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THE VANISHING REFUGE: A MECHANISM FOR ECOGEOGRAPHIC SPECIATION

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ABSTRACT

Some populations of forest-restricted species may be pre-adapted to life in open formations. If, during the dry part of a climatic cycle, they happen to be confined to a refuge that eventually vanishes, they may, in the process, become completely adapted to open formation conditions and constitute a full ecological vicariant.

In tropical regions, at least, whether on continents or islands, there is one very common situation in which the application of the orthodox model of speciation by geographic isolation is not immediately obvious. It is that of closely related species inhabiting contiguous, even interdigitating, areas characterized by sharply contrasting plant formations. This is a situation which both of us, working with the herpetofaunas of South America (Vanzolini) and the West Indies (Williams), have confronted. We have independently come to the same modification of the geographic isolation model as a possible explanation of this very general phenomenon of climatically strongly differentiated yet very closely related vicariant species.

It is well known that many euryecious species span most of the range of conditions that any continent (or even more than one continent) can offer. The observation that populations in complete genetic continuity may cross the interfaces between different plant formations is trivial. What has not been clear is how the genetic continuity is broken — how complete stoppage of gene flow across an interface between two vegetational formations can be achieved, particularly in the absence of strong physiographic barriers. Alternatives to the geographical model have been proposed (e.g., Endler, 1977, White, 1978). We do not here or at this time wish to dispute these alternatives but instead to place on record a simple modification of the geographic model which can adequately explain vicariant distributions in contiguous contrasting environments.

Our conception is that the physiologically profound changes and concomitant speciation involved in ecological vicariance are not preceded by the colonization of a new environment, but that adaptation to the new ecology and genetic divergence proceed *pari passu* during drastic climatic cycles, while the origi-

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nally favored environment is being reduced in area and broken up into isolated patches, some of which may eventually vanish.

Since South America has recently passed through a maximum of humidity (Vanzolini, 1974: 70) and is now proceeding down the dry leg of the cycle, it is more convenient to use as illustration the case of animals strictly coupled with the rain forest. Let us suppose a large forested area, surrounded by open formations, during mesic times (see figure). When the climate moves toward semi-aridity, the open formations begin to invade and dissect the forest, until the latter is reduced to a set of isolated refuges, where segments of the original fauna survive.

Let us suppose, next, that one of the patches of forest does not last the whole cycle, but dwindles and eventually vanishes, and that one of the forest animals that had found refuge in it happens to become adapted to the new semi-arid conditions. We would then have the original species represented by disjunct populations in one or more refuges of its normal environment (forest) and in one isolated location (that of the vanished refuge) in the middle of the open formations. These populations would be geographically isolated and undergoing very diverse selection pressures; they will have already differentiated to some degree.

Originally the new dry-adapted population may have been small and then drift might accelerate selective pressures, pushing it to a new norm — quite possibly at the species level of difference. But if that new norm of adaptation to open conditions is achieved, buildup of the newly differentiated population is to be expected and it can then achieve, in classic fashion, secondary contact with the forest refuges and so with the populations within them belonging to its parental stock. The descendant stocks, the forest-adapted populations, perhaps themselves differentiated, and the new open formation-adapted population are now ecological vicariants.

One of the points the model has to explain is that, since Quaternary climatic cycles are known to be rapid and drastic, the probability of a forest form having enough time to adapt to semi-arid conditions should be very small. This probability, however, would be much larger if the population involved were in some way pre-adapted, i.e., tolerant of (or perhaps even preferring) edge or other situations intermediate between the two extreme ecologies.

It is possible to cite some actual examples of the critical steps of the process. In fact, it is the very obvious presence of a number of such examples that first attracted our attention to the problem. A first stage is shown by the South American sphaerodactyline gecko *Gonatodes humeralis*. One of us has been able to make reliable observations of this species at 42 Amazonian localities, along some 10,000 kilometers of waterways. At 37 of these localities this diurnal lizard was found on the lower meter or so of tree trunks, always in shade situations, under canopy, either of natural forest or of dense orchards (cocoa, rubber). At four localities it was in edge and second growth situations, and in one place it was frankly in the open, on backyard fence posts, where one would rather expect to find *Anolis aeneus* instead. This backyard population of *G. humeralis* would be a likely candidate for survival during a dry episode, even if the local forest disappeared completely.

