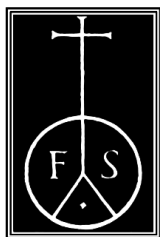


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# EVOLUTION IS A COOPERATIVE PROCESS: THE BIODIVERSITY-RELATED NICHES DIFFERENTIATION THEORY (BNDT) CAN EXPLAIN WHY

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KEYWORDS: Cooperation, Evolution, Niches differentiation, Biodiversity.

ABSTRACT: A. McFayden [1] and G.E. Hutchinson [2] defined a niche as a multidimensional space or hypervolume within the environment that allows an individual or a species to survive, we consider niches as a fundamental ecological variable that regulate species' composition and relation in ecosystems. Successively the niche concept has been associated to the genetic term «phenotype» by MacArthur [3-4] stressing the importance on what a species or a genome can show outside, either in the environmental functions or in body characteristics. Several indexes have been developed to evaluate the grade of overlapping and similarities of species' niches, even utilizing the theory of information. However, which are the factors that determine the number of species that can coexist in a determinate environment and why a generalist species do not compete until the exclusion of the remaining species to maximize its fitness, is still quite unknown. Moreover, there are few studies and theories that clearly explain why the number of niches is so variable through ecosystems and how can several species live in the same basal niche [5-6], intended in a

comprehensive sense as the range of basic conditions (temperature, humidity, food-guild, etc.).

Here I show that the number of niches in an ecosystem depends on the number of species present in a particular moment and that the species themselves allow the enhancement of niches in terms of space and number. I found that using a three-dimensional model as hypervolume and testing the theory on a Mediterranean, temperate and tropical forest ecosystem it is possible to demonstrate that each species plays a fundamental role in facilitating the colonization by other species by simply modifying the environment and exponentially increasing the available niches' space and number. I resumed these hypothesis, after some preliminary empiric tests, in the Biodiversity-related Niches Differentiation Theory (BNDT), stressing with these definition that the process of niches differentiation is strictly addressed by species. This approach has various consequences, first in consideration of relations among species and second in terms of a better understanding of cooperation/competition dynamics.

**K**AUFFMAN in the 1993 published a book titled *Self-Organization and Selection in Evolution* [7]. In this masterpiece of biology he argued that the complexity of biological systems and organisms might result as much from self-organization and far-from-equilibrium dynamics as from Darwinian natural selection. Some fellow biologists and physicists working in Kauffman's area reserve judgment on Kauff-

man's claims about self-organization and evolution. Kauffman explored complex systems and science that focuses on the emergent and adaptive behaviors between multiple systems and their interactions, as well as environmental, social, economic, technological systems.

Recently, Levine and HilleRisLambers [8] suggested that niches differences stabilize competitor dynamics by giving species higher per capita population growth rates when rare than when common and that coexistence occurs when these stabilizing effects of niche differences overcome species in overall competitive ability. Bastolla *et al.* [9] argued that nestedness reduces interspecific competition and enhances the number of coexisting species. These new ecological approaches conduct towards other assumptions on the role of species and their niches.

Basically, the Competitive Exclusion Principle [10] affirms that it is impossible that two species that are in competition for the same resources or ecological rules can live in the same ecosystem. This principle looks at niches as static [11] and predetermined «ecological volumes» [12] that species can fill. Mathematical models [13-14-15] and empirical analyses [16-17-18] confirm that without a clear differentiation of niches the common species become more common and rare species rarer, suggesting that niches' differentiation strongly stabilizes the coexistence of species [19]. However, this is not a univocal relation. Thinking in terms of non-linear/non-equilibrium systems with feedback and dissipative [20] mechanisms, we can say that not only do niches enhance species coexistence but really species increase the number of niches available, thus they allow a biodiversity increment in resources exploitation within an ecosystem.

Said that, we can formulate the BNDT as follows:

in natural conditions of immigration and emigration, with every environmental condition, species tend – directly or indirectly, thanks to their simple presence and life roles – to increase the number of potentially available niches for the colonization of other species, enhancing the limit imposed by the basal hypervolume, until the reach of the carrying capacity of the ecosystem.

