

REFUGE MODEL SIMULATIONS: TESTING THE THEORY<sup>1</sup>Dalton S. Amorim<sup>2,3</sup>

**ABSTRACT.** The refuge model has been proposed and developed in the last two decades only descriptively. The absence of a general method of biogeographical analysis in the refuge model free from prior assumptions demands a search for such a method elsewhere. However, the structure of the model itself can be critically and profitably analysed. The model is here tentatively formalized, with an algorithm for the number of species generated in a region. This formalization allows simulations that result in objective predictions, which can be compared with actual data. According to the simulations, the expected number of descendent species for each ancestral species existing in a region just before the beginning of the Quaternary would be, in the most conservative hypothesis, one order of magnitude higher than the total number of species known from actual data. It is shown that it is nearly impossible to accept that extinction and failure of populations to differentiate could have had the necessary intensity to reduce this number of potential species in a region to the numbers observed. The expected geographic distribution of species under the predictions of the model is also unverified, considering the postulated phase of the present climatic cycle. Finally, assuming equal rates of evolution of classes of proteins, information from molecular distance studies indicates a history of Tertiary, rather than Quaternary divisions in Neotropical and Australian taxa. This would force the conclusion that the Quaternary promoted almost exclusively expansions and retractions of the distribution of biotas around refuges, which are spatially coincident with areas of endemism generated during the Tertiary or earlier.

**KEYWORDS.** REFUGE THEORY, TERTIARY, QUATERNARY, BIOGEOGRAPHY, EVOLUTION.

## INTRODUCTION

Discussion of biogeographical theories during the last few years has shown that a biogeographical reconstruction should not begin with a preconceived model, but should be based on a biogeographical method of analysis (CROIZAT, 1964; PLATNICK & NELSON, 1978). This implies that the refuge model should be abandoned as an *a priori* causal explanation for large scale speciation events in any region, despite the number of coincidences between refuge areas and areas of endemism.

The refuge theory does not offer a general method of biogeographical reconstruction. However, it does contain a model and, although poorly developed in the literature, some hypotheses can be deduced from it. At least three predictions can be made under the refuge model. The first concerns the total number of species expected to be generated in a region from a single ancestral species after a given length of time. The second accounts for the geographic distribution of species or populations at a given moment in any cycle. The third concerns the expected substitution rates of molecules between species of a group if regular rates are assumed.

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2. Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Av. Bandeirantes 3900, 14100 Ribeirão Preto SP, Brasil.

3. Bolsista do CNPq.

PALEOCLIMATIC FLUCTUATIONS IN THE QUATERNARY  
AND THE NUMBER OF PRESENTLY KNOWN SPECIES IN  
NEOTROPICAL GROUPS

The number of descendent species of any given ancestral species is a function of the number of successive divisions of that species after a given length of time and of the number of vicariated areas or areas simultaneously occupied by dispersal at each division. In the refuge model, the major causal factor of vicariance is a succession of climatic cycles, with alternate phases of glaciation and interglaciation (see VANZOLINI & WILLIAMS, 1981: Figs. 1-6). Species, within the whole biota, would expand in range during favorable climates and retract and fragment during unfavorable phases. Refuge theory necessarily implies that the number of descendent species of a group in a region would be a function of the number of climatic cycles that have been effective in generating (spatial and, later, reproductive) isolation and of the number of refuges in that region.

Few authors working with refuge theory seem to have made any attempt to determine what kind of climatic cycle, in terms of length and periodicity, would affect evolution of taxa in a region. The peak of glaciation of about 18,000-12,000 y.a. (AB'SABER, 1974) is frequently cited as having generated divisions in a great number of Neotropical groups. A less severe and more recent peak of glaciation, about 2,600 y.a., affecting areas at least at the sea level, is also cited as being possibly effective in generating divisions within some groups (VANZOLINI & AB'SABER, 1968; VANZOLINI, 1973). There are few comments on the influence of earlier glacial cycles.

