

Species richness in isolated environments: a consideration on the effect of time

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ABSTRACT

The widely accepted MacArthur & Wilson model of island biogeography proposes a number of species that, after an initial growth, stabilize on each oceanic island at an equilibrium point. This species number depends on the available space, the vicinity of mainland, and the habitat diversification, thus being directly correlated with space characteristics. This space based model, however, does not explain some astonishingly evidences of species richness. The story length (the age) of each environment, possibly associated to the stability of conditions, should offer a better interpretation of species richness in each situation. Lakes, as water islands, more than land islands, have been considered in the present review as evidences of such an affection of the time on the species richness. The high species richness in the most ancient lakes is probably completely due to the genetic drift which produces diversification within each population possibly without any dependence from variability of conditions and habitats.

KEY WORDS

Ancient lakes, Evolutionary time, Island biodiversity; species richness.

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INTRODUCTION

The ecological frame: space and unstable conditions as responsible of species richness

Hutchinson (1959) justified the embarrassing abundance of species on the earth with the existence of trophic nets. According to this proposal, small sized species, characterized by short life span which does not encompass many developmental stages, can concentrate themselves upon narrower trophic specializations, thus living together in high numbers in the same site, without competition. Complexity of trophic nets was intended as higher when specialization occurs, such a specialization being the possible result of evolution under stable environmental conditions.

This assumption indirectly gave a role to the time: is the environmental stability (intended as time passed under invariant conditions) which allows the existence of complex trophic nets.

But this implicit admission was never evident; in fact Hutchinson did not develop it in the future. Only 2 years later the same scientist (Hutchinson, 1961) was convinced that the stability (homogeneity) of the water environment could not explain the high biodiversity in to the plankton, for which the seasonality (time instability) could be the actual reason.

In accordance with the principle of competitive exclusion (Gause, 1934), only variation allows the co-existence of ecologically similar species (= constant conditions lead to the affirmation of only one subject in each ecological role). In the water of the pelagic habitat, microalgae of phytoplankton do not affirm themselves because in a variable space, but probably because in a variable time, so avoiding the competitive exclusion. The time was a determining factor, but the variability, and not stability, was the cause affecting the species richness. Probably due to this double, contradictory time implication in the justification of species richness, successive ecologists did not take care of the time role.

To tell the truth, the role of the evolutionary time in the biological diversification (enrichment) of the planet is probably given as obvious and, avoiding to discuss it, scientists wanted to demonstrate how many and what causes were involved in addition.

Sepkowsky (1984) demonstrated that the number of taxa has a positive, although interrupted, trend in the whole earth story. On the other hand, however, Gould (1989) pointed out that after the Cambrian explosion, only extinctions occurred on the earth regarding phyla, and the biodiversity growth was relative to exaggerated speciation inside one or few phyla. Along the evolutionary time, the bio-richness at level of phylum was considered as impoverished notwithstanding the evident growth of the species number.

Coming back to the Gause principle, just to certify that time for ecologists is not the same entity of that for evolutionists, it implicitly admits an impoverishment of the species number with time (the ecological exclusion destroys locally the diversification if conditions became constant).

After Hutchinson, in '60s of the XX century, the scene has been monopolized by the model of MacArthur and Wilson (1963; 1967) where the species number possibly existing on an island is linked to the available space (island size) and to the distance from the continent (both problems of space). The role of time in that model is limited just to what would be necessary to reach the equilibrium point (to replenish the available space). The model is true only for newly formed islands, e.g. for the oceanic ones. What could change in an oceanic island at its biological equilibrium, when new arrivals equal the extinctions, is the type of species present, not their number. A number of studies tending to demonstrate the validity of this rule on a general scale were realized in the successive 20 years considering mountain tips, lakes, marine life around the islands, as isolated biota subjected to the same rule.