At same time, niches and mutualistic networks of the ecosystem allow, through circular and feedback mechanisms, the rise of the number of species, generating a non-linear autopoietic system [21-22].

In other words, we can argue that the species themselves, creating favourable conditions for the colonization of other species, allow the concurrent presence. This is nothing more than coexistence and the fundamental mechanism that supports the coexistence of species is the creation of *diversity-related niches*. The higher the number of species is, the more likely the possibilities that other species can colonize that environment are.

Trying to model the previous definition we can determine that the number of niches in a discrete time depends on the number of niches related to the initial number of species:

$$\frac{dN}{dt} = [Nt - n(t_0)] \times \varrho$$

assuming that  $N$  is the number of niches,  $t$  is the time,  $n$  is the initial (at time  $t_0$ ) number of niches and  $\varrho$  is the coefficient of niche' facilitation (intended as  $\varrho = S_t + i_{\Delta t} - e_{\Delta t}$ ,

where  $S$  is the number of species at time  $t$ ,  $i$  is the rate of immigration/speciation and  $e$  the rate of emigration/extinction).

Solving this differential equation the number of niches at time  $t$  becomes an exponential function of the initial number of themselves elevated to the number of species multiplied for a variable  $c$ :

$$N_t = c \cdot N_0^{e \cdot dt}$$

If we consider the carrying capacity ( $K$ ) of the ecosystem ( $e$ ), the equation can be rewritten as follows:

$$\frac{dN}{dt} = [Nt - n(t_0)] \cdot e \cdot \left(1 - \frac{N}{K}\right)$$

Taking discrete intervals of time, the systems (ecosystems) tend to be subjected to an increase of the number of species proportional to the number of species already present in the environment at time  $t$ , with available niches that rise in an exponential way. Systems with different initial number of species, even if they have the same chemical-physics basic conditions, after a discrete interval of time  $dt$ , will count a different number of species, directly proportional to the number of potential niches developed and to the initial number of species.

Running, instead, the model towards an infinite time ( $t \rightarrow \infty$ ) every ecosystem, in identical chemical-physical conditions, tends to reach the same number of species that is maximum at climax and at carrying capacity level. However, as every model, it is only a simplification of reality and cannot completely represent the whole ecological roles and relations among species and the complete dynamics of niches formation. Anyway, taken with many precautions it is an easy exemplification of the theory.

Going deeper into niches formation and evolution and remembering Hutchinson's [23] concept of multidimensional space, I would suggest a three-dimensional model of diversity-related niches differentiation, as showed in FIG. 1. The two-dimensional system of basic variables evolves towards a three-dimensional niche's space (a sphere) of multiple variables. When one or more species are able to fill this niche's space, and because most of species are strict for some ecological condition but tolerant for other variables, the hypervolume (considered as the sum of every single range of variables) enhance its dimensions allowing other species to colonize the environment. In this way a niche that was originally forbidden to some species for some ecological characteristics becomes available because of the simple presence of a species that can tolerate initial conditions.

Graphically it could be imagined as a sphere that represents the basal niche's space and a big tree (FIG. 2) that fills the whole space. Roots of this tree are pioneer species (r-selected [24]), that partially are substituted during growth and trunk is one or few dominant generalist species (we can call, G-species). As successional ecological stages develop, the tree expands its crown. Doing this, it develops branches that represent more selective species (K-selected [23]) and that little by little enhance the limit of the basal hypervolume and allow super-selective species (we can call, S-selected), as leaves, to fill the whole niche's space created. The grade of overlapping of these leaves represents the overlapping level of niches.