Glaciation cycles are probably generated by distinct, nonexclusive, and interacting causes. Each causal factor seems to have its own periodicity. There is evidence of cycles of 400,000 (SMITH, 1974), 100,000 (FAIRBRIDGE, 1972; MUIJS, 1983; POLLARD, 1983; SMITH, 1984; BOYD *et al.*, 1984), and of about 10,000 year intervals (WHITE & VALASTRO, 1984; DENTON & HUGHES, 1984, etc). The extent of the Quaternary period, during which there have occurred exceptionally intense global climatic variations, is also a point of some disagreement. Most authors indicate a period of 2 m.y., although there are some more conservative (1 m.y.) or more extreme opinions (7.5 m.y.; ZUBAKOV & BORZENKOVA, 1983).

An estimate of the total number of climatic cycles that have affected the biological history of any region depends on the length of the cycles (time of isolation) one accepts as sufficient to influence the history of the organisms. If one accepts short cycles as efficient for generating differentiation (and reproductive isolation), a larger number of splitting events must have affected the history of the groups. However, the lack of a definition for the kinds of cycles that affects the history of groups makes it very difficult to estimate this variable in a simulation. In a simplistic calculation of the numbers of each kind of cycle, we would have, in a period of, say, 2 m.y., 5 complete cycles of 400,000 years, 20 complete cycles of 100,000 years, and about 200 cycles of 10,000 years.

It is evident that interactions among different causal and local factors imply loss of regularity in the final pattern. However, this is simply irrelevant in the

simulation, since what affects the final number of species in the region is the **total number** of cycles which have occurred, not their regularity. So, the values presented below correspond only to possible minimum and maximum numbers of cycles (respectively 5 and 200) that may have affected the history of groups in the region, with an intermediary value.

The number of refuges is also a point of poor agreement among authors. VANZOLINI & WILLIAMS (1970) have proposed four refuges for Amazonia, while BROWN (1977) proposed 38 refuges for whole tropical South America, there being numerous other intermediate opinions. Different ecological requirements imply that a refuge can be adequate for a group but not for others, to survive during unfavorable phases. That is, the effective number of refuges can be higher or lower depending on the group and the extreme values must be taken to fit all kinds of groups in the simulations.

The simplest algorithm to calculate the final number of potentially generated species under a model of regular expansion and retraction is

$$(1) \quad N = R^C,$$

where N is the final number of species, R is the total number of efficient refuges, and C is the number of cycles that affected the history of the taxa.

Table I includes the results obtained with 9 different simulations, in which values of 6, 15, and 40 have been assumed for R and values of 5, 20, and 200 have been assumed for C.

Table I. Total number of differentiated descendent species or subspecies that would be expected by a refuge model to exist today, beginning with a single ancestral species in the end of the Tertiary. Different simulations were made, in which different values are attributed for the number of cycles (C) and for number of refuges (R). The algorithm itself does not take into account processes that would reduce the final number of species.

R/C	5	20	200
6	$7,8 \times 10^3$	$3,7 \times 10^{15}$	$6^{200}$
15	$7,6 \times 10^5$	$3,3 \times 10^{23}$	$15^{200}$
40	$1,0 \times 10^6$	$1,1 \times 10^{32}$	$40^{200}$

The validity of tests of a theory depends on the correct choice of objects in the real world to be compared with the simulation results. In the present context, these objects are groups that have some precise historical features: the taxon must be monophyletic, endemic of a geographic region, and its (supposed) origin must have been earlier than the Quaternary. Some examples of taxa with these characteristics, as may be inferred from their biogeography and/or paleontology, are *Rhynchosciara* (Diptera, Sciaridae), the *Rhipidita* group of Ditomyiidae (Diptera), the Platyrrhini (Primates), and the Passalinae (Coleoptera, Passalidae).

