid fixation of an allele in the descending population. The divergence increases the potential genetic incompatibility and this incompatibility causes reproductive isolation, generating a rapid speciation phenomenon.

Peripatric patterns are mainly supported by patterns of species distribution in the wild. Oceanic islands and archipelagos provide the strongest empirical evidence on how peripatric speciation appears.

**Centrifugal speciation.** It is an alternative variant or model of peripatric speciation. This model contrasts with the peripatric speciation, by virtue of the origin of the genetic novelty, which leads to reproductive isolation. When a population of a species experiences a period of expansion and restriction of the geographical areal, a small, fragmented, isolated, peripheral population may remain. These isolated populations will contain evidence of genetic variation from the larger parental population. These variations lead in all probability to the specialization of ecological niches and to the evolution of reproductive isolation.

Centrifugal speciation has long been neglected in the specialized scientific literature. However, the researchers supported the model, and most part of this model was not rejected. An example concerns the possible center of origin, which took place in the Indo-West-Pacific region.

**Microallopatry** refers to allopatric speciation, which occurs on a small geographical scale. The examples are referring to the microallopatric speciation that has been described in nature. Rico and Turner (2002) founded the hypothesis of the intralacustrine allopatric divergence of the species *Pseudotropheus callainos* - endemic cichlid in deepest Lake Malawi (from East Africa) is separated only by a distance of 35 m. Then, Gustave Paulay (1985) founded also the hypothesis about Cryptorhynchinae subfamily of neotropical curculionids, having microallopatric speciation in Rapa Island and the smaller surrounding islands. Lynch (1986) described new species of leptodactylid frogs from the Ecuadorian and Peruvian Andes.

A triple sympatric spread of diving beetle species (of *Paroster* genus from Dytiscidae family) living in the aquifers of the Yilgran region of Australia having microallopatric speciation on an area of only 3.5 km<sup>2</sup>. The term was first proposed by Hobart M. Smith (1961) to describe a resolution of a geographical level. A sympatric population may exist at a low resolution, while those seen at a higher resolution (*e.g.*, on a small population to a small-scale) are "microallopatrics". Fitzpatrick *et al.*, (2006) argued that this original definition "*is erroneous because geographical and ecological concepts are confused.*"

**Ecological speciation** can be allopatric, sympatric or parapatric, the only requirement being that it appears as a result of an adaptation to different ecological or microecological conditions. Ecological allopatry is an inverse form of allopatric speciation, in connection with reinforcement.

First, the divergent selection separates the appearance of a population from prezygotic barriers, from which genetic differences evolve, due to complete obstruction of gene flow. The terms alloparapatric and allosympatric have been used to describe the speciation scenarios, where there are differences in allopatry, but the speciation appears only on a secondary contact. These are the actual models of reinforcement or the phenomenon of "mixed-mode" speciation. Because allopatric speciation is widely



accepted as a common mode of speciation, scientific literature abounds in studies documenting its existence. We already mentioned that Ernst Mayr (1942, 1954, 1963) was the first to synthesize his contemporary literature and Poulton (1904) was the author of the concept of biological species and of term aposematism, for the warning colors.

Many of his examples have remained conclusive today. However, modern research on molecular phylogenies - methods unavailable to early researchers, came to edifying conclusions in support of geographical speciation.

The most recent and careful work on allopatric speciation (and on speciation research in general) is by Jerry Coyne and H. Allen Orr (2004), entitled *Speciation*. They mentioned six main arguments, which lead to the support of the concept of vicarious speciation:

- 1 - In most cases, the pairs of closely related species are in geographical areas close to each other and separated by a geographical or climatic barrier.
- 2 - Pairs of young species (sibling-species) often appear in allopatry, even without any known barrier.
- 3 - Where apparently several related species share the same large areal, they are distributed in close areals, without strictly delimitation between them and therefore are named areals of hybridization.
- 4 - In regions where geographical isolation is questionable, species do not have sister (cryptic) pairs.
- 5 - The correlations of the genetic differences between the closely-related species to the phylogenetically distant species correspond to current or historical geographical barriers.
- 6 - By measuring the reproductive isolation it was found that this isolation increases with increasing geographical distance, between two species. Most often this refers to reproductive isolation by distancing.

Allopatric species have resulted from numerous biogeographic and biodiversity models on Earth: on islands, continents and even around the mountains. The islands are often the sites of endemic species – most of them existing on only one island. This is the case for species that do not exist anywhere else in the world except on certain islands, on which almost all taxa (from isolated islands) are located, but which species have resulted from a common ancestor and for the species on the nearest continent.