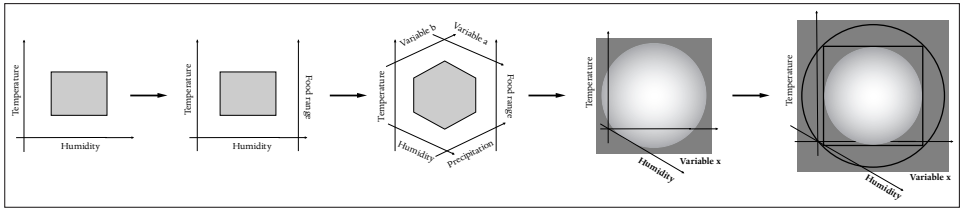


FIG. 1. Process of niches formation and expansion due to the presence of new species. The two-dimensional niche's space shaped by two variables (Humidity and Temperature) becomes more complex step by step adding new components (variables, i.e. Food range, Precipitation, etc.). The niche's space assumes a hexagonal, octagonal, dodecagonal, etc. shape until it becomes spherical with infinite variables. The expansion of these latter over the two-dimensional limit leads the niche's space to a spherical form of three-dimensions. This sphere can represent the hypervolume (or multidimensional space) of a niche. When this niche's space is filled by one or more species, because each species cannot fit exactly into the niche's space but is tolerant for some of the variable, the available hypervolume enhances its ranges (the cube, showed frontal as a square) becoming a bigger sphere where other species can survive. In this way one species that occupies a limited niche's space creates the condition to allow new colonisations by other species. This process will continue, if there are available colonizers, until the carrying capacity of the environment.

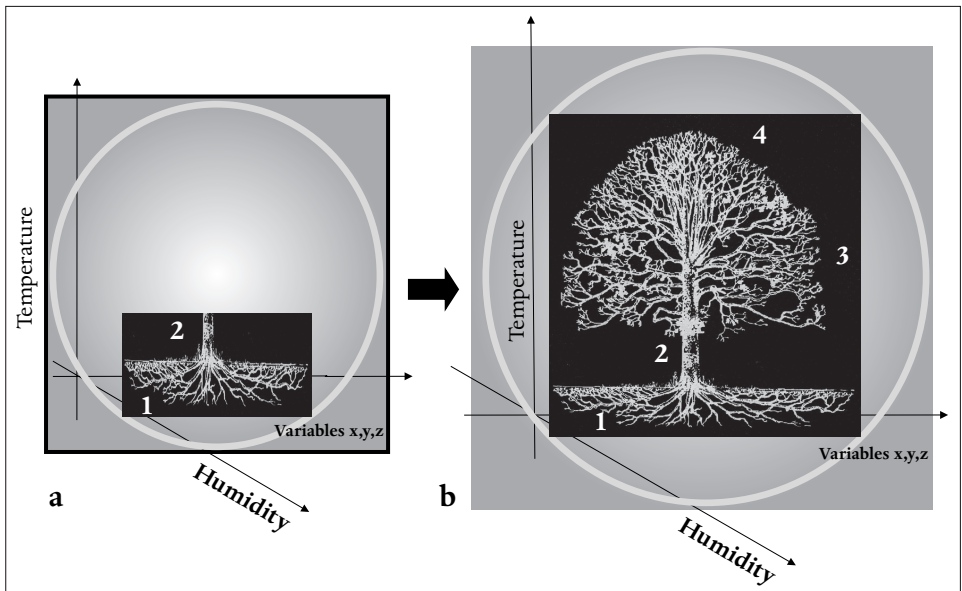


FIG. 2. The development of niches differentiation and the respective role of species. The sphere represents the basal niche's space and the tree fills the space. Roots (1) of the tree representing pioneer species (r-selected), that partially are substituted during growth and trunk (2) is one or few dominant generalist species (we can call, G-species). As successional ecological stages develop (from part a to b of the figure), the tree expands its crown. Doing this, it develops branches (3) that represent more selective species (K-selected) and that little by little enhance the limit of the basal hypervolume (red square) and allow super-selective species (we can call, S-selected), as leaves (4), to fill the whole niche's space created. The grade of overlapping of these leaves represents the overlapping level of niches.



To test empirically the BNDT I realized three preliminary field analyses. The first was conducted into a Mediterranean forest ecosystem [25]. A square plot into a burned forest in the South-Italy region was selected. Four squared areas equally surrounded by wood (at same mean distance) were extracted within this plot. The number of survived species after fire (3 months before the experiment) was zero for each area. I planted respectively 1, 5, 10 and 30 endemic shrub species randomly selected, belonging to the close forest. The rate of immigration and emigration for each area was statistically the same. No speciation and extinction processes were documented due to the strict time of the survey. I came back two times, at one year distance, to count the number of species present in each sample area. The first year I found that the plot accounted respectively 7, 14, 19 and 43 species of plants and animals. The second year the number of species was respectively 13, 28, 35 and 66 (TAB. 1).

