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A conceptual model of new hypothesis on the evolution of biodiversity

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Abstract: The mechanisms that allow species to evolve, coexist, compete, cooperate or become extinct are becoming always more understood. At the same time, the factors that allow species to coexist in a given time within the same environment are still debated. Many theories and hypotheses suggest that competition tends to differentiate the ecological requirements after repeated interactions and to allow the presence of many different species in the same area (i.e. biodiversity). After all, a thorough understanding of the evolutionary dynamics of biodiversity, which could somehow explain the current distribution patterns and mechanisms of coexistence, must consider the biogeographic and phylogenetic approaches. Here I propose a new graphic model that reviews the past and present, and sometimes debated, trends in biodiversity and evolutionary science, pointing out the importance of the avoidance of competition, the biological history, the *endogenosymbiosis* and the three-dimensionality as the main forces that structure ecosystems and allow the evolution of biological diversity. This model is an attempt to explain and summarize some of the mechanisms that underlie the current presence of the awesome number of species that currently inhabit our planet.

Key words: avoidance of competition; endogenosymbiosis; evolution; biodiversity; phenotypic plasticity; niches differentiation

Introduction

The understanding of the mechanisms that allow the origin of species (Darwin & Wallace 1858; Darwin 1859) and explain their current presence on planet Earth has shed light on many processes such as speciation, adaptation and extinction. In the last decades many hypotheses and evidence have corroborated the mechanisms that allow species to evolve, coexist, compete, cooperate or become extinct. Founder effect ant genetic drift represents some of the most corroborated ideas about speciation (Barton & Charlesworth 1984). More recent models adopted computer simulations to extend previous theory and show how gradual adaptive change can generate nonlinear population transitions, resulting in the rapid formation of new, reproductively isolated species (Flaxman et al. 2014). These authors suggest that small effects of adaptive change act synergistically and precipitously split one population into two discontinuous, reproductively isolated groups.

Certainly, one of the most debated aspect of the hypotheses which have been developed (Hubbell 1980; Tilman 2004) is actually finding out which factors allow species to coexist in a given time within the same environment. Genomic approaches have been recently implemented to understand the genome-wide effects of accumulating reproductive isolation and of genomic properties that influence the process of speciation (Seehausen et al. 2014). Starting from the principle of competitive exclusion of Gause (Gause 1934; Hardin 1960) until Connell's ghost of competition in the past (Connell 1980), the importance of intra-and interspecific competition for the evolution of biodiversity has been stressed. These theories and hypotheses suggest that competition tends to differentiate the ecological requirements after repeated interactions and to allow the presence of many different species in the same area (Sommer & Worm 2002). Recently, the principles based on competitive reasons for the explanation of biodiversity have been criticized from both theoretical and empirical approaches (Chesson 2000). Strong multi-species interactions and genetic interactions, such as horizontal gene transfer, have been proposed as factors able to alter evolutionary outcomes and either dampen or promote evolution of constituent species, depending on the number of species and the distribution of interaction strengths across the interaction network (Barraclough 2015), which might also affect evolutionary outcomes.