The consideration of temporary ponds as islands added also a time point of view to the problem. According Ebert & Balko (1987) the length of periodical existences of temporary ponds (the so called hydroperiod) affects the number of species possibly present in each pond independently from the basin size. The Authors proposed a time based re-interpretation of the MacArthur & Wilson space based model with the area dimension corresponding to periods of existence of the pond, and distances from

continent corresponding to periods of water absence. The time they considered, however, was an ecological factor, because related to something as the seasonal absence/presence cycles, and not useful for the realization of evolutionary modifications.

In a book Rosenzweig (1995) describes as in the periphery of the geographic distribution of large populations (where the pangamy is not real) small populations differentiate, giving new species with time. The process, intrinsic to the population dynamics, is completely disconnected from the environmental diversification and it occurs also in homogeneous habitats.

Notwithstanding this evolutionary (timely) approach to the problem of the species richness, Rosenzweig officially adhered to the hypothesis of Therborg (1973) who gave to the land extension the responsibility for the geographic distribution of species on the whole earth. In fact, even if is only the time which can allow the realization of genetic differences and their affirmation, for Rosenzweig this can be possible only for large populations, hence for those populations which occupy large spaces.

More extended areas contain a larger number of rare species because each lonely individual in each site is connected to other scattered individuals distributed in a larger space. On the contrary, a lonely individual on an island (a delimited space) cannot maintain such a connection with the rest of its own population and the species will extinguish with his death on that island.

Therborg (1973) and Rosenzweig (1995) did not affirm explicitly what this can represent for the species number on each isolated system, but it is easy to deduce that when a continental island is formed (e.g. with the sea level uplift) the number of species can only diminish (for the extinction of the rare ones) from that moment onward, until a new situation of equilibrium. This is just the opposite case of the species richness on oceanic islands (they grow until the equilibrium).

The hypothesis of Rosenzweig, however, admits a role of the time on the variability of the species number, absolutely independent from the environmental variations. Species richness spontaneously evolves towards a growth due to a mechanism intrinsic to the population dynamics. In addition, and in opposition with the Hutchinson's thought, the Rosenzweig's hypothesis is funded on the sympatric/parapatric speciation.

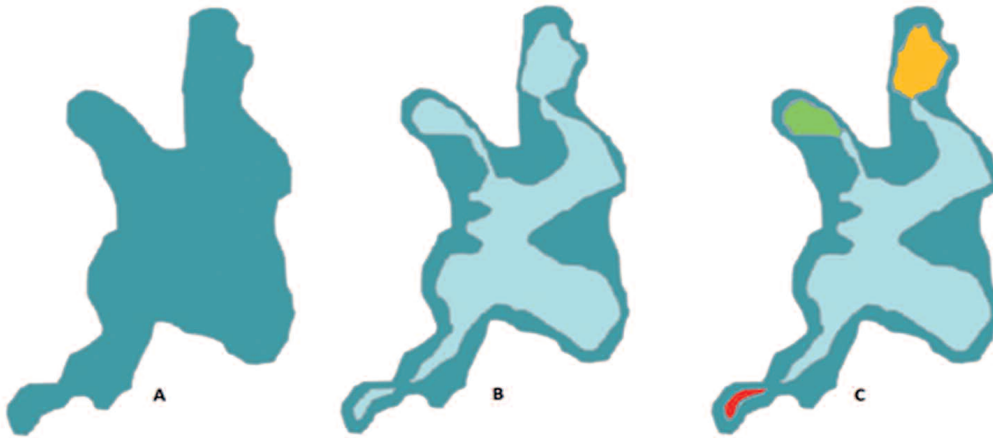


Figure 1. Hypothesis of the species number growth in a delimited area (island). A, the area is empty. B, one species establishes successfully on the area, occupying as much as possible space, with a high number of individuals. C, according to the Rosenzweig's Hypothesis, periphery subpopulations undergo genetic drifts due to the impossibility that pangamy is realized. This situation will give more species than the equilibrium situation due to the model of MacArthur and Wilson, without neither immigration, nor environment variability.

