

The equilibrium theory of island biogeography: paradigm shift over 50 years

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Abstract

The equilibrium theory was created over 50 years ago and it is considered the first paradigm of ecology. But how does this theory apply to the knowledge of today? Studies done to test the equilibrium theory showed that for undisturbed situations a dynamic equilibrium was attained but not for islands with occasional disturbances (be that anthropogenic or natural).

Furthermore, over time flaws have been discovered in the equilibrium theory, like other variables besides size and isolation affecting immigration and extinction, different effects of size and isolation, no differentiation between species and a lack of speciation as a mode of species enrichment. Newer models that try to incorporate some of these basic elements are mentioned in this paper, e.g. the General Dynamic Model and finally, based on all the arguments presented, it is concluded that the equilibrium theory is a perfect null theory because through the reasons we find why an equilibrium is not obtained, we expand our knowledge of what factors play a role in shaping insular species compositions.

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Introduction

Islands are very important to ecological research worldwide. They are a naturally isolated area separated from the mainland. If we assume that an island was newly formed unconnected to the mainland there should be no living animals or plants on it yet. Thus, how do species come to this place of wonder? Animal immigration is the solution. As insects, birds, mammals, plants and reptiles swim, fly (uncontrolled or controlled) or are brought there by drifting upon wreckage, they have a chance of establishing themselves on this newly-formed island. But species that colonize an island also have a chance of not being able to keep their population at a sustainable level. What follows then, is extinction. Based upon this constant interplay of immigration and extinction the equilibrium theory was conceived by MacArthur and Wilson (1963).

MacArthur and Wilson assumed that at a certain point immigration and extinction would equal each other. At that point there would be a species richness balance where as many new species would immigrate to our island as many as there would go extinct. MacArthur and Wilson furthermore suggested that the species composition in such an equilibrium would be constantly changing as some species become extinct while new species immigrate. Before MacArthur and Wilson came up with this theory it was widely accepted that islands were in an archaic, static state (Dexter, 1978). Thus, a state in which species composition barely changed.

Fig. 1 shows the model MacArthur and Wilson designed to explain their theory. The descending curve is the immigration rate of **new** species (species that immigrate to our island might already be present, so it is important to note only new species are considered) to our island. This rate declines because the more species there are, the less likely the chance for a migrant to be a **new** species. Also, the curve declines more steeply at first; a result of dispersal capability differences between species. Some species migrate relatively easily and those are usually the species that are first present on an island. The curve falls to a rate of 0 when all species of the mainland's species pool have migrated to the island. The ascending curve is the extinction rate of species on our island. As there are more species the curve goes up, because there are more species available to go extinct, while there is also an increased competition for space and resources. Furthermore, the curve starts at a rate of 0 extinction because there are no species present at our newly-formed island at the start of its

life. The reason why there is an equilibrium that is being maintained can be explained with the following: imagine species richness exceeding the equilibrium value. In that case, extinction will be higher than immigration and the equilibrium will be re-attained. When species richness is lower than the equilibrium value immigration will be higher than extinction and again the species richness equilibrium will be re-attained.

It is important to note that immigration in the meaning of MacArthur and Wilson is considered to be immigration followed by establishment. It has been found that propagule sizes of three pairs of a certain species have an almost 100% colonization chance if only genetic variation is considered as a limit for their settlement (Schilthuizen, 2008) .