Since Hutchinson's provocative "paradox of plankton" (Hutchinson 1961) a series of hypothesis, with different approaches, has been proposed to explain why the principle of competitive exclusion is not found in "real nature". The reason probably lies in the fact that ecologists have not questioned some of the principles of evolution. Most ecological models are too simplistic and are often considered as outdate (Pilkey & Pilkey-Jarvis 2007).
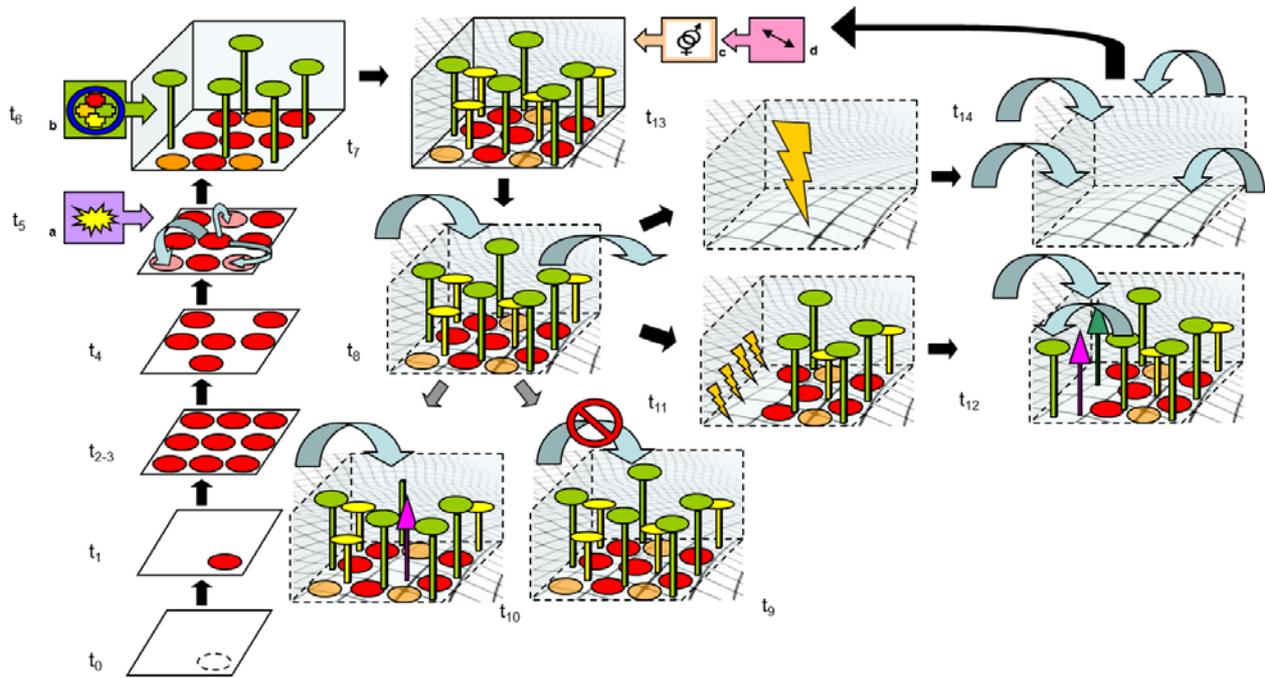
That niches are important to attain a genetic

Fig. 1. The graphic model of the evolution of biodiversity. Different steps towards species coexistence (see text for more details). t(0-14) are discrete times of the evolutionary process. Dotted-line circle is a potential species at t0. Red circles are "two-dimensional" species. Pink circles are polymorphic meta-populations. Orange circles are new species. "Tree-shaped" species are those that exploited the 3-D niche's environment. Grid landscape at t7 represents the heterogeneity of the environment. Dotted cube and blue arrows at t8 represents, respectively, the removal of barriers and the immigration and emigration processes. Small lightning at t11 symbolises local extinctions and big lightning at t13 is mass extinctions. a,b,c,d squares with arrows are, respectively: virus and bacteria's new alleles integration (*endogenosymbiosis*); BNDT effects including symbiosis, endosymbiosis and mutualism; sexual reproduction and predation/grazing/parasitism events.

equilibrium that favour species is a well-known eco-evolutionary pattern (Levene 1953). Recently, Levine & HilleRisLambers (2009) have argued that niches are critical for the maintenance of species diversity, challenging the neutral theory of biodiversity (Hubbell 2001) which on the contrary explains the coexistence with the equivalence of competitors. This study, like many others (Purvis & Hector 2000), does not take into account the effects of evolutionary history (in geological time) on biological diversity. Hubert et al. (2015) recognized that studies on speciation and community ecology have converged towards similar general principles by acknowledging the central role of metacommunities and dispersal dynamics in ecological framework. A thorough understanding of the evolutionary dynamics of biodiversity, which could somehow explain the current distribution patterns and mechanisms of coexistence, must consider both the biogeographic and phylogenetic approaches (Kottelat 1995; Cazzolla Gatti 2014).