This evolutionist position appeared in a context of great success for Ecology which accepted without problems the Connell (1978) theory of the intermediate disturbance, evident descent of the continuous instability of Hutchinson, as the main responsible of species richness and/or ecological diversity in each geographic site.

Hence Rosenzweig opposes his evolutionary theory (there are more species in large areas where large populations can exist, and this is true also under constant conditions) to the ecological one of Connell (there are more species where the environment is variable and subjected to intermediate disturbance). One thesis affirms that species richness is independent by environmental conditions, although favoured in mature and stable situations; the other thesis affirms that species richness is favoured by variations which maintains in a state of immaturity the system (Fig. 1).

Isolated environments as witnesses of the role of time and stability on species richness

Lynch (1988) summarized the refugia hypothesis from which the present biodiversity could derive. During such a fragmentation period, species were separated in many and not communicating populations which had the time to accumulate genetic novelties with the mechanism of the genetic drift

(in condition of allopatry). The same interpretation (fragmentation of the system leading to isolation of many populations) has been proposed also for the flock speciation of Cichlidae fish in the African rift lakes (Sturmbauer, 1998).

What has been always distant from the ecological interpretations is just the island situation and the existence of ancient lakes (water islands). These last evidently do not follow the MacArthur & Wilson rules, and the ecologically based predictions on the number of species they should host are constantly disobeyed. The most ancient lakes today existing on the earth are all characterised by an elevated number of species, coupled with an elevated endemism. They confirm so simply the dependence of species number from the time, an unconsidered element from the island biogeography model of MacArthur & Wilson.

It remains to be discussed if the numerical growth of species can be attributed to the condition variability or to the stability in the time of the lake's lifespan. Lakes as Bajkal, Tanganika, Malawi, Victoria, Biwa, Ohrid, seem to show a species richness directly proportional to their own age, more than to their geographic position, their size, and/or episodes of fragmentation which could be succeeded during their existence. The dependence of the species number from the time (on an evolutionary scale) is evident because sites with high species number (the

mentioned lakes) show also a endemism grade directly correlated with their presumed age. Consequently, species present in such environments did not arrived there from elsewhere, because they formed in situ according to a mechanism (speciation) which required time and, according to the Rosenzweig hypothesis, they simply need large initial populations.

The evolutionary phenomenon of speciation produces endemism, and needs, in lakes, probably more than 10,000 years because postglacial lakes (formed from 10,000 years ago) in the boreal hemisphere have not endemics among their species. The necessary time for evolution is, on the other hand, completely compatible with volcanic islands of the MacArthur & Wilson model. For example, Galapagos or Hawaii, well known for the studies on the presence of endemics, have ages of some million years. Howarth (1990) admitted the time as main responsible of the high species richness of Hawaiian Drosophilidae (at least 1000 species recognized), giving importance not only to the biota fragmentation (the Hawaiian archipelago) but, more, to the presence of similar conditions on all the archipelago islands, during million years of story.

Briggs (1995) reports as the marine fauna richness from the two islands Saint Helen and Ascension, notwithstanding they should be colonized according to the MacArthur & Wilson model, shows numbers compatible with the different ages of the two islands, and not with their distance from the continent, or their size.

Notwithstanding Ascension is closer than St Helena to the African continent (1500 Km against 1850 Km), it has less fish species. If we look at the position of the two islands relatively to the middle Atlantic ridge, we discover that Ascension is closer to this fracture line, hence it is younger (it is the last which has been formed, being the closest to the ridge). In the marine dominion also other environments add data to the time-species model. One of these situation is the continental slope between 500 and 2000 m depth. Some pioneer data of benthonologists have astonished the scientific community showing the diversification of such an environment. Here not only species are numerous (862 species on a total sampled area of only 21 m²), but they sometimes reach maxima of possible abundance, with no species more abundant than another (Grassle, 1991). Also here the reason was searched among

ecological cues and the intermediate disturbance of Connel (1978) was considered as the only possible cause. Nobody has never found what is the intermediate disturbance which determines such a situation, but the continental slope has considered as inevitably interested by turbid falls of the just strength, extension, ad frequency, to authorize such a species diversification.