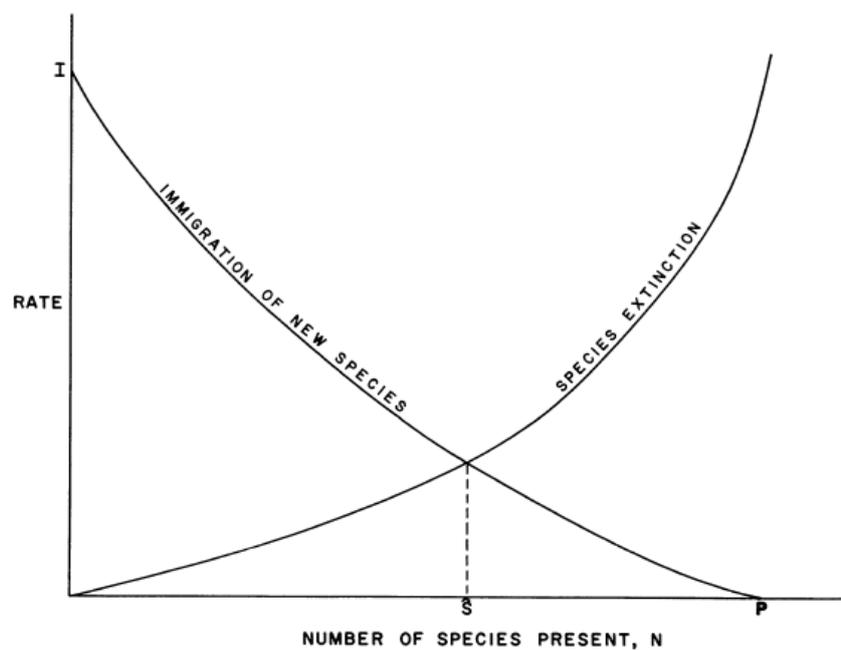


Fig. 1: The equilibrium theory model of MacArthur and Wilson

MacArthur and Wilson then added 2 variables that could change the number of species at which an equilibrium value would be reached, namely, distance from the mainland and island size. Mayr (1940) showed that there was a decline in species richness as distance from the mainland progressed, while Preston (1962) and Wilson (1961) found that species richness increased almost logarithmically with island size. MacArthur and Wilson thought these 2 variables would be the most important deciding factors of where an equilibrium between immigration and extinction would be found.

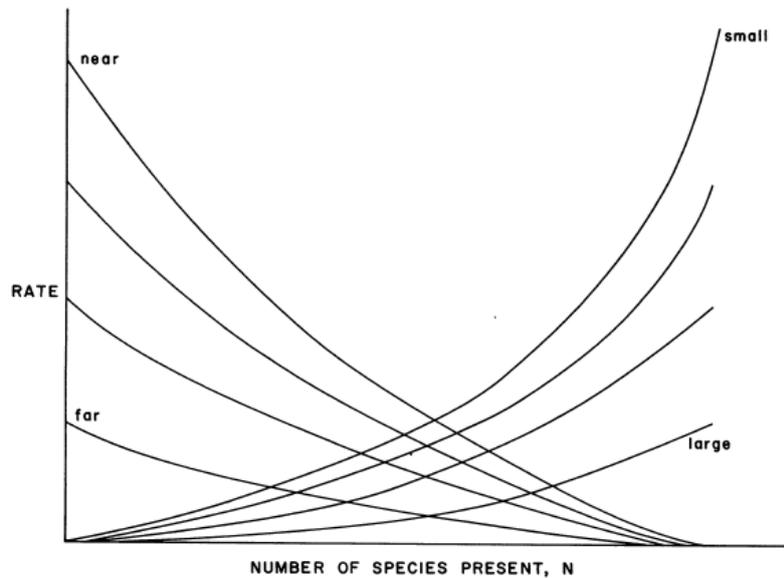


Fig. 2: The equilibrium theory model with the 2 variables of island size and isolation.

MacArthur and Wilson suggested that differences in isolation of islands changes the immigration rate. A higher rate of immigration with a smaller distance from the mainland, as the distance is within reach of the dispersal capabilities of more species. The island size on the other hand, affects the extinction rate with smaller islands having higher extinction rates due to less space, leading to smaller population sizes; smaller population sizes being more prone to extinction. Considering this, species richness should be highest in large, nearby islands while the lowest species richness should be observed in small, distant islands. Fig. 2 shows the representation of these ideas.

Mathematically the change species richness is calculated as:

$$\Delta s = M + G - D$$

Where Δs is the change in species richness in a certain time interval, M is the number of new species being added through immigration in that time interval, G the number of species added through speciation and D is the number of species being removed by extinction.