Here I propose a new graphic model that reviews the new, and sometimes debated, trends in biodiversity and evolutionary science, pointing out the importance of the avoidance of competition, the biological history, the *endogenosymbiosis* and the spatial three-dimensionality as the main forces that structure ecosystems and allow the evolution of biological diversity. This model takes into consideration geological, evolutionary and ecological dynamics in the context of natural history (see Gavrilets 2004; Doebeli 2011 for detailed re-

views of the models and mechanisms in speciation and diversification theory) to present a clearer and more complete picture (Jackson 2001) of the evolution of biological diversity.

Methods

A simple evolutionary graphical model of biodiversity is presented (Fig. 1) to explain, using the latest scientific evidences, the mechanisms involved in species coexistence. I voluntarily avoided formalize it in a mathematical model being our current knowledge and analytic techniques still too simplified and embryonic if compared to the natural system I describe.

As Von Bertalanffy suggested in his masterpiece *General system theory* (1934) "the advantages offered by mathematical models – non ambiguity, rigorous deductions, verifiability through data of observation – are well known. But this does not mean that models expressed with a common language should be rejected or despised. A verbal model is still better of no models or of a model that, being mathematically formulated, is forced to reality, falsifying it. The history of science attests that, frequently, the expression in common languages precedes the mathematical formulation, i.e. the invention of an algorithm".

To implement the model a graphical symbolization has been adopted. The "external forces" of evolution have been depicted as arrows towards the system; the evolution/distribution patterns of biological diversity have been represented by single-cell circles of different colours, and the ecological niche has been symbolized by an open cube (and a

net has been used to represent environmental heterogeneity within the niche).

Results

The model

I began to consider a two-dimensional environment (Fig. 1) where any form of life is lacking at time 0, which may be the Earth a few moments before the formation of the first living beings. I supposed that this area is isolated by a physical barrier (island, mountain chains, acidic waters, closed pool, etc.). The first cell that will be formed at *time 1* will probably consist of a single individual that through asexual reproduction, when resources are available, will reproduce itself exponentially until *time 2*. While the amount of time before the formation of the first living organism is infinitely long (billion of years), the one between the first individual and the exponential increase of the population is relatively short. We can assume that all individuals that have reproduced so far belong to the same biological species. When the maximum abundance allowed by the limited resources and carrying capacity of the environment at time 3 is reached, density-dependent effects (which have an impact on birth rates and mortality) will take back the population within the limits of the carrying capacity (time 4). In this simplified environment, the death of individuals regenerates resources (byproducts) for the birth and the development of other conspecifics with (syntrophy; see Sachs et al 2004).

After a relatively long time (millions of years), by chance, some integration of genome parts coming from successively evolved non-living cell parasites (such as virus and bacteriophages) can appear. These latter non-living cell parasites are just fragments of genes encapsulated in protein coats moving among cells and using them to replicate. Then, after the integration, the genetic sequences of the first species transcribe, leading to the formation of some individuals that are slightly or hugely (in punctuated equilibrium; see Eldredge & Gould 1972) different from their ancestors. I call them polymorphic meta-populations (Smith 1998). I did not suppose that random mutations were the main drivers of genetic differences able to produce these new meta-populations being recent hypothesis suggesting that natural selection maintains what acquired genomes create (Margulis & Sagan 2008). When these differences are not big enough to separate the meta-populations reproductively (not only genetically but also behaviourally), we cannot consider them as two different species. The population is constantly in a dynamic equilibrium that oscillates around the carrying capacity level. After many cycles of oscillations around the limits imposed by the environment, one meta-population could not manifest a density-dependent effect reduction of populations. So, it is possible that during a phase of exponential growth the meta-population, with the accumulation of new genes, would be able – due to its phenotypic plasticity (Via et al. 1995) – to utilize a different resource from those used by the in-