Plot	Species at time t1	Species at time t2	Species at time t3	Increment of species dS
a	1	7	13	12
b	5	14	28	23
c	10	19	35	25
d	30	43	66	33

TAB. 1. Trend in species number during the time. For each plot in the second column (time t1) the initial number of planted species is indicated. Time t2 and t3 columns indicated the number of species counted during the two surveys phases at one year distance. dS indicates the total increment of species number during the time (as Species n. at time 3 minus Species n. at time 1).

These results mean that the increment of species from the original situation, after two years, was of 12, 23, 25 and 33 for each sample plot, excluding the original planted species, and that this increase strictly depends on the number of initial species. The curves follow, as predicted by the model, the exponential trend (FIG. 3).

The result could appear apparently strange, particularly if we consider that in the sample area with one initial planted species there was much more potential niche's space available to be colonized compared, for instance, to those available in the area with 30 initial species. Instead, contrarily to what expected, we found an increased number of 12 species for the first area with one initial species and 33 for the sample area with the highest number of species.

This preliminary results show that, as predicted by the BNDT, not only the available space or the vacant niches play an important role in determining the number of colonizers but also the presence of species induces and somehow encourages the presence of others.

Another research in Indonesia conducted last year, within the Bali Barat National Park, seems to confirm the previous results. I surveyed two different tropical forest ecosystems. One was a lowland unmanaged pristine tropical forest. The second was a selective-logged lowland tropical forest. I found that the species composition was quite similar in both forests and that the selectively logged one followed a niches development similar to the pristine one. Because in the logged for-

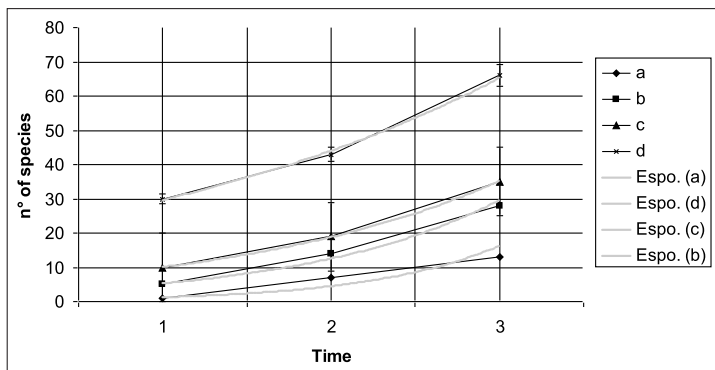


FIG. 3. Exponential trend in niches formation. After a three time period (one year each) it is possible to find an exponential trend in the number of the species present in each sample area. The line -a- shows the trend of the area with one initial species. If only the available space and the potential vacant niches were to determine the colonization trend we could expect a higher number of species increment after a time  $t$  in the less initial species number area than in the highest one. Instead the plot -d- showed a higher difference of number species than plot -a- confirming what it was foreseen by the BNDT: the species themselves allow other species to colonize as a positive feedback, simply by making available niches space that was not available beforehand.

est some selected species were removed (indicated as  $\beta$ ), we can expect a total number of species ( $S$ ) differing by the close unmanaged forest ( $\alpha$ ) only in the number of logged species ( $S = \alpha - \beta$ ). On the contrary, the total number of species in the selectively logged forest was very low compared to what we can expect merely deducting  $\beta$  to  $\alpha$ . This confirms that the removal of one species takes out many other species (>5% of the total number) from the ecosystem as predicted by the BNDT.