In equilibrium we have:

$$M + G = D$$

The question to be answered in this paper is whether the theory of MacArthur and Wilson is applicable to natural systems. And if so, how does it apply to natural systems in the present where an increase of our knowledge surely must have sparked some new theories and ideas.

Studies: Then and now

The first study that was done to test the theory that MacArthur and Wilson had published was done by Wilson himself and Simberloff (1970). They wanted to see the process of colonization from scratch and they did so with an experimental setup. For this they chose 6 islands of the same size but at different distances from a very large island as their experimental areas (2 of them as controls). First, they measured the species richness currently living on the island after which they fumigated the 4 islands with methyl bromide which in the process killed all arthropoda upon those islands. It was expected that colonization of the 4 islands would start shortly after and so it did. Taking the species richness measurement they did before the experiment as the island's equilibrium they took frequent censuses to see if and when this equilibrium would be reached. The species richness prior to defaunation (the equilibrium) was re-attained within a year on the 3 most nearby islands, while the 4th one was still in the process of reaching it. And so it was proven for the first time that a balance between immigration and extinction was indeed observed on islands. Important to mention as well is that the species composition differed enormously from the pre-defaunation composition.

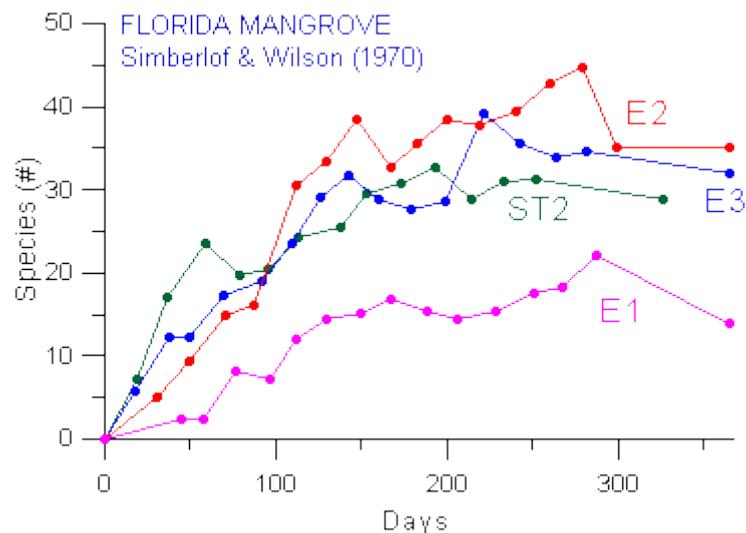


Fig. 3: The results of temporal species richness changes observed by Simberloff & Wilson in which E2, E3 and ST2 are the islands which reach equilibrium within a year, while E1, being the most distant island, took longer.

Does the equilibrium theory work when disturbance events are taking place? This was one of the arguments against the equilibrium theory that had to be tested in the field (Whittaker, 2000). It was believed that an equilibrium would not be able to persist if dynamic events would affect the extinction and immigration of species on an island.

Morrison (2010; 2010) studied plants and ants at islands that were prone to hurricanes to examine whether there would exist an equilibrium. He found that there was a continuous non-equilibrium state over a course of 17 years. Extinction rates during periods of hurricane activity were found to be much higher than immigration rates and caused by indirect effects of the hurricanes, such as increased herbivory, decreased nutrient availability, an increase in

temperature and a decline in rainfall. Morrison pleaded that when hurricane activity was low, the system was moving towards a long-term equilibrium as can be seen from fig. 4 where immigration is higher than extinction during the first “decade”. But disturbances from hurricanes interrupted this process and thus species richness never balanced out. Furthermore, Morrison found that the state of an island’s bio-geological features plays an important role in whether species can be present. In this case, ants were shown to require terrestrial vegetation, something that is not mentioned in MacArthur and Wilson’s theory.

