



Sources of diversity

- Speciation areas
- Refuges (as proposed by the Brazilian zoologist)
- Refuges (as proposed by the German geologist)

A theory endures

A lizard from the Amazon region studied by Vanzolini reinforces a German geologist's position on forest refuges

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Developed more than 40 years ago by the German geologist Jürgen Haffer and, indirectly, by Brazilian zoologist and *samba* musician Paulo Vanzolini, the Refuge Theory, associating the Amazon region's biodiversity with periods of arid climate and geographic isolation, was declared obsolete on numerous occasions over the years by various other researchers. In the words of one of Vanzolini's own songs, however, the theory "got over" this setback and, after being brought somewhat up to date, is now seen as valid within various research circles – valid not only in the sense of explaining the emergence of species in the Amazon region, but also the emergence of those in the Atlantic Forest, where the theory's principles have also been applied.

Settled snugly into his favorite armchair in one of the upper rooms of his home in Aclimação, an old neighborhood on the south side of the city of São Paulo, Vanzolini, now 88, claims not to have come up with any theory at all: "It was just some work I did with an animal species. What I did ended up being

a concrete example of what Haffer had proposed from a theoretical viewpoint. It's nothing more than a model – a conceptual one – that can be replicated, even in other regions.” In 1970, one year after Haffer presented his theory in an article published in the journal *Science*, Vanzolini and the American researcher Ernest Williams published a study of nearly 300 pages about the emergence of a species of lizard of the genus *Anolis* without making a single reference to the Refuge Theory.

Haffer, a geologist who had studied the geographic distribution of bird species in the Amazon region, advanced the theory that changes to the region's vegetation accompanied naturally-occurring climatic shifts during a given period in geologic history. This process dispersed the species' various points of origin, isolating some of them in ecological refuges where they lived separated from the others. These relentless climatic changes effectively pulverized the forests of the Amazon region. The resulting patches of forest, separated by barren areas, set the stage for the development of new species and sub-species. Three developments likely occurred in these areas: the defining or evolution of new species, the extinction of certain other species, and the adaptation of others that managed to survive the changes to their ecosystems without undergoing significant genetic mutation.

LESS-DEFINED PATCHES OF FOREST

In an 2005 interview with the newspaper *Folha de São Paulo*, Haffer stood by his Refuge Theory, but not without suggesting some corrections to how his work should be approached: “It's likely that these patches of rainforest during the dry periods were larger and far less-defined than those on many of the maps that illustrate the location of the refuges in the pluvial tropical forest.” Haffer died in 2010 at the age of 77.

One of the criticisms of Haffer's theory that has been presented over the years has come from Vanzolini, whose objection relates precisely to where Haffer claims the Amazon region's barren areas were situated, as well as to the fact that evidence of these areas has never been firmly established. According to Haffer, however, many erroneous interpretations to his refuges idea have been presented over the years: “Our data show climatic shifts occurring at least on a

A theory that explains how the Amazon rainforest's tremendous biodiversity emerged from instabilities in the earth's climate millions of years ago



Anolis chrysolepis, the species that served as a basis for Vanzolini's general understanding of the process of speciation in the Amazon

localized and roughly regional basis. Of course, extensive expanses of pluvial forest, all very ancient, have always existed in the Amazon.”

Research groups from São Paulo have conducted studies over the past few years on the emergence of new species in the Atlantic Forest that have buttressed the theory that was proposed towards the end of the 1960s. At least Vanzolini's idea and that of his German colleague can still be considered valid or at least of sufficient interest to reanimate the controversy that surrounds it.

The two men became friends around 1970 after exchanging correspondence about their respective studies. Vanzolini likes to say that Haffer, besides being a first-rate scientist, showed generosity. “And, like every good German,” adds Vanzolini, “he couldn't pass up a beer.” Vanzolini recalls that he received the article from the German scientist by mail after finishing his article with Williams. “Ernest thought they had pulled a fast one on us,” says Vanzolini about their reaction to the publication. Vanzolini was soon in touch with Haffer, who immediately put aside a research project in South Africa to go to Brazil for an in-depth look at Vanzolini's lizard refuges.

Different times and new research follow more or less the same course. In a 2008 article about the sauba ants of the Amazon published in the journal *PLoS One*, Brazilian and American scientists proposed a kind of re-examination of the Refuge Theory. According to Maurício Bacci Jr., a biochemist at São Paulo State University in Rio Claro, the huge explosion in the diversity of ants in the Amazon region occurred despite the geographic barrier created when the region's rivers were being formed. Bacci explains that this extraordinary diversity in sauba ant species is a recent phenomenon that occurred approximately two million years ago. Ant nests may have migrated throughout the region through the river system by floating atop plants.

Genetic research points to another important process besides the Refuge Theory – one that predates it – involving the transformation of the landscape of the Amazon that was a determining factor behind the diversity of the region's ant species. Fifteen million years ago, before



Now in his 88th year, Paulo Vanzolini is pessimistic about the preservation of the Amazon

the Amazon river was formed, the rise in sea level led to an influx of the oceans' waters into the region which, according to scientists, led to the isolation of certain swathes of land mass that eventually became islands. This fragmentation of the ecosystem would then be further brought to relief with the formation of the refuges. According to this study, the great upswing in diversification of ant species occurred some 8 to 14 million years ago.

The theory of areas isolated in the Amazon for a certain period may – while bearing in mind its limitations – help explain much of the diversity of the Atlantic forest. Cinthia Brasileiro, an expert in ecology at the Federal University of São Paulo (Unifesp), supports the claim that a number of speciation areas, veritable centers for the manufacture of species, must have existed in

the region between the states of Bahia and São Paulo.

The refuge hypothesis as applied to the Atlantic Forest arose from the eval-

The theory also serves as a valid explanation for evolutionary processes observed in other regions, such as the Atlantic Forest

uation of genetic data on two species of frog. The study of phylogeography (the mapping of the genetic diversity of a species over time) shows that some areas of the forest remained covered and had a more or less stable climate for millions of years. These areas underwent neither periods of extensive draught nor excessive cold temperatures. There is also no evidence of dramatic changes in sea level in these areas.

Over the past 12 million years, however, a number of refuges existed along the coast of Brazil. One of these probably developed in the area between São Sebastião and Cananeia in coastal São Paulo. When, for example, the area's sur-

rounding sea-level declined, drylands emerged that later became forested for longer periods, thereby enabling these regions to sustain an influx of different species. This is how the speciation process that Vanzolini and Haffer imagined occurred in the Amazon region.

Regardless of whether the theory that has been advanced is entirely valid, it is clear that phenomena such as fragmentation, isolation, climate change and environmental stability are constant factors behind the development of new species. This is but another way to say that the debate surrounding the refuges question is now more pertinent than ever. With human activity at once accelerating climate change and diminishing the forests in many parts of the world, a process may well be in place – one that may be invisible to us – that is running counter to the speciation process also underway. The consequences of these developments remain uncertain.

Topics such as climate change and an extinction of biodiversity leave Vanzolini quite pessimistic about preservation of the Amazon region's ecosystem, a region he came to know so well through decades of 3-month expeditions conducted just about once a year. "The Amazon is done," Vanzolini laments, "There's a lot of cattle and soybean there, but the people of the Amazon – who have to survive – are also the ones most interested in increasing these kinds of economic activities." ■

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