Undoubtedly, there is a typical correlation between island endemics and biological diversity. This means that a greater diversity (a wealth of species) on an island, also implies an increase in the number of endemics. In turn, increasing diversity is the source of speciation. Moreover, the number of endemics on an island is directly correlated with the relative isolation of the island and its surface. In some cases, island speciation occurs rapidly.

In the case of dispersed and *in situ* speciation, a number of agents are responsible, which, for the biodiversity in Hawaii, explain the origin of organisms. In the Hawaiian biota, different modes of geographical speciation and especially of angiosperms have been studied, which seem to have been predominant, through the allopatric and parapatric modes of speciation.

But not only islands are the places of endemic species. South America has been extensively studied with its endemic areals, which represent ensembles of allopatrically distributed species groups. Species of *Charis* butterflies from the Riodinidae family are a prime example, limited to specific regions, consistent with the phylogeny of other species of butterflies, amphibians, reptiles, birds, marsupials and rodents. For all these groups, the models indicate a repeated, vicarious speciation. It is believed that rivers may have acted as geographical barriers for some species of the genus *Charis*.

Beyond the hypothesis regarding the role of rivers as barriers, in the Amazon Basin, the allopatric speciation offers the explanation of the high rate of biodiversity. It is also estimated that the dispersal of the allopatric species has been a significant source of diversification throughout the Neotropical Region.

The pattern of growth of endemism in both karst shelters and at high altitudes has been proven both for islands and continents worldwide. As the topographic altitude increases, the species become more isolated from each other, often being constrained by the zonal category.

This isolation from the "mountain top islands" creates barriers to genetic flow and stimulates allopatric speciation, generating the formation of endemic species.

The appearance of mountains (through orogenic phenomena) is directly correlated with biodiversity, which directly affects them. The formation of the Himalayan Mountains and the Tibetan-Qiunghai Plateau (for example), stimulated the speciation and diversification of many plant and animal species: - the species of *Lepisorus* genus - evergreen ferns; - glyptosternoid fish of the family Sisoridae; - *Rana chensinensis* species complex.

The raising of mountain ranges has also favoured the vicarious speciation of *Macowania* carnations (*Crinum macowanii*) and *Dianthus caryophyllus*) in the Drakensberg Mountains in South Africa, as well as the same speciation of *Dendrocincla* woodpeckers in the Andes of South America.

The Lamannride orogeny of the Upper Cretaceous stimulated vicarious speciation and dinosaur

radiation in North America. Adaptive radiation, as in the case of the Galapagos finches observed by Charles Darwin, is often a consequence of rapid allopatric speciation between populations. However, in the case of the Galapagos finches, among other islands, island radiation (such as the Hawaiian finches) is a case of limited geographical separation and has led to ecological speciation.

The results of geological research are showing that the last closure of the Panama Isthmus was about 2.7 to 3.5 million years ago. Recent research has highlighted an older and more complex emergence of the Isthmus, with fossils of the extinct species (as part of American biotic exchanges), and it is estimated that there were three large pulses to and from North America to South America.

Later, changes in the terrestrial biotic spread on both continents (as it was the case with some ant species of the genus *Eciton*) were possible based on the existence of an older deck or the existence of a series of decks.

As for the exact timing of the closure of the Panama Isthmus, biologists can study the species on the Pacific and Caribbean coasts. The emergence and submersion of the Isthmus of Panama was what was called "one of the greatest experiments in evolution".

In addition, as in most geological events, the closure was not rapid, but in millions of years, when a mixture of seawaters took place.

Shrimp studies of the genus *Alpheus* have provided evidence of an allopatric speciation. Phylogenetic reconstructions support the relationships of 15 pairs of sibling-species of *Alpheus*, on each side of the Isthmus and the molecular chronometer data support their separation between 3 - 15 million years ago.

The recent separations of the species took place in the brackish waters of the mangroves, while the older separations took place in the deep waters, in correlation with the gradual closure of the Isthmus.

The confirmation of an allopatric divergence also comes from the Experimental Laboratory on the pairs of species that are showing a reproductive isolation, almost complete. A similar situation of wildlife retreat and spread across the Pacific and Atlantic coasts has been demonstrated for other species-pairs. In the case of vertebrate species, the speciation was favored by the glacial periods, when the fauna withdrew from unfavorable conditions.

