Biological Diversification in the Tropics

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Amazonian Inundation Forests
Their Role as Short-Term Refuges and Generators of Species Richness and Taxon Pulses

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ABSTRACT Central Amazonian inundation forests, especially along blackwater rivers, are considered to be short-term refuges and additional long-term evolutionary centers. The importance of flood cycles on speciation rate and vagility of arthropods, particularly carabid beetles, is discussed. Biogeographic definitions of "dispersal," "vicariance," and "taxon pulses" are given.

A good theory points to possible factors and relationships in the real world that would otherwise remain hidden and thus stimulates new forms of empirical research. Even a first, crude theory can have these virtues.

—MacArthur and Wilson 1967

Haffer (1969) and subsequent followers have accumulated data sufficient enough to offer such a theory, which, if supported by tests, will help answer G. E. Hutchinson's (1959) oft-quoted query "Why are there so many kinds of animals?"

As pointed out by Haffer (1978), the 6 million km² of "apparently" uniform tropical lowlands of the greater Amazon region "harbor the most species-rich flora and fauna on earth." A search for the explanation of this diversity has commanded the attention of biologists and others for over 100 years. Three main allopatric speciation models or theories have been proposed to explain this diversity (Haffer 1974, 1978; Simpson & Haffer 1978). According to these, allopatry was caused by either 1) the formation of numerous islands caused by high seas (or low land) during the Tertiary period with subsequent biota differentiation; 2) isolation of biota components due to development of the present river system in the Quaternary period; or 3) climatic influence on the vegetation during the Quaternary that separated blocks of "refuge" forest between which organisms could not disperse. An additional idea, that of "sympatric speciation," was proposed by many early biologists (see Mayr 1963; Bush 1975; Endler 1977). The time has come to suggest that the three allopatric speciation models are not mutually exclusive and that they need to be synthesized into a single model to explain evolution of the Amazonian biota. That is, neotropical species-richness can be accounted for by accumulative historical events involving climatic shifts and microgeographic changes which impose differential allopatry on a biota already influenced by a mosaic of edaphic factors. As for sympatric speciation, it is a problem of semantics, in that sympathy, allopatry, and parapatry are thought of as...
macrogeographic by some (traditionalists) and microgeographic by others. Often discussants with identical views do not communicate at all because of this definition problem. Usually the problems come up between systematists and ecologists. Herein we use "allopatry" as a "vicariant event" and this can be at any level from host plant switching to continental drift (Erwin, in press). The separation of two or more portions of the gene pool is the only mechanism by which differential selection by agents external to the organism can take place. It is this separation, or vicariant event, that appears to be the most important (but not only) evolutionary process for the attainment of species diversity (see also Endler 1977 for thoughts on parapatric speciation and Yen and Barr 1975 for discussions on cytoplasmic incompatibility).

Allopatric models have been discussed, especially the forest refuge aspect, but little attention has been paid to the evolutionary driving forces once isolation has occurred. It seems that these should be viewed concurrently.

There is now accumulated evidence of terrestrial arthropod movements into the subcanopy and canopy of inundation forests at periods of annual flooding. Since this would be a driving force, we viewed the literature and some unpublished data regarding Amazonian flood cycles, hypothesized river barriers, speciation rates, vagility of species in the region, taxon cycles, and climatic cycles.

From this review we now believe, in general, that tropical species diversity can be accounted for by accumulative historical events involving climatic and geographic changes. One of these events, or series of events, was embodied in the Haffer refuge
theory (Haffer 1969). However, we feel that other possibilities also exist as supplemental or alternative theories, alternative, that is, for a portion of the Amazonian region that perhaps did not experience drying out. Our data lead us to believe that flood waters in the Amazon Basin are important in two ways: 1. Rising waters annually inundate riverine habitats, driving the terrestrial arthropod faunal components toward the canopy (trunks, branches or foliage areas) or into the soil, or to terra firme habitats, thus adding species to other biotopes for part of the year. These other biotopes already have a complex of species, thus an evolutionary driving force potentially exists through increased competition and predation. 2. Cyclic flooding of major tributaries during the Cenozoic formed lakes and wide rivers that separated portions of otherwise contiguous populations and thus allowed allopatric conditions that may have resulted in speciation events.

We wish to address both of these points in their own right and also see if there is a connection between them which somehow influences the biota.

The question now arises, why even consider water side habitats at all? Our reason is that the forest refuge model as stated only deals with terra firme forests and their replacement by “savannas sensu lato.” As far as we know there has been no suggestion that riverine forest disappeared along the length of the rivers, but rather, savannas were behind such forests as they are today. It seems reasonable, too, that the leaders in forest refuge studies have concentrated on terra firme forests because that is where their animals and plants are most diverse, as Prance pointed out in this volume.