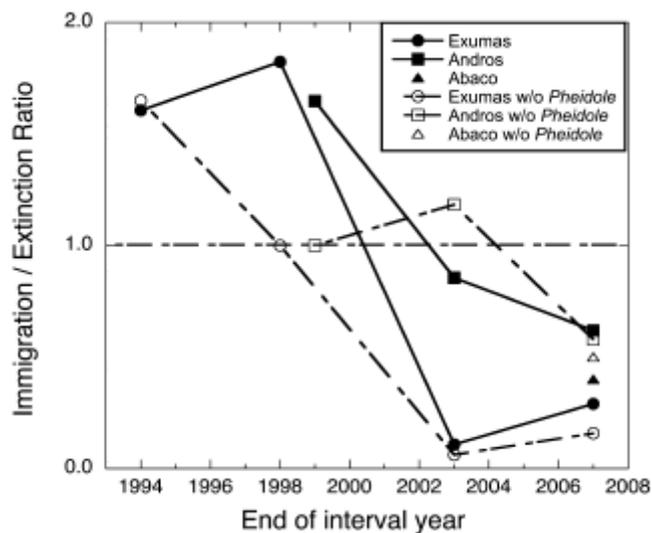


Fig. 4: Morrison’s immigration/extinction ratio of ants at the Bahamas. As can be seen the ratio did not balance out as predicted by the equilibrium theory.

Many other authors found that when disturbances are taking place an equilibrium is not attained. Panitsa (2008) and Burns & Neufeld (2009) also found this non-equilibrium. In the article by Panitsa grazing disturbances by sheep (placed there by humans) were the reason for plants not being able to reach an equilibrium. For Burns & Neufeld it was ocean-born disturbances that did not allow for an equilibrium to be reached by plants.

In all these cases extinction was found to be higher than immigration. This shows that when there are disturbances, be that natural or anthropogenic, an equilibrium is not reached.

New insights/theories

Non-equilibrium state

Based on the findings of an equilibrium not being attained as shown in the previous chapter and other states of equilibria, Whittaker (2000) coined three hypotheses, namely the dynamic equilibrium hypothesis, the dynamic non-equilibrium hypothesis and the static equilibrium hypothesis.

The dynamic equilibrium hypothesis is actually the equilibrium theory of MacArthur and Wilson in which there is a state of equilibrium but with constant turnover of species composition.

The dynamic non-equilibrium hypothesis is exemplified by the studies of Morrison, Panitsa and Burns & Neufeld where a non-equilibrium state was found with turnover. This has always been found as the result of a disturbance.

And last, the static equilibrium hypothesis in which turnover is completely lacking or so minimal as to make the species composition appear static over time. This is often found in birds. This is probably because they have a high dispersal capability and populations of a certain species on an island are unlikely to become extinct, because they are rescued by immigration, unless the bird species is in general threatened with extinction (Lack, 1976). Thus turnover is not easily observed and thus a good example of a static equilibrium state. Abott (1983) observed the same pattern in mammals but this is due to a very low dispersal capability.

Based on these different states that can occur on an island, island biogeography is made more complex than just the equilibrium state. A dynamic non-equilibrium state is the one that is most often observed under natural circumstances, as disturbances run rampant across the globe at rates that affect extinction and immigration rates. But the equilibrium theory is a perfect null theory as it describes an “optimal” state. As divergence from its equilibrium on an island is noted, analyzing the causes for this divergence can provide us with more knowledge of the biogeography of islands. Whittaker pleads to advance non-equilibrium models however, which is perfectly sound as they are the most occurring, but there are also many processes that can be the cause of a non-equilibrium state making it an arduous task.

Other variables

In addition to island size and isolation there are many variables that affect immigration and extinction patterns. Size and isolation are singled out, however, because they always play an important role. But as many authors claim; so do time and elevation. Other than those, as also mentioned in the previous chapter, Panitsa found that grazing affected species richness significantly and Burns & Neufeld the same, but with ocean-born disturbances. While Morrison saw that ants needed terrestrial vegetation to even be present on an island. MacArthur and Wilson themselves also mentioned these other variables in their 1963 paper, as they gave an example where severe climate affected the extinction rate instead of island size.