dividuals of the original population (e.g. by-products of it) or to metabolize some resources more efficiently. Therefore, in the first case it is the effect of the acquired genomes, through the phenotypic plasticity and the characters displacement of individuals of the meta-population that allows the adaptation to a new niche. This process, defined as sympatric speciation, may occur by means of a shift in the fundamental niche of a meta-population from the original one (time 5). It has been argued that true sympatry may not exist in nature, or can be – at least – genetically constrained (Felsenstein 1981; Bolnick & Fitzpatrick 2007). This is because small variations in the microhabitat preference can still create allopatry and recent investigations in habitat suitability studies seem to reveal these differences (Raxworthy et al. 2007; Rissler & Apodaca 2007). If we consider sympatry as a spatial variable, the "microhabitat preferences" are not properly sympatric but instead represent a niche displacement. I suggest that sympatric speciation should be reconsidered as one of the main mechanisms that lead to species coexistence and to the evolution of biodiversity. In fact, if interspecific competition and the principle of competitive exclusion of natural selection between different meta-populations (and then, species) were to take place, probably there would never been the coexistence of different species, but rather the survival of the most efficient one (which accumulates enough mutation to adapt and not to differentiate) and the extinction of the ancestor or those species belonging to other phyletic lines. The coexistence of two species in a sympatric way can happen only if there is low competition or weak competitive exclusion between them and a kind of *avoidance of competition* that leads to a slight shift of the niche of a meta-population, which accumulated a series phenotypic difference due to genomic inclusions coming from other sources of genes. Thus, eventually, it's the avoidance of competition and the process that I will call *endo-geno-symbiosis* (hereafter, the capacity of endogen "genes carriers" to share parts of their genome in a symbiotic relation with their hosts; following "endosymbiosis" proposed by Sagan 1967) that drives the ability to produce the diversity of living beings. Competition and mutation (i.e. natural selection) on the other side, lead to preserve and adapt species and not to diversify them. This confirms what has previously been pointed out: in reality we cannot attend the competition in the present since all niches of the relevant species in an ecosystem seemed to be unique and different, even though overlapping on various degrees. This is a concrete possibility since there has never been competition between two species living in the same area because of their common evolutionary history and phylogeny. Nuismer & Harmon (2014) used mathematical models to show that phylogenetic relationships among species can influence trait evolution and rates of interaction among species, but only under particular phenotype matching.

Continuing with the evolution of the system (time 6), further species formation is achieved by characters

displacement and the new realized niches, through the avoidance of competition and the endogenosymbiosis. This can lead to reach, again, the limit of the carrying capacity with minimum viable populations of many species. The ability of species to change their external environment (e.g., the production of oxygen, nitrification, carbon fixation, etc.), to develop in a three-dimensional space (and not only in two dimensions) and to create relationships which take advantage of symbiosis and mutualism (Forsey 2013), may allow the expansion of the basal hypervolume and the formation of new species (even multi-cellular). At this stage, facilitation (Cazzolla Gatti 2014; Barraclough 2015) and co-evolutionary processes (Wade 2007) play a major role, such as the process that allows the development of new species taking advantage of the presence of the others (autocatalysis of biodiversity and hypervolume expansion; Cazzolla Gatti 2011).

Going further (time 7) the interaction between the biotic and the abiotic components increase the spatial heterogeneity of the ecosystem and this encourages the further evolution of new species that adapt to the new possibilities (formation of by-products, new chemical elements, erosion of the rocks, biochemical and physical changes, etc.). Obviously, at the same time, it is likely that some species could not be able to survive to the changing of external conditions (lack of robustness; Wagner 2012) to become extinct, consequently making niches freely available for the speciation of the others. The possibility of extinction due to environmental changes is, thus, more concrete than that due to inter-specific competition (Erwin 2001). It is at this stage, interactions of predation, grazing and parasitism between species could originate. They will maintain, through the principles discussed above, the various populations in dynamic equilibriums. This situation could persist for a long time or change after the removal of environmental barriers hitherto considered (continent shifts, climate change, drying up of rivers, etc.). At time 8, the species, whose populations fluctuate around the carrying capacity, will by chance or selected movements to reduce the effects of density and, therefore, aimed to avoid competition, migrate to neighbour territories and, thus, immigrate into new areas. Here they find two situations. The first is that the environment into which these individuals migrated does not have available niches so, as a consequence, they will be rejected (time 9). The second is that the immigrant individuals finds a niche available and settles in that territory (time 10). More and new evidences show that in intact ecosystems the chance that an alien species can survive is very low (Gurevitch & Padilla 2004) and that ecosystems under stress are more prone to having available immigrant niches to let alien species settle in (Wilson & Peter 1988). Emigration can either still keep the meta-populations in contact and thus genetically belonging to the same species or, because of the distance and/or the rebuild of physical and geographical barriers, it could lead to the formation of two distinct species (parapatric/allopatric speciation). Allopatric speciation then, although it can

occur suddenly after the formation of physical barriers or dispersal forces (for a review of speciation mechanisms see Templeton 1981), seems to be less likely to appear than sympathy, considered as the result of the inclusion of new parts of genomes and phenotypic adaptation to new niches.