*Rhynchosciara*, an exclusively Neotropical group, has its sister-group in Madagascar. The genus has 22 presently known species (AMORIM, 1987). The *Rhipidita* group has as its sister-group a circum-antarctic taxon; this group has 21 known Neotropical species (AMORIM, 1987). In both groups, the number of known species is profoundly affected by sampling errors, because large areas in South America have never been collected for these groups. They provide, however, at least an

order of magnitude as a reference. The Passalinae, a group rather easy to collect in Neotropical forests, has about 200 known species, and its sister-group is outside the Neotropical region. Finally, in the Platyrrhini there are probably slightly less than 250 valid names for species and subspecies in the Neotropical Region. The sister-group of this taxon, the Catarrhini, is distributed mainly in the Afrotropical and Oriental regions. The Platyrrhini are quite well collected and studied taxonomically. Forthcoming work on primatology most probably will not modify the order of magnitude of the number of known differentiated populations in the taxon.

All these taxa have "Gondwanic types" of distribution. Since they are supposedly older than 2 m.y., we could use their present number of species as data to be compared with the simulation results. The fact that these groups may have a Neotropical distribution due to a mid-Tertiary introduction by migration (a hypothesis herein considered improbable), rather than to a Mesozoic, Gondwanic origin, does not affect the line of reasoning developed here; in both cases they would still have a pre-Quaternary origin.

The differences between predicted and actual data are in the best case of one order of magnitude. This forces us to abandon the model or to modify its algorithm. This algorithm, in fact, was developed as a first step only to present the general structure of the problem. It does not include evolutionary processes which reduce the number of potential species; "deleterious" evolutionary processes must now be included. The two most important processes in this category are extinction and fusion between previously geographically isolated populations that failed to differentiate.

If fusion (or hybridization) between previously vicariated populations occurs, the last cycle would have produced little or no increase at all in the numerical diversity of species in the area. In the case of the refuge model, to justify the reduction in the final number of species produced by the simulations with this process would imply necessarily that shorter cycles would have little or no influence on the process. We do not necessarily need to modify the algorithm to verify the influence of fusion between populations in the simulation: we can just alter the values attributed to  $C$ , what limits the "acceptable" results of Table I to those of the left column.

Extinction, on the other hand, reduces the number of populations isolated in the  $R$  refuges that would effectively generate species in a vicariant event. A new algorithm that includes this process can be given as follows:

$$(2) \quad N = (R_T - R_{EX1}) \cdot (R_T - R_{EX2}) \dots (R_T - R_{EXn}),$$

where  $N$  is the number of produced species,  $R_T$  is the total number of refuges, and  $R_{EXi}$  is the number of refuges in which extinction took place for the descent of a group in the  $i$ -th of  $n$  cycles.

Although extinction may be a random process, we can admit that groups with similar ecological features would not survive in certain refuges (e.g., because the refuges are too small) in any or most cycles. Consequently, it would be acceptable to admit a mean rate of extinction in each cycle in relation to the total number of

existing refuges. In this case, we can use the results of the first simulation, simply reducing the values attributed to R. The effect of extinction can be visualized by ignoring the lower lines in Table I.

The inclusion of the effects of fusion between populations and extinction in our simulations leads to a curious result: It is still necessary to consider the results of Table I, in which the most conservative hypothesis indicates  $N = 7.8 \times 10^3$ . This is 30 times higher than the known number of Platyrrhini.

Some additional comments must be made for the results of the simulation. First, it is necessary to consider that rejection of lines 2 and 3 of Table I, to try to adapt the model to the known data, requires a "model of extinction" within the refuge model. However, in such an extension this implies a contradiction to a basic assumption of the refuge model, namely that refuges are supposed to be stable areas. Additionally, such a model assumes different ecological features and consequent differential survivals for various groups, so that there would be at least some groups in the biota with a higher number of species (e.g., line 2 of column 1 of Table I), which certainly cannot be verified in any group.

As a clarifying example, consider a simulation in an "extinction refuge model" of 15 refuges on the continent, 5 cycles of 400,000 years in 2 m.y., and extinction in 11 of the 15 descendent populations at each of the five cycles. A single ancestral species at the beginning of the Quaternary would have about  $2^{10}$  descendent species in the region. That number cannot be verified. Additionally, such a Quaternary history of the group would be very different from the original formulation of the theory.