So why are elevation and time such important variables? Just like size and isolation these two variables are more static in time and play a key role on every island. Minor variables like grazing are situational. Elevation has many times been found to be positively correlated to species richness (Foufopoulos & Mayer, 2007) and is assumed to, just like island size, be a good predictor of niche diversity. Furthermore, a higher elevation may enhance the target effect (which will be explained in the next paragraph), as higher islands are easier visible (Brown & Kodric-Brown, 1977)

About time, MacArthur and Wilson wrote “The impoverishment of the species on remote islands is usually explained, if at all, in terms of the length of time species have been able to

colonize, and their chances of reaching the remote island in that time.” This is an idea that would make island size the only real deciding factor of species richness because if given enough time even distant islands will reach the same species richness as nearby ones, if they are of the same size. A study by Badano *et al.* (2005) with ants found that age plays a significant part in species richness. The older an island, the higher the species richness. They assessed that area plays the most important role in determining species richness, but isolation and age contribute to it. This strengthens the concept that if given enough time even very isolated islands of the same size as less isolated ones, will reach the same species richness. Due to this, I would personally argue that distant islands are not in equilibrium if they have fewer species than a similarly sized, less distant island, as they are still in the process of attaining it. But it is required to remain realistic with our thoughts, as mammals which overall have low dispersal capabilities, have a very slim chance of ever reaching a distant island and this might be the taxon that will be the difference in the species richness reached between a distant and a nearby island.

Furthermore Whittaker (2000) provided evidence that sometimes, given enough time, older but smaller islands might have more species than younger and larger islands. An example of this are the Hawaiian *Rhyncogognus* Weevils (Paulay, 1994).

And last but not least, time might add niches as was observed by Friðriksson (1987) and when those are added the equilibrium value might shift. Friðriksson saw that when high nutrient areas were formed due to gull guano on Surtsey (a volcanic island that had risen in 1963) the equilibrium shifted from 12 to 50 plant species within several years. This, however, might also be a pattern of succession as an island gets all the more habitable over time. But even succession measures itself in time and shows us the importance of this variable. Heaney (2000) argues that due to the amount of niches changing over time an island is always in a state of disequilibrium due to these constant changes and species richness is always a step or two behind in reaching its equilibrium. In conclusion, all conditions on an island decide how species richness, extinction and immigration will be shaped and not just size and isolation.

Other effects of size and isolation

MacArthur and Wilson had strictly theorized that island isolation is the deciding variable for immigration and island size for extinction. Wright (1980) and Buckley & Knedlhans (1986) respectively found that isolation also influences extinction rates through a phenomenon known as the **rescue effect** and that size plays a key role in the extinction of species with the **target effect**. The rescue effect is described as a supplementary immigration of species present on the island which were on the brink of extinction. While the target effect is described as the size influencing the immigration of randomly dispersing individuals as it is an easier target while also affecting non-random immigration through being easier visible compared to smaller islands.

And last, there is the **small island effect** which was mentioned by MacArthur and Wilson themselves, in their 1967 book. When islands become relatively small, species richness no

longer has a relationship with island size (MacArthur & Wilson, 1967). A pattern that was also observed in nature (Burns & Neufeld, 2009).

Difference between species

In the equilibrium theory of MacArthur and Wilson all species are considered equal in their possibilities for colonizing an island and becoming extinct on it. Nature shows this is far from the truth though. Species differ enormously in their dispersal capabilities, their strength in maintaining a population and their speciation rate. For this reason Lomolino (2000) pleaded for species specific theories as to remove this issue. In my opinion this sounds like a tremendously arduous task as there are so many species to model. But I would argue that it is an important task as more knowledge about every species provides us with a better chance of conserving every single species.

Interaction between species is neglected by Lomolino but internal dynamics of assembly rules (Belyea & Lancaster, 1999) show species being very reliant on other species already present in their ability to colonize an island. Some species are just not able to coexist with each other due to competition over e.g. resources and/or space or cannot survive on an island because the basic prey item of a certain species is missing. Thus, in the creation of species specific models I would plead for interspecific interactions to be incorporated as well.