Continental slopes are, however, the most ancient marine habitats of the planet, and depths below 1000 m are those where temperature is invariably fixed around 3 °C, where the light is completely absent, differences of pressures are relatively minimum, and probably also turbulence is weak. Due to the continental drift which is opening the North Atlantic Ocean, the slope studied by Grassle is opening from about 190 million years. While, however, surface coastal areas suffer the variability of seasons and climates, the cited slopes (1000 – 2000 m depth) represent the zones of maximum age where present conditions has been realized first (and they are possibly remained constant).

The time seems the most responsible of species richness according the Rosenzweig's hypothesis of spontaneous formation of species from a large initial population, and the strongest alliance for this results comes from the stability of conditions which should stay there. This is completely opposite to the ecological monopoly of reasons to explain species richness (space or time variability, intermediate disturbance, fractioning of habitats, and so on) (Fig. 2). Unfortunately, the short time scale (1-50 years) which our studies can use to establish a rule, has not efficacy from the evolutionary point of view.

The area of an environment, or its variability, can sure be the cause for a temporary enrichment of species, coming from elsewhere. But all the biogeography can be better understood if interpreted in terms of environment ages. Latitudinal and altitudinal gradients are strictly correlated with the age of environments, due to the fact that cold environments (at high latitudes and/or high altitudes) have obligatorily less years than the warm ones, due to the last ice expansion during the last glacial era.

The polar caps retraction on high latitudes, and the rising on high altitudes of the mountain glaciers, are the certification of the young age of nowadays periglacial isolated environments. On a short time scale, the effects of climate variations, of the human activities, and of ecological successions, are all mo-