Because, either in the short or long-term, environmental conditions tend to vary, it might happen that ecosystems that face low and time-limited instability see some species become extinct because they do not adapt to those new conditions (time 11). These areas have a high rate of immigration since some niches remain empty due to extinction. Even in this case, it will be very unlikely that competitive exclusion between immigrant and local species to occurs, as immigration depends on the distance (MacArthur & Wilson 1967). It is more probable that a species of neighbouring territories, and therefore phylogenetically close to those extinct, emigrates filling the niches gap without potential competition (time 12).

In case of environmental instability of greater intensity or duration, the extinction of species in a given ecosystem is likely to be massive and so, therefore, the rate of species immigration from the surrounding environment, in an attempt to reoccupy the many empty niches, would be very high (time 13). Certainly, at that stage, the need of speeding up the ability to face variable environmental conditions and the appearance of parasites (Smith 1978) have encouraged and allowed the evolution of sexual reproduction. The latter, through the recombination of two different genetic pools and the increase of the probability of favourable mutations, adapts the species to new external conditions, but does not evolve new ones (even in the long term). Such a change results from a compromise between the need to transmit in the long-term as much as possible genetic material to future generations and the need to address the environmental variability, while halving its fitness potential (Hamilton 2002). In this perspective, the evolution of sexual reproduction appears as an extreme and ultimate action to preserve the species or, in other words, to adapt them to external changes and not, as hereto suggested by evolutionary biologists, as a mechanism capable to produce new species due to mutations. It is furthermore likely that the same cause of the evolution of sexual reproduction, the parasitism, represents also the beginning of biodiversity. In fact, it seems that sexual reproduction acts as a conservative system (related to natural selection) against the inclusion of new genetic variations into cells' DNA (supported by the mutations reparation systems; see Generoso et al. 1980) and, instead, the evolution of a new species appears only when this preservative system fails to contrast the inclusion, within the host genome, of hexogen parts of DNA coming from "parasitic" cells (viruses, phages) or of whole individuals (mainly cells; Sagan 1967). As two parallel evolutionary lines, sexual reproduction preserves what endosymbiosis and *endogenosymbiosis* drive to diversify. Following the first, the species can adapt slowly and indefinitely to the ex-
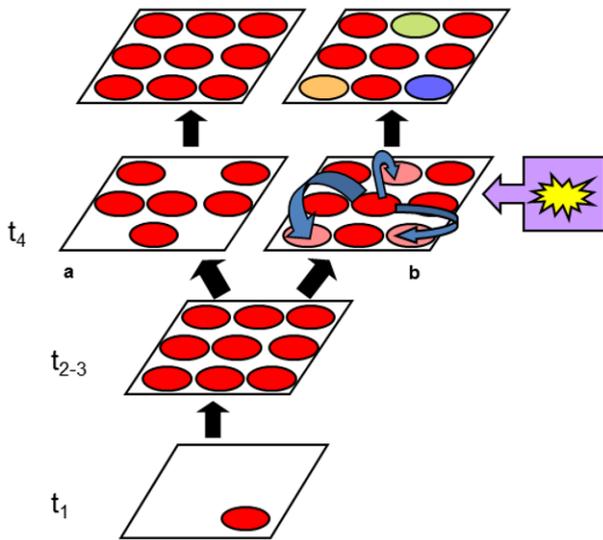
Fig. 2. The avoidance of competition leads to species coexistence. At t4 the empty space due to cyclic fluctuation of populations around the carrying capacity is filled by individuals of the same species (a), with mutations that allow them to adapt, but not to evolve in different species. (b) with *endogenosymbiosis* and phenotypic plasticity (purple square with arrow) some polymorphic meta-populations can evolve in different species, following the principle of the "avoidance of competition" (see text for more details).

ternal factors, adjusting themselves (adapting) but not "creating" novelty. The second line leads to speciation due to sudden changes in genes sequences.