Speciation

Speciation or phylogenesis is the divergence of two or more species from one through a process of genetic changes. The importance of speciation upon islands can be seen from the amount of endemism that is present on them (e.g. 50-85% endemism on islands that were present during the pleistocene) (Heaney, 1986). The most drastic form of speciation on islands being adaptive radiation. A famous example of this are of course Darwin's finches where a single species colonized an island and from there on covered all niches within its reach and in that process many new species of finches were formed.

But, when looking at the equilibrium theory models, speciation is not mentioned in it. Many authors have therefore criticized the equilibrium theory as it lacks this basic mode of new species becoming present on an island (Heaney, 2000; Lomolino, 2000). These same authors consider that speciation is most powerful on distant islands where immigration and extinction are low. When immigration is not the process through which the niches are filled, speciation can act to fill those gaps. Before explaining speciation further though, it must be noted, in MacArthur and Wilson's defense, that as can be seen in the mathematical models described earlier ($\Delta s = M + G - E$) speciation was an alternative to immigration in their thoughts, but it was just never fitted into the famous equilibrium theory model (Whittaker, 2000).

For a speciation event to occur there must first be, at least, one occurrence of successful colonization of a species. And with time, this one species may diverge into more. On very isolated islands Heaney (2000) observed that speciation was the process by which addition of species was 14 times more on average compared to immigration. Another example by Heaney was his research on murid rodents in which an estimated 4-8 colonization events

resulted in an average of 7-14 species produced through speciation per colonization event on a timescale of about 5 million years.

Time is a very important variable when talking about speciation. Heaney (1986) found that for a completely isolated island the rate of speciation was 3% new species per 100.000 years. A timescale that is by far not covered by MacArthur and Wilson and thus decreases the importance of speciation in their model. This, however, does not discard the importance of speciation in the overall process of species composition on islands.

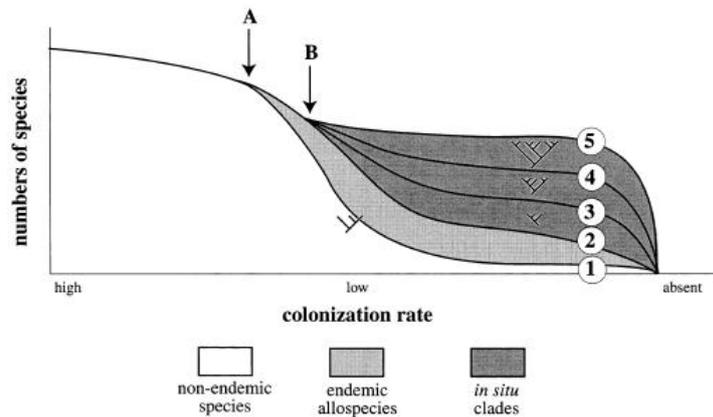


Fig. 5: A model by Heaney that depicts the influence of speciation for varying degrees of immigration rates and based on the total species richness of an island.

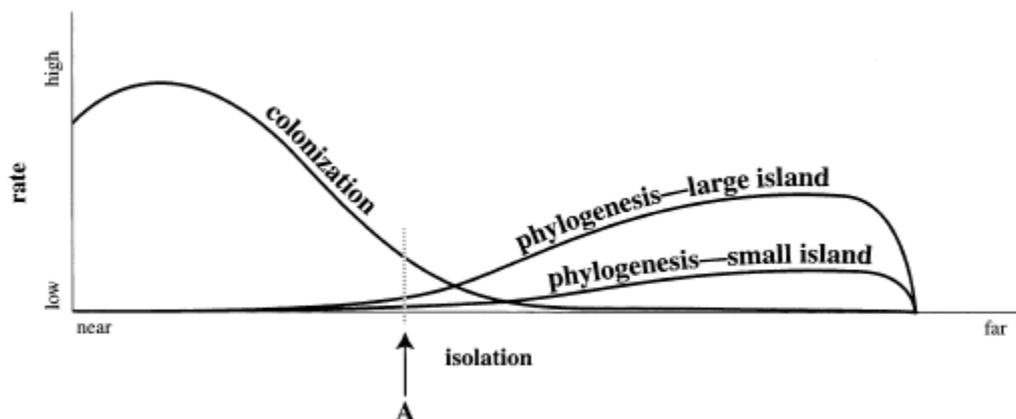


Fig. 6: A conceptual model by Heaney that visualizes the influence of colonization and speciation on different scales of island isolation and size for speciation.