A second point is that the Platyrrhini are at least 30 m.y. old. That is, the group has a history extending at least 28 m.y. before the Quaternary, if not since the beginning of the Cretaceous. To accept the total number of species in the Platyrrhini as adequate to compare with the simulations would imply accepting that the ancestral species of the group had not subdivided during that whole period. This is really an improbable hypothesis. If a group had a number of divisions ( $d$ ) in its history through the Tertiary (i.e., during a period of 80 m.y.), the final number of species to be compared with Table I would be something between  $250/d$  and  $250/2^d$  (minus extinctions). This number, smaller than 250, puts the refuge theory into a further jeopardy.

#### THE PRESENT PHASE OF THE CLIMATIC CYCLE AND KNOWN GEOGRAPHIC DISTRIBUTIONS OF NEOTROPICAL SPECIES

Another approach to verify predictions of the refuge model is to analyse congruence between present geographic distributions of species or differentiated populations in many groups with those expected by the model.

Information about the distribution of taxa adequate for such analysis may be obtained, for example, from HAFFER'S (1978) study of avian groups in Amazonia. His results (for similar data, see HERSHKOWITZ, 1977; BROWN, 1982; KINZEY, 1982; PRANCE, 1982, etc) show that most species have distributions centered in nuclei, considered by him as spatially congruent with the areas of past refugia. In other words, it is possible to detect today existence of areas of endemism in many groups,

a trivial task for any taxonomist. There is information, on the other hand, that the maximum level of rainfall in the present cycle of climatic fluctuation has already been surpassed. We are now moving into a phase of increasing aridity (FAIRBRIDGE, 1974; VANZOLINI & RAMOS, 1977; VANZOLINI, 1982; RODRIGUES, 1984).

These two classes of data together disagree with the refuge theory. Should the theory have been correct, at the beginning of the regressive phase of each cycle forest species should have maximum distributions and be largely sympatric with their sister-species, which later become subdivided when the forest retreats. However, if information about the climate is correct, expansion of the population distribution during the last favorable phase of the climate did not lead to sympatry between previously vicariated populations. The retraction of the forest, consequently, will not generate new descendent species from the earlier fractioned ancestral species in most or all refuges.

This is certainly an inconsistency of the model, but one capable of immunization from falsification. One could argue that the present decrease in rainfall (if the information is true at all) may be part of a "short" cycle and, as we have demonstrated above, it would not have much effect on the speciation process.

#### MEAN RATES OF MACROMOLECULAR EVOLUTION AND DEGREE OF MODIFICATION OBSERVED IN PROTEINS IN NEOTROPICAL GROUPS

Another kind of pertinent information in this analysis has been furnished by studies of macromolecular divergence in biological groups. Many different techniques and methods have been developed to analyse differentiation in homologous macromolecules (for general views, see WILSON *et al.* 1977; FARRIS, 1985). These analyses provide hypotheses of genealogical relationships among taxa and include information about degree of modification found between them at each level. Using the premise that particular classes of proteins in certain groups have relatively constant rates of evolution (WILSON *et al.*, 1977), one may establish a "molecular clock" for evolution. These data have been used in biogeographical studies, since they furnish an approximation of absolute age of groups. Many studies have been made on amphibians, particularly for Neotropical (HEYER & MAXSON, 1982, 1983; MAXSON & HEYER, 1982) and Australian groups (MAXSON & WILSON, 1975; MAXSON *et al.*, 1979; MAXSON & MAXSON, 1979; DAUGHERTY & MAXSON, 1982; BARENDSE, 1984; MAXSON & ROBERTS, 1984; ROBERTS & MAXSON, 1985). These papers are almost unanimous in concluding that most (in some cases all) events of subdivision of monophyletic assemblages into species and groups of species probably occurred during the Tertiary, rather than during the Quaternary period.