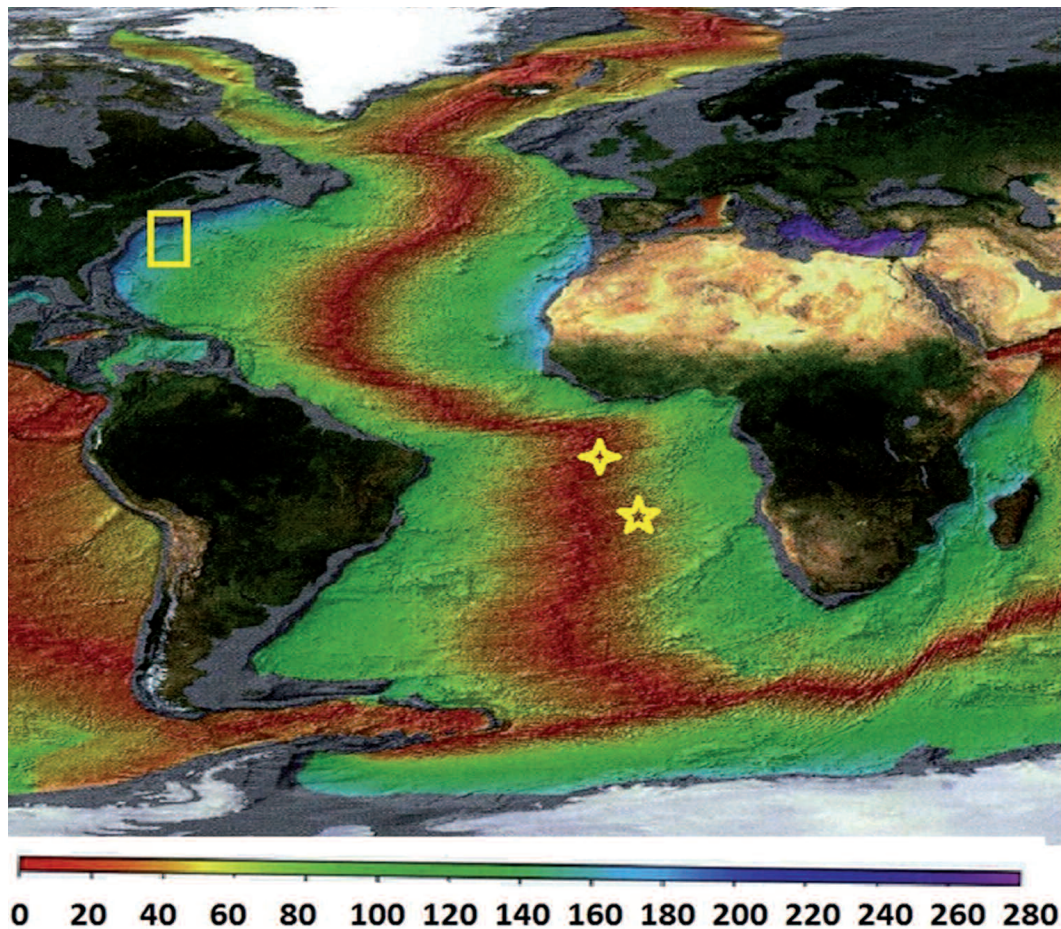


Figure 2. A map of Atlantic Ocean with colours indicating the different ages of its bottoms (see the reported colour scale from 0 to 280 million years). The yellow square indicates the area from where Grassle (1991) described astonishing high species richness. Four arms star indicates the position of Ascension island. Five arms star indicates the position of St.Helena island.

dern effects, and field of Ecology, which subtract attention to the evolutionary (long time scale) field.

Islands (isolated environments) of millions years of age can offer the possibility to easily evaluate the correlation of species number with the system age. Such a challenge has been accepted by Limnologist more than land Island Biogeographers. The ancient lakes allow us to explain the species richness avoiding to search a solution into the dispersal/immigration and to point on the in situ speciation.

The case of lake Aral

The Aral Sea (today reduced at 14% of its past extension) had a surface about 20 times that of lake Ohrid, in the Balkans. This notwithstanding, and contrarily to the rule which wants the area correla-

ted with the species number, Aral has an evident low species richness (maximum 310 species according to Aladin, 1995) if compared with the "small" Ohrid (about 1200 according to Albrecht & Wilke, 2008). Reading from more sources it is possible to advance the hypothesis that the Aral did not existed in ancient historical times, and its story has only some centuries.

The expert Arab geographers of the middle age did not indicated a great lake in the position of the present Aral, and the lake has been reported on maps only from Russians after the conquer of those steppe lands after 1620. The history tells about the Sultan of Khiwa who turned the Oxus river into the desert to avoid it could be used by the Czar's soldiers to individuate the city and invade it. Oxus is very possibly what now is called Amu Daria, the river southern tributary of the Aral; and it possibly

arrived into the Caspian Sea, from where the Czar soldiers easily could reach Khiwa. This is probably only an hypothesis to be confirmed, but the present retraction of the Aral leaved dried lake bottoms where in 2004 an ancient city with architectural remnants of the XIII-XIV century has been recognized. Hence it is now evident that the Aral Sea, as we remember it, was a young environment and, although exaggeratedly large, the species it hosted were only those which arrived from elsewhere, according the process described by MacArthur & Wilson, and no one of them had the time to undergo the genetic process of the multiple speciation.

Dodson (1991; 1992) confirmed the ecological rule area/species number on the crustacean species abundance in lakes of the northern hemisphere. But this Author considered mostly postglacial lakes, hence those (as the majority of boreal lakes) formed in the post-glacial era, hence with a comparable age (20,000 - 10,000 years).

In the study of 32 European lakes (Dodson, 1991) the regression line on the area/species log plot, shows an evident scattering distribution of points around the x value (area) of about 1×10^5 km² where it is easy to recognize the Finstertaler (a dam), the Port Bielh (at 2700 above the sea level), and the Latnjajaure (near the Arctic polar circle), as the youngest lakes and at the lowest y (log species) values; a different hypothesis could be at-

tempted with lakes arranged according an age/species plot (Fig. 3).