As mentioned before, speciation is of a higher rate when the isolation of an island is higher, resulting in a lower amount of immigration as seen in fig. 5. This can be explained by the fact that if colonization is very high, any genetic change will vanish due to gene flow. And thus, if isolation increases and colonization declines, genetic change persists more until irreversible speciation occurs. It is described by Peterson & Heaney (1993) that less than one individual from the mainland per generation will cause genetic change to persist to a point where phylogenesis is more important than colonization in shaping the species richness of an island. Fig. 6 depicts that phylogenesis is higher on larger islands as it is assumed there are

more niches with a larger area. Small islands thus have a faster saturation from immigration, leaving little “space” for speciation to play its part. So, as islands become larger niche occupation can be influenced more by speciation events. But let us not forget, as Heaney forgot to mention, the target effect which increases the immigration rate to larger islands (and thus decreasing the role of speciation).

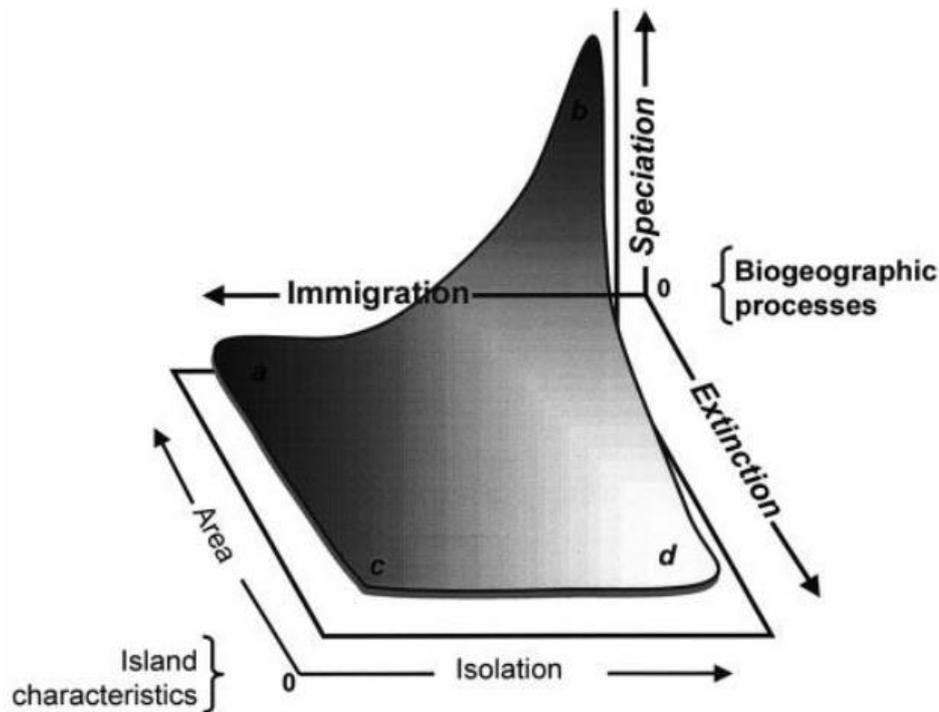


Fig. 7: A model by Lomolino that is based on the equilibrium theory of MacArthur and Wilson but incorporates speciation.

Based on the arguments made by Heaney (2000) and Lomolino (2000) the model shown in fig. 7 was designed which includes speciation, next to immigration and extinction. Immigration and extinction rates are determined in the same way by the factors size and distance from the mainland as in MacArthur and Wilson’s model. It also depicts the earlier mentioned speciation theories in which speciation is higher when immigration and extinction are low. Furthermore shading indicates the height of the species richness (the darker, the higher the richness).