Again, the conclusions can be immunized from falsification. The "molecular clock" is based on an assumption of mean rates of evolution for some proteins, which may be false. However, even if macromolecules do not present such regular rates of modification, this would not necessarily favor the refuge model. Errors in measurements may have increased or decreased the actual age of the groups

analysed. As a mean rate, it departs too far from the rates expected by the refuge model. Moreover, the "molecular clock" has been calibrated against fossils, which give only minimum ages: the actual ages would tend to be still greater.

### CONCLUSIONS

A theory has scientific status, following POPPER'S (1959) criterion, if hypotheses can be deduced from the general theory and tested against reality. The refuge theory, interestingly, has the characteristics of a general theory from which hypotheses can be deduced, although no defender of the refuge theory has ever formalized it. On the other hand, accumulation of knowledge about coincidences between refuge areas and areas of endemism does not furnish additional strength to the theory, although this is frequently claimed by the proposers of the theory. Repetition does not test the causality proposed by the model in any sense, but rather confirms the existence of an observed pattern.

Studies of the supposed "axioms" of the theory in the literature (although not formally proposed) allows some formalization. The formalization proposed here resulted in objective predictions about the number of descendent species and the spatial distribution of the species (or subspecies). Both showed very poor congruence with actual data, and an additional source of information (macromolecular data) also argues against the model.

This would be sufficient to falsify the theory when it proposes that climatic fluctuation during the Quaternary is the *causal factor* for most of the speciation events in the history of subdivisions of biological groups. Climatic variation more likely would have occurred during the Quaternary over a pre-established biogeographical pattern of distribution, promoting only expansion and retraction of the biota as a whole around each area of endemism originated during the Tertiary and before.

ENDLER (1982a) has also proposed some predictions of the theory - especially based on expected ecological behaviour of different groups or species of a group in different refugia - that are not observed in available data. MAYR & O'HARA (1986) tried to show that Endler's data are too imprecise to allow some of his conclusions. Also, the bird species analysed, the distributions of which would supposedly dismiss the theory, are actually allopatric, "never having come into secondary contact" (MAYR & O'HARA, 1986:55). However, this kind of pattern, as we have seen, is one of the evidences against the refuge theory, although not favoring ENDLER'S (1982a, b) parapatric model (CRACRAFT & PRUM, 1988).

The generally observed coincidence between core areas of endemism and areas believed to be refugia should not be overlooked. An explanation for this fact may be due to aspects of relief. At least some of the breaks in the history of terrestrial groups in South America have been demonstrated to be spatially and temporally congruent with epicontinental sea formation during the Tertiary (AMORIM, 1987; see BROOKS *et al.*, 1981, for aquatic groups). The sea introgressions covered lower areas, with terrestrial species occupying the vicariated higher terranes. These same higher areas would offer the adequate climatic conditions (especially pluviosity)

for the survival of rain forests and the development of forest refuges during the Quaternary. Tertiary areas of endemism that were not refuges during the Quaternary may have suffered severe or complete extinction. A "Tertiary model" of divisions in the history of groups, still to be further developed, is compatible with the three kinds of data presented above.

Obviously, objections can be proposed against the formalization above, since one can consider that it does not represent the theory. However, the algorithms presented are mathematical representations of the theory very similar to its description in the literature. Actually, as showed by NELSON (1979), refuge theory is vicariance applied to a specific situation in Quaternary. The algorithms proposed can be applied to any case of vicariance, refuges being just one particular case. The second algorithm, in fact, may be further improved (e.g., deducing a number of refuges for the cases of fusions between populations at each cycle) and a study could be made to determine whether mean values of extinction are acceptable. However, the enormous differences between the predictions and the actual data imply that the model cannot be sustained, at least not in the way it has been presented. Certainly, a different formalization of the model may be proposed, but to reject the algorithms as inadequate without a substitute proposition - if possible at all - would throw the discussion to a rhetorical level, placing the theory in the realm of metaphysics (*sensu* POPPER, 1959).

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**Note from the Editor.** This paper received from different referees comments both decisively favourable and frontally against its publication. Thus, as the subject of the paper seems to be controversial, it was decided: (1) to publish it; (2) to open in the RBE a section "Points of view" where comments on the subject will be eventually published.