The growth of species number with time is obvious at the start of the story of each island (and lake). The Krakatau "son" (an island remnant from the explosion of 1883) has been considered as replenished of species after not more than 35 years. Simberloff & Wilson, 1970) demonstrated the restoration of the insect number in experimentally defauned islets after only 2 years. Also a study on dams (lakes of a young, known, age) in southern Italy (Alfonso et al., 2010) confirmed that the species number in the plankton grows until 50 years from the lake birth, but not more. The time necessary to the biological replenishment of newly birth islands is relatively short but, however, it is only the first part of the story. Successively to the reaching of the equilibrium, the number of species stop to grow only apparently. This number grows with a slower rhythm, over a longer time, and only great age differences among islands can unveil this time effect. Aral, in Kirghiz language, means Island. The species richness of this large island of water was just that which has been possible to recruit from water environments geographically around.

According MacArthur & Wilson they reached the maximum number possible at an equilibrium point between new immigrants and local extincts; the large area allowed the presence of demographi-

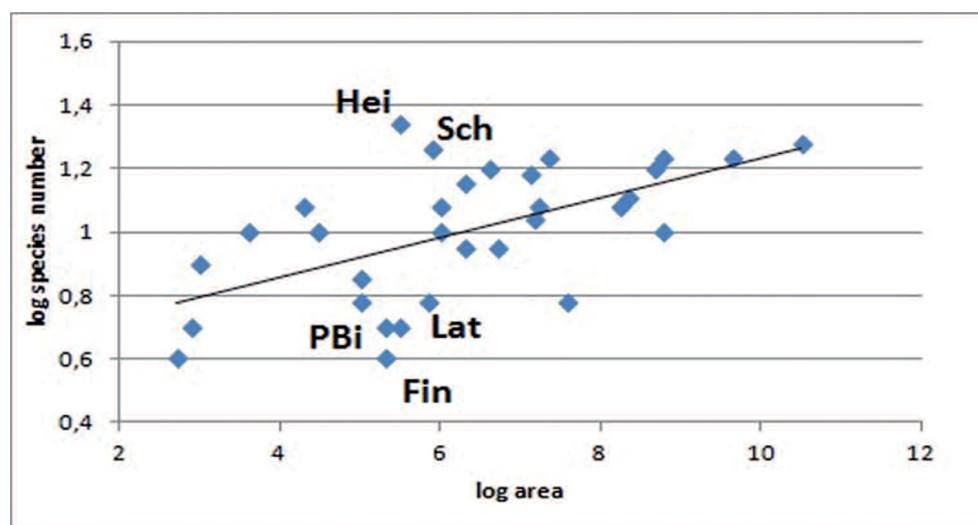


Figure 3. The Dodson's correlation Area/Species as reported from 32 European lakes. Lakes of about 1×10^5 km² are visibly scattered around the regression line. Fin is the Finstertaler dam (less than 100 years old), PBi is Port Bielh, an alpine lake at 2700 m above the sea level (less than 6000 years old), Lat is the Latnjajaure (near the Arctic polar circle, less than 6000 years old)

cally enormous populations, but the lake age (400-500 years) was too short to allow the system to enter the phase of the speciation even for single groups (the species flock) as Rosenzweig suggested as possible. The case of the Island=Aral also suggests that, differently from what proposed by Hutchinson (1959) at least for long time intervals (million years) the species richness is probably directly correlated with the stability of the system (in the case of Aral its existence). The speciation according the model of Rosenzweig, in addition, needs not variability of conditions. The Age/Species curve, hence, has to be corrected into a sum of species curves acting each for a different time duration, and nothing can be said on the existence of a limit to such a number (Fig. 4).

According to the recent model of Hubbel (2001) on a neutral theory of species geographic distribution, it exists a species number, typical for each environment, which depends not simply upon the MacArthur & Wilson model, but also on speciation and evolution. This number, however, obeys to a sort of zero-sum game where the number of species cannot exceed the carrying capacity of the system. If the carrying capacity is a biomass value, the number of species can grow in combination with a decrease of the number of individuals per population, and/or a decrease of the size for each species.