General Dynamic Model

Advances in the modelling of island biogeography are taking place and the General Dynamic Model (GDM) is an example of this in which speciation and time are incorporated for oceanic islands. Oceanic islands have a limited existence as they rise with volcanoes and eventually submerge. Whittaker (2007) noted that oceanic islands undergo a natural succession over time with the island’s rise, its maturation, old age and the eventual loss of it. During this succession the equilibrium value is constantly changing as when an island is formed it provides only a couple of niches and in due time the amount of niches start to accumulate until an island reaches its maximum area and elevation. After this maximum, an

oceanic island will slowly erode and thus, niche amount will decline and finally, the island will submerge.

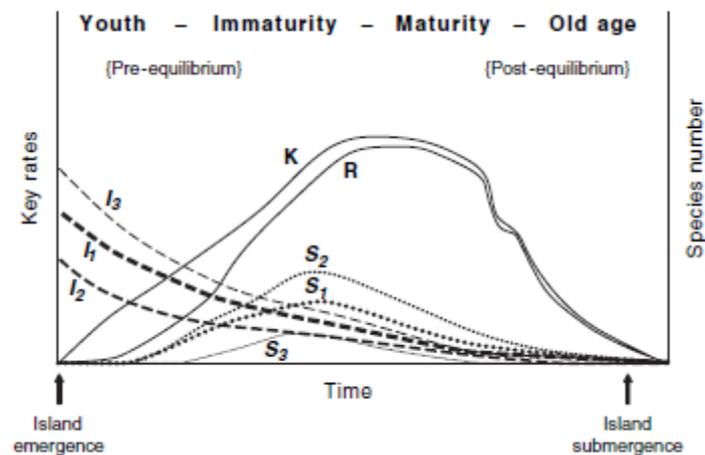


Fig. 8: The General Dynamic Model created by Whittaker (2007) which depicts the rise and fall of an oceanic island and how immigration (I), speciation (S), realised species richness (R) and carrying capacity (K) change over time inbetween the rise and the submerging of an island.

The General Dynamic Model shown in fig. 8 follows the basic principles of the equilibrium theory. Immigration rate is highest when an oceanic island is in its **youth**. I_1 , I_2 and I_3 representing different rates of immigration. At **immaturity** speciation starts to play its part as soon as at least one colonization event has occurred. And depending on the strength of immigration filling up the empty niches, speciation strength will vary represented by S_1 , S_2 and S_3 . At **maturity** species richness peaks represented by R which is the realised species richness but always below the actual carrying capacity K , since as mentioned before, in time, species richness always lags behind its actual equilibrium (also evidenced by Valente *et al.*, 2014). As an island starts to lose its heterogeneity at **old age**, species richness starts to decline as extinction increases (not shown in this particular model but it is described explicitly by Whittaker) and finally an island submerges.

Furthermore this humped shape found in the species richness, depicted in the general dynamic model, was also found in analyses of real islands in most cases (Azores, Hawaii, Galapagos and Canary) by Whittaker (2007) as well as in analyses done by Valente *et al.* (2014) although the hump in their case was found to be of a smoother nature.

Application in other fields

The theory of island biogeography is supposedly possible to be applied to other insular areas besides islands. Fragmented areas are an example of such insular areas, like forests, where different patches become separated from others. With the equilibrium theory, attempts are made at predicting the amount of species richness loss due to an increase in extinction and a decline in immigration. Due to this application of the equilibrium theory it was made clear that one large area, of for example, a forest, should provide a home for more species than several fragmented pieces of forest. Besides size, an increased connectivity between the

different patches should also increase species richness as that results in a decline in distance (Gillespie & Clague, 2009).

Conclusion

To conclude, I would say that the equilibrium theory is a brilliant model. It provides the background for an optimal state in which species richness remains constant. Although most of the times this equilibrium is not observed, it provides the will to pursue the reasons for why this equilibrium is not obtained. This resulted in the arguments that for example time and elevation also play a significant role in determining species richness. Some newer models were showcased earlier in this article and they are the start of a revolution in a paradigm that has been around for so many years. Agreeing with many authors I would also argue that for future research the model should focus on single species, its interactions with other species, be island specific, incorporate speciation and time as in the GDM and keep in mind the rescue, target and small island effect.

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