A third evidence of the theory can be observed in many different ecosystems like on the top of the Monte Venere, in Lazio region in Italy. In the east slope of the mountain grows an old beech forest and in the western slope an oak forest. While oak allows a rich brushwood and the presence of vines, lianas, epiphyte and other tree species, the beech creates the condition to be quite a monocultural species. On the edge of the Monte Venere's top it is strange to suddenly pass through a richness of biodiversity ecosystem to a monotonous sweep of one species. Considering that the climatic and environmental conditions are quite the same (even if the solar radiation and the exposure to the winds that come from Vico Lake are a bit different) it is very strange to see this situation in less than one hectare. I can suggest that the fundamental reason that leads to this phenomenon is strictly linked to the BNDT. Oak-dominated forests follow the successional evolution foreseen by the theory, where a species creates the conditions for the growth of other species rising exponentially the available niches and the limits of basal hypervolume. Beech-dominated forests instead do not seem to follow the previsions of the BNDT, mining its va-

lidity. Recently, however, has been evidenced that the *Bos primigenius*, before their extinction caused by human hunters, was the controlling factor of *Fagus* overgrowing, giving more emphasis to the role of natural history to species' relations in shaping the ecosystems and determining the creation of new niches (through the biodiversity-related niches differentiation mechanism) or the maintaining of a mono-species dominated environment, that frequently is the result of an ecological stress.

These fast surveys and evidences could confirm the results of the Mediterranean ecosystem plots where, because of the artificial differences in the initial number of species, the number of species at certain time periods resulted different among plots. There is necessity to better understand the validity of the BNDT in a complex tropical ecosystem and I am going to do it in the African tropical rainforest next two years.

However, theoretical and preliminary empirical approaches could lead to other questions that need to be answered: is the rule played by each species in an ecosystem indifferent in terms of niches differentiation or are generalist species more relevant to allow specialist ones to fill niches that are created in the late stages? and how does the evolution of niches change in relation to the different species that colonize the environment during the first stages?

The BNDT, following this preliminary results can be the answer to the reason why we have a higher number of species in the plot with higher initial number of species, if the immigration/emigration tax is the same in the four plots. Furthermore, a future step towards an empirical confirmation of the BNDT could be the evaluation of the behaviour of the four plots in long time to verify if the carrying capacity of the system will keep under a unique threshold the number of species living in that ecosystem, shaping the four curves in a sigmoid way to converge towards a common level of niches filled.

If these empirical evidences are consistent with the BNDT it will be possible to better understand the species' relations and the rule they play within the ecosystems. At the same time it will be simpler to predict the behaviour of a complex system and shift our idea of niches from a static to a dynamic and biologically (biodiversity) determined vision.

More importantly, a confirmation of the BNDT validity could represent a new way to see the dominant force among species and reconsider the importance of the competitive exclusion towards a less competitive nature where one species itself, enhancing the possibilities offered by the environment, allows other species to live in the same ecosystem.

Moreover, the BNDT could offer an opportunity to link as a bridge the criticized Unified Neutral Theory of Biodiversity (UNTB) [26], that promotes the concept of irrelevancy of adaptations, with the older theory of competitive exclusion.

Finally, the BNDT increases the urgency to arrest the loss of biodiversity, because if the theory were to be confirmed right, the loss of one species could lead to the disappearance of many other species 'hosted' into the niche hypervolume created by that. This dramatic evidence of the theory could take place when it is too late to revert the process.

## METHODS SUMMARY

To develop the BNDT I reviewed the latest theoretical, modelling and empirical approaches and extracted the common features that can adapt to real ecosystems well. The graph of the evolution of a niche space is the result of a long modelling process to better and easier represent the theory.

I followed a transect to individuate the best square plot to carry out the Mediterranean ecosystem experiment. The area is located in the region of Puglia in Italy in a semi-deciduous forest burned two years consecutively before the experiment. To be sure that no plant was present at the beginning of the experiment, not even seeds or cryptophytes, the soil beneath 10 cm deep was completely monitored and ploughed up. The 4 sample areas were of  $10 \times 10$  m and formed a bigger square. To ensure that the rate of immigration/emigration was similar in each area the plots were located exactly in the middle of the forest and at the same distance from the unburned trees.

I selected after 2 years of forest survey 30 most common shrub species and I randomly selected some for each plot. To evaluate the rate of biodiversity change I counted every species present at moment of surveys in a single day for 3 times every year. Only species that can be detected by eyes (no microscopical species) were counted.

I assessed the validity of the hypothesis, confirmed by the Mediterranean plots, during a field research within the Bali Barat National Park, in Bali, Indonesia with 3 consecutive surveys that gave to the BNDT another empirical confirmation. Obviously, the short-terms of researches and the preliminary result need to be confirmed by other studies.

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