The dynamic process just described may, therefore, continue to be used for further endless cycles of sexual reproduction, while maintaining the basic patterns set.

These dynamics, considered in biogeographical and evolutionary terms, seem to be the most likely to have led to biodiversity and the coexistence of the species that we see today on our planet, both in aquatic and terrestrial ecosystems.

Discussion

The simplified model of the evolution of biodiversity described so far leaves out two aspects of microevolution that cannot be omitted in a comprehensive view of the processes that influence species diversity.

In particular, it is necessary to investigate what happens at time 3, at the maximum carrying capacity of the only species present and at time 5 with different species (Fig. 2). Exceeding the carrying capacity by some populations, in case of no possibility of emigration even on the microscale, leads to the appearance of a series of density-dependent effects (mutual interference, resource depletion, diseases, grazing, predation), which bring populations under the limits allowed by the ecosystem (increasing mortality rather than birth rates). According to the statement of the principle of competitive exclusion, when a balance between population/resources is reached and all individuals of the same species (obviously) have identical niches, there would be

no ways for the expansion of the species or for evolution of new ones. What actually happens, instead, follows precise steps that lead to an increase in the number of species. A series of random changes in genomes induced by either endosymbiosis, *endogenosymbiosis*, environmental or reproductive (less frequent if asexual than sexual) causes may lead to an accumulation and a change in genotype of some individuals of the species. This will generate a phenotypic plasticity that, through characters displacement and polymorphisms, can be used to shift slightly the niche and avoid the competition for space and resources with non-mutated (wild type) individuals. In this way new species can form (following the accumulation of behavioural differences as a result of niches shifting and, then, by sympatric reproductive isolation), which are able to coexist in the same area as they have different ecological needs. It is well known, for instance, the case of the coexistence of predators, whose ancestors of different phylogenetic lines, during their evolutionary history, established trade-offs in the use of the same prey, but in different ways, ensuring the survival in the same territory, precisely through the avoidance of competition (Durant 2000).

Something similar happens in the plant world, where (especially in tropical forests) many species with apparently the same ecological requirements, whose niche were slightly differentiated from their phenotypic plasticity driven by the avoidance of competition, coexist (Platnick 1991; Wright 2002).

The avoidance of competition, therefore, not only resizes the importance of the competition among species, but also explains why climax ecosystems with intermediate disturbances show great levels of biodiversity (as in the case of coral reefs and tropical forests). These steady ecosystems are characterised by an iteration of the cycle of the model described above.

For instance, temperate ecosystems, which have experienced recent phases of glaciations with high climatic variability and deep stress because of anthropogenic activities (logging, fires, etc.), have reset many times the cycles of "speciation through the avoidance of competition" leading to poor diverse environments.