This concept of refuges has been applied to numerous species groups and to the explanation of their biogeographical distribution. The glaciation and successive withdrawals stimulated the speciation of birds from many boreal forests, as it is the case of the woodpackers (- yellow ventrally; - with the red neck; - with the red breast); setophaga warblers (*S. townsendii*,

*S. occidentalis* and *S. virens*), *Oreothlypis* genus (*O. virginiae*, *O. ridgwayi* and *O. ruficapilla*) and *Oporornis* (*O. tolmiei* and *O. philadelphia* now classified as *Geothlypis*) sparrows of the genus *Passer* (subspecies *P. (i.) unalaschensis*, *P. (i.) megarhyncha* and *P. (i.) schistacea*); species of the genus *Vireo* (*V. plumbeus*, *V. cassinii* and *V. solitarius*); Pacific-slope Flycatchers of *Empidonax* genus (*E. occidentalis* and *E. difficilis*); chickadees from Paridae family (*Parus. rufescens* and *P. hudsonicus*); and Turdidae (*Catharus bicknelli* and *C. minimus*).

As a special case of allopatric speciation is the peripatric speciation, often invoked as an example of isolation in glacial refuges, when a small population becomes isolated due to habitat fragmentation, as it was the case of red fir (*Picea rubens*) and black fir (*Picea marina*) or the case of prairie dogs *Cynomys mexicanus* and *C. ludovicianus*.

**Superspecies:** Many pairs or groups of species have close distribution patterns and these reside in the case of geographical regions, located next to each other. They often have common boundaries, many of which are hybridization areas. Some examples of neighboring species and superspecies make up an unofficial hierarchy, which refers to the spread of a complex of allopatric related species. These are also called allospecies. Among them we quote:

- 1 - The western and eastern passeriformes of North America, which belong to the genera *Sturnella* and *Leistes*. They prefer the dry regions of the West and the wet regions of the East (as geographical regions), with rare cases of hybridization and most of them result in sterile hybrids.
- 2 - The endemic monarch Muscicapidae for Solomon Islands; a complex of several species and subspecies from Bougainville Island (muscicapids with white head and brown abdomen) together with related subspecies.
- 3 - North American woodpackers and members of the *Setophaga* genus (the red and black eyes, with the green chest, and the Townsend warblers).
- 4 - A number of 66 subspecies of the genus *Pachycephala* are living in the Melanesian Islands.
- 5 - Bonobos – *Pan paniscus* - small chimpanzees and common chimpanzees.
- 6 - Relatives of *Climacteris* sylviiids from Australia.
- 7 - Birds of paradise in the mountainous areas of New Guinea (genus *Astrapia*).
- 8 - Red-collared and yellow-collared pigeons; black-headed and pink-breasted grosbeakmoths; Baltimore and Bullock orioles (from British Columbia, Canada); Lazuli bunting and purple/indigo bunting etc.

All these pairs of species are coming into contact with each other in the hybridization zones, which corresponds to the great geographical barriers.

"Flatworms" of the genus *Dugesia* (Platyhelminthes) exist in both Europe and Asia, and the circum-Mediterranean region.

In the case of birds, some regions are favorable for the formation of superspecies (see bird speciation), as it is the case of the 105 Melanesian subspecies, representing 66% of all bird species in the region. Patagonia is the country with 17 superspecies of forest birds, while North America has 127 superspecies of terrestrial and freshwater birds. Sub-Saharan Africa has 486 species of passerines, grouped into 169 superspecies. Australia also has many superspecies of birds - about 34% of all species, grouped into superspecies.

These superspecies are cryptic species or groups of closely related species without clear differences between them. They have had a common ancestor in an early stage after speciation. They should be known for correct measures applied in the disease control, in pest control as well as in conservation of biodiversity.

### III. Conclusions

1 – Because different organisms are either sexually or asexually reproducing there are tens of species definitions, but no one is entirely satisfactory.

2 – Every time, natural selection and microevolutionary processes are determining all species to adapt and permanent changing, and grading into one another.

3 – After Darwin's explanations how natural selection can arise new species, geneticists and ecologists explained the genetic variability as a result of mutations and recombinations, followed by geographical, ecological and sexual (genetical) isolation.

4 – In the same areal of a species can exist two end populations, which in spite of their genetically connections, they are too far each other and are not interbreeding. These are very rare cases of „ring" species.

5 – According to different scientists, the speciation can be sympatric, allopatric, parapatric, peripatric with centrifugal alternative of speciation, vicariant, microallopatric, geographical, ecological and superspecies or allospecies.

6 – Considering biological significance of the species, its definition should take into consideration the evaluation of morphological, geographical, ecological, behavioral, and molecular information about natural interbreeding populations, which are reproductively isolated from other populations.

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