Another case is that of the iguanid *Plica plica*, that typically lives high on columnar trunks of thick and tall trees in the forest. It is not as common a species as *Gonatodes humeralis*, but we have reasonable observations at 17 localities in the same general geographic area. At only one of them, Os Patos, on the river Maicá, near Santarém, it was frequent outside the forest, on isolated mango trees. A few kilometers to the south, at Taperinha, without any discernible ecological gap, it has been seen many times, but only in its normal habitat.

These are then two cases of presumable pre-adaptations that would permit survival in open formations following disappearance of the forest. The animals are not independent from the forest domain yet: they have only moved from the shade of the canopy to the network of juxta-fluvial open formations (Vanzolini, 1978: 321).

We have published (Williams and Vanzolini, 1980; Vanzolini, 1981) an example of a further step of the process, happening in a mesic enclave in the semi-arid caatingas of northeastern Brasil. This enclave, the Cariri, 350 km inland from the Atlantic forest, is determined both by rainfall (1100 mm — caatinga does not withstand more than 800 mm) and by many springs that flow from the slopes of a sandstone mesa. The lower slopes of this mesa, on its north side, and an adjacent belt of lowland some kilometers wide, were forested as late as the middle nineteenth century. The area has since been entirely cleared by man, but a few faunal relicts of the recent maximum of humidity (when the Atlantic and Amazonian forests were connected) still survive.

Important among those is *Anolis chrysolepis brasiliensis*. *A. chrysolepis* is a broadly distributed lizard, that has been studied in some detail, from the morphological and distributional viewpoints by ourselves (Vanzolini and Williams, 1970). We have personally encountered it in the field in Amazonia at 20 localities, always inside the forest. We have reliable information on a further dozen localities, and only at Villavicencio was it found in (perianthropic) semi-open situations. This situation would be analogous to that of *Gonatodes* and *Plica*. The subspecies *brasiliensis*, essentially extra-Amazonian, is very unevenly distributed, and has been previously found in localities (especially in Central Brasil) whose general ecology suggests tolerance to open situations. For example, the type series is from Barra do Tapirapés, in the domain of the cerrados, and was collected in gallery forest. In the Cariri this lizard is found frankly in the open. Given the very broad range of the subspecies, roughly one million square kilometers, it was indeed probable that some population would survive worsening climates and fulfill the scenario we propose.

Anolis chrysolepis brasiliensis at the Cariri did not noticeably differentiate in morphology from other populations studied, in spite of the large distances involved. One of the other mesic relicts of the area, the snake *Sibynomorphus mikanii*, shows apparent differences in scale counts (Vanzolini, 1981) but we cannot at present evaluate its degree of specialization, for lack of comparative materials. There is one lizard, however, *Mabuya arajara* Rebouças-Spieker, 1981, that has undoubtedly reached species status.

The type series of the new species comprises 119 specimens. The species from which it seems clear *arajara* derived, *M. bistrata*, is also known from several hundred specimens. The differences, mostly in color pattern, are small enough to make the relationship evident, but extremely consistent. *M. bistrata* has a disjunct distribution, on one side all over the hylaea, on the other on the northern end of the Atlantic forest; the differences between the disjunct populations are incomparably less than between either and *arajara*.

The Cariri, as said, was forested until the mid-nineteenth century (Vanzolini, 1981) and very probably *M. arajara* evolved in a proper forested refuge and not in a vanishing one. This is not, however, the point of the example, but the fact that a refuge has now vanished leaving behind one species inhabiting open formations contiguous to forested areas where the parent species survives. *Mabuya* makes also a strong case for preadaptation, because the forest forms of the genus are heliophils that frequent clearings and edge situations. They seem to be still incompletely adapted to the umbrophilous environment, and still capable of doubling back evolutionarily.