A second mechanism of microevolution happens at time 6, when the species begin to exploit the three-dimensional space (Fig. 3). Both in laboratory and in the field experiments, the three-dimensional space of biodiversity is often deliberately omitted, conducting studies that force species to interact in a two-dimensional environment (Holmes et al. 1994). In fact, the three-dimensional space provides a greater exploitation of the niches made available by the environment (Cazzolla Gatti 2012). With the Biodiversity-related Niches Differentiation Theory (BNDT; Cazzolla Gatti 2011), I recently proposed that species themselves are the architects of the greatest biodiversity of a given environment because, through the realization of their fundamental niche, they allow the autocatalytic expansion (also in the third dimension) of the available niches' space for other species. I consider three, and not more,
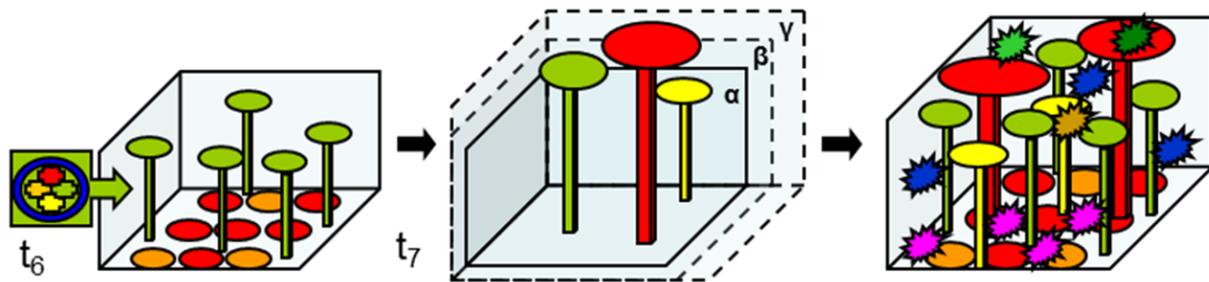
Fig. 3. Species exploit the 3-D space and the BNDT effects. As suggested by the BNDT, the exploitation of 3-D space and the species facilitation allow the increase of basal niche space and enhance the number of species that can fill the ecosystems (see text for more details). Green square with arrow represents the mechanisms foreseen by the BNDT. α, β, γ cubes are different basal niches shaped by environmental variables (in particular temperature and humidity). α could be intended as a polar ecosystem with limited space and few species, β a temperate ecosystem and γ a tropical ecosystem with higher temperature and humidity and, consequently, bigger 3-D niches space that key species can exploit allowing more (as in the last cube of the figure) specialist species to survive.

dimensions as fundamental for the evolution of biodiversity because they are the main physical dimensions in a spatial landscape that a species can exploit (imagine the water column for marine life, the forest canopy structure, the micro-scale volumetric landscape or the vertical air space). In this context it is important to clarify that it is only the volumetric space that is intended to be 3-dimensional in the BNDT, and this latter can increase the available niches including multidimensional niche's hypervolumes. As in the original graphical representation of the concept (Cazzolla Gatti 2011), the enlarged physical niche's space is represented by a cube (of 3-dimensions), but the available hypervolume inside is spherical (meaning that many, and not just three, behavioural and physiological niche's variables are involved).

Although every species is able to support the establishment of many others, it is especially the generalist and structuring ones (key-species) that greatly increase the hypervolume available in the ecosystems (Bruno et al. 2003). They do this by extending the three-dimensional space that allows the specialist species to establish themselves in that habitat (autocatalysis of biodiversity; Cazzolla Gatti 2011). According to this theory, factors such as the overvalued intra and inter-specific competitions are overtaken, reconsidering their real importance in the evolution of biological diversity, by mechanisms as facilitation, mutualism, symbiosis, coevolution (for a review of the genetic bases of the co-adaptive process and co-speciation see Wade 2007), which all lead to the coexistence of species.

Much emphasis has been put on the competitive interactions between individuals of the same species and different species in ecological and evolutionary studies rather than on cooperative approaches. Darwin himself wondered how the simultaneous presence of many species in one ecosystem could be justified in the struggle for existence. The allopatric speciation has often been cited as the main cause of species formation, underestimating the importance of the mechanisms of sympatry. Recent researches and developments of new theories on the mechanisms of cooperation and facilitation between individuals (Nowak 2010) and species (Cazzolla Gatti 2011) and the old ideas about the role

of sympatric speciation (Gorur 1973; Maynard 1966) should be reconnected to better understand the main factors in the evolution of biodiversity.

Critics of this approach may highlight the fact that many alien species that have been introduced deliberately or accidentally into territories far from their habitat in recent decades, contradicting what hereto argued, have developed competitive behaviour up to eliminating or greatly reducing native species with their similar realized niche. However further analysis is needed to observe two elements. The first is that alien species are rarely able to settle in areas not subjected to anthropogenic stresses (alteration, fragmentation, selective logging or hunting, etc.; Meyerson & Mooney 2007.) and that when an allochthonous invasion takes place, it is very unlikely for the alien species to completely eliminate the endemic one, which usually tends to reduce their density or migrate to neighbouring areas, when it has the phenotypic plasticity to do it (Didham 2005). Only in rare cases and in localized environments, resource and habitat limitations may lead to the extinction of native species (Wauters 2005). This latter event, however, cannot be considered as an effect of the principle of competitive exclusion. The two species that come into contact in this way, usually carried by human activities over long distances, arrive often from different continents, whose biological histories and phylogenetic relationships are distant and generated through allopatric speciation or parallel evolution. This suggests that the evolution of biodiversity itself has the tendency to avoid the competition. Competition can never happen between two species that come from a common biological and phylogenetic history and can occur only in case of deep alterations of the ecological dynamic equilibrium (stresses and invasion of alien species). Richardson et al. (2014) suggested that micro-geographic adaptation and its driving mechanisms can fundamentally alter ecological and evolutionary dynamics in nature. They identified seven main mechanisms known to facilitate the adaptation at fine spatial scale, such as: strong natural selection; landscape barriers; spatially autocorrelated selection regimes; habitat choice; selective barriers against migrants; evolutionary monopolization effects; and sexual selection against migrants. In invasion