But this model deserves an appropriate set of data to be completely accepted.

CONCLUSIONS

The time has undoubtedly an effect on the species number which stay in an environment. This effect, however, is not simply that indicated by MacArthur & Wilson on oceanic islands, due to the immigration/extinction rate of species. The role of the time on the species richness starts to be recognizable only on isolated environments where contaminations from neighbors are limited or null, and after many years to allow the evolution to do its job.

This action is so slow that it cannot be recognized in terms of ecological times, and even a limit (a maximum number of species) is probably difficult to be found. Time, however, elegantly explains the disobeying faunal situation of St. Helens and Ascension in the middle of the Atlantic, the species richness of ancient lakes (or the species poorness of Aral), the latitudinal gradient of the species number, the species diminution with the altitude, the astonishing species richness of benthic fauna on the continental slope of the north Atlantic Ocean.

The temptation to re-describe each pattern and geographic situation is great. In Italy, for example,

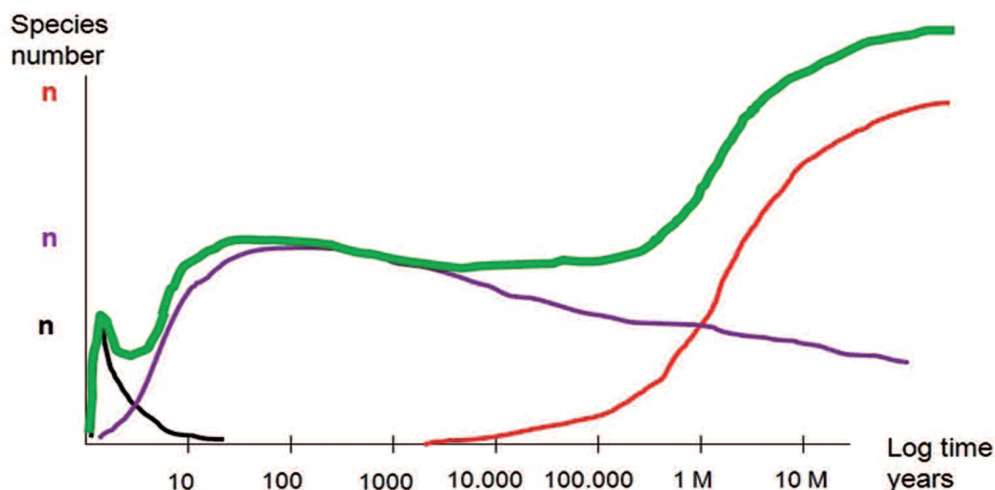


Figure 4. The species number in each island grows according different phases. 1 early colonization, arrival of pioneer species (r-strategists) which sustain the successive immigration (Ecological Succession). 2 immigration from neighbors (MacArthur and Wilson model) up to a constant number (the equilibrium point) of species (k strategists) where new arrivals equal extinctions. 3 speciation and species flock appearances. The species number grows for intrinsic, evolutionary reasons and independently from the ecological ones.

a series of faunal geographic provinces have been recognized on the ecological basis of the climate.

If we look at the lakes, however, we can note as the Padano-veneta province has large lakes at low altitudes, formed at the beginning of the ice retraction (about 40,000 years ago), whereas the Alpine province host small lakes over the tree altitudinal line, hence ice free from only 5,000-7,000 years.

Along the Italian peninsula (Apennine province) are concentrated the several Volcanic water basins which have ages of hundred thousand years, and at the extreme south, and on islands (insular provinces), the most of the lakes have been realized only recently with dam buildings (ages lower than 100 years). In this brief case the biogeographic subdivision of a territory could be based not on ecology, but on environment age, and it proposes the age of environments as an alternative key in the understanding species distribution, other than the species richness.

In any case is probably time to start with a deeper consideration of the age effect in the biogeographic framework.

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