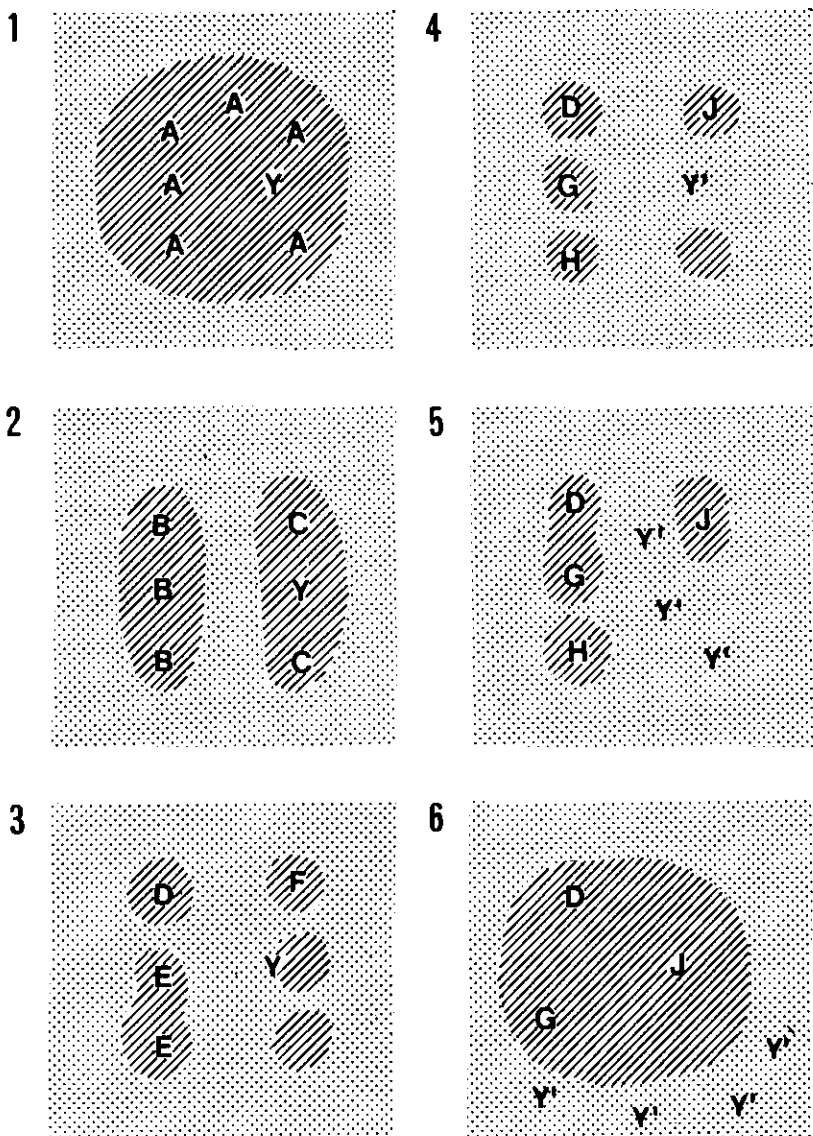
In *Mabuya arajara* we see the completed process, but it should be noted that in the Cariri the forest has completely disappeared but the climate is

still relatively mild. However, an example of survival in actual semi-arid conditions is available. Laurie J. Vitt collected in the area of Exu, Pernambuco, just south of the Cariri and in the core of the caatingas, the small sphaerodactyline gecko *Coleodactylus meridionalis*. This is typically a forest leaf litter dweller, known from the Atlantic forest and its relicts, and from mesic enclaves in the caatingas (Vanzolini, 1980). Near Exu it was found in what possibly was a vanished dry forest enclave, definitely in a semi-arid environment.

We propose that the examples above illustrate all steps and demonstrate the feasibility of the vanishing refuge model.

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Hypothetical example of the vanishing refuge model

1. Continuous forested areas (hachured) surrounded by open formations (stippled). "Y" is an ecotone-tolerant population of "A", a forest-restricted species.

2. Desiccation of the climate: beginning of the dissection of the forest by open formations and of the differentiation of A in refuges.
3. Further dissection of the forest and differentiation of A; Y becomes definitely ecotone-adapted.
4. Maximum aridity: full process of differentiation in refuges; Y's refuge has disappeared and the population has become fully adapted to open formations, and spatially isolated from the populations within the surviving refuges.
5. Ammelioration of the climate: beginning of the recovery of the forest; refuges begin to coalesce; Y is now a fully adapted open formation form.
6. Process completed: continuous forest area reconstituted; Y a widespread, parapatric open formation species.