events the two species in contact, belonging to distant branches of the evolutionary tree, have not been able to establish a series of trade-offs which might prevent competition and have to interact when their coexistence is forced. In nature, therefore, competition seems to be the exception and the avoidance of it by any means the rule (even in intraspecific relationships, rituals are put in place to prevent damages caused by competition for resources, space or mating; Smith & Harper 2003; Branch 1975). There is a large number of defence mechanisms (inedibility, poisons, spines, allopathic substances, dispersal in plants, animals migrations, etc.) evolved in order to avoid competition between species belonging to the same or, even, different trophic guilds and among individuals of the same population (Lambin et al. 2001). The mechanisms that have been interpreted so far as competitive are in reality nothing more than ways to avoid competition and save energy, which consequently allow the coexistence of species with similar niches.

Conclusion

The abovementioned ideas have often been criticized for their lack of formalisms able to model these patterns. Some attempts to unify the most interesting mathematical approaches have been done. Kirkpatrick & Ravigne (2002), for instance, identified and formally described five major elements that determine the outcome of speciation caused by selection, such as a form of disruptive selection, a form of isolating mechanism (assortment or a mating preference), a way to transmit the force of disruptive selection to the isolating mechanism (direct selection or indirect selection), a genetic basis for increased isolation (a one- or two-allele mechanism), and an initial condition (high or low initial divergence). They showed that allopatry vs. sympatry can be viewed as a form of assortative mating. Gavrilets & Losos (2009) using modelling approaches identified 10 general patterns concerning the temporal, spatial, and genetic/morphological properties of adaptive radiation. Despite this huge models review, their conclusions were not definitive: lineages vary in manifold ways, various evolutionary factors act simultaneously, similar evolutionary outcomes can be achieved via alternative paths, and the contingencies of place and time play a large role in guiding the evolutionary process. This follows because we must admit that the complexity, non-linearity, feedback mechanisms make the networks of relationships in any ecosystems is virtually impossible to be represented with the current mathematical tools. The same stability against stress of more complex systems has been questioned (McCann 2000) by mathematical models, against the empirical evidences. This may be due not to the fact that ecosystems with high biodiversity are really more vulnerable but to the evidence that non-linear mathematical models, with many variables, are not easily manageable with current analytical techniques and therefore tend to generate erroneous results.

Finally, the review of the old hypotheses and the new ideas suggested in this study recall the urgent need to halt biodiversity loss caused by human beings. Marine and terrestrial ecosystems are subjected to a level of depletion that do not match with their ability to regenerate. The great extinctions of the past, such as the Permian-Triassic or the Cretaceous-Tertiary, were all caused by climatic and geological changes (Courtillot & Gaudemer 1996; Purvis & Hector 2000) and not by the competition for resources and space between species. This should motivate our species to think before it is too late about how human competition, for the first time in the history of life on Earth, has been leading to the extinction of animals and plants systematically. The simple model of evolution that I proposed here does not only explain some of the mechanisms that underlie the current presence of the myriad forms of life, but it also sheds new light on the need of periods of geological, rather than biological, time scale to generate the awesome number of species that currently inhabit our planet. If humanity does not stop its "unnatural" competitive spirit in the massive elimination of species, it could another billions of years before the diverse set of living beings, that we now call biodiversity, be regenerated. And the extinguishing sun's power will not allow it.

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