For our group, the carabid beetles,
the case is opposite. These beetles (fig. 19.1-19.4) are most numerous in species, species groups, and genera along waterways, in marshes, swamps, and in the canopy. Therefore, there must be some additional mechanism, besides terra firme refuges, working. The evidence presented by Irion (pers. comm. and Irion and Adis 1979) and some of his work with Absy suggests that water levels have fluctuated quite a bit over the last few million years, especially during the Pleistocene, in the Amazon drainage system. It may be this water-level fluctuation that will help explain carabid beetle richness. Also, we now know that annual inundation has a dramatic impact on riverine arthropod communities.

If it can be shown that riverine forests also have fragmented, that blocks were not connected by gallery forest so that organisms could disperse, it would help explain extensive carabid speciation. This would compliment the terra firme forest refuge model.

Definitions of Terms

Jargon usually associated with biogeography has caused confusion among even experienced biogeographers. Before going further it is necessary to state definitions of certain words or concepts.

Dispersal. Dispersal is the actual movement of an individual or group of individuals from one geographic point to another. The potential for this movement, its mode, speed, and distance can be thought of as species vagility. Careful analysis must be made to assure biogeographic usefulness. An understanding of a group's vagility must be a forerunner to any biogeographic study.

The importance of dispersal to a taxon is the attainment of cosmopolitanism, that is, acquiring, maintaining, and altering geographic range and continuing genetic contact between populations. Individual dispersers are merely genetic carriers from one population to another across an intervening gap. So long as this connection exists, a species maintains its integrity and genetic diversity; separated populations are at the same time gradually diverging, yet maintaining a commonness in direct proportion to amount of contact or genetic exchange. It is only if dispersants fail to carry their genetic material between separated populations that allopatric speciation can proceed. Failure to do so results from the intervening "gap" becoming an uncrossable "barrier." This potentially can occur in two ways: 1) physical features of the earth surface change and/or climate shifts, or 2) intrinsic changes occur in the genome, behavior, or dispersal capabilities of members of a semi-isolated population. That (1) can occur is undisputed; that (2) occurs is open to conjecture and in much need of study (see e.g. Endler 1977).

Biogeographers often think of barriers as large, dominant features of the landscape. Oceans between continents and oceanic islands are good examples. We know that insects disperse to remote islands; they even cross the Atlantic Ocean (Johnson & Bowden 1972). This capability of animals and plants spurred Mayr (1942) to suggest the "Founder" principle, that is, one-time transportation across a barrier of a gravid female or small deme which becomes established (with subsequent family) in an area not previously occupied by that species. Speciation then proceeds. Given that insects, some plants, and some other animals do disperse long distances, the theory of "founderism" seems reasonable. The chances of it actually happening in nature, however, are remote and cannot account for very many cases of species distribution patterns even in remote areas. This is because weather patterns, ocean currents, or other means of dispersal are not "freakish" when viewed on the geologic time scale or especially the evolutionary-rate scale. In other words,
if dispersal conditions are such that a founder finds its way across an ocean to an island today it is likely that the potential for such an event is going to occur often over the next several thousand years until dispersal conditions change. The pattern is one of attaining cosmopolitanism, not isolation, and it is repeated year after year, or decade after decade. The connection to the semi-isolated population may be tenuous but it exists and the island therefore is within the cosmopolitan distribution of the species. When the tenuous connection is broken for a long enough time, speciation may take place. The event that breaks the connection is called a vicariance event; it may be climatic change, continental-rifting, glaciation, host plant switching or anything that prevents the genetic carrier from crossing the gap long enough for a speciation event. In the case in point, the ocean was not the barrier because the species members crossed it, rather it was the weather pattern change that stopped dispersal; this concept is fundamental to biogeography. All too often biogeographers have considered some imposing geographic surface feature to be the barrier because it was visible. We doubt that this is often the case at least for vagile arthropods and suggest we focus on more subtle features such as climate shifts or, in the case of the Amazon, the mosaic and shifting riverine system.

Of course, in the case of continental rifting the developing ocean does eventually, after a long period of time, become a barrier to a majority of the fauna and flora, but this happens gradually and differentially on various biotic elements. An analysis of barriers and species vagility is an important first step in any biogeographic project.

Vicariance. Vicariance, as alluded to above, is usually thought of as the separation of populations of a species by some geologic or ecologic feature in the biosphere (Platnick & Nelson 1978). It is the result of two or more portions of a species range becoming separated, thus disjunct or allopatric. If the separation is maintained long enough speciation takes place.

Vicariance is not established so long as dispersal or genetic exchange takes place between the populations. However, we view vicariance events as having potential coincidence with a wider scope of historic perturbations, from climate alternations, grand continental rifting, and glaciation patterns to host switching traditionally thought of as “sympatric” speciation (Bush 1975). Vicariance to us is merely the separation of genetic resources available to a species into two or more isolated pools by some external or intrinsic mechanism which allows the two or more pools to be differentially selected by agents external to themselves. The resolution at which one looks at vicariance depends on taxon level. There should be a general correlation between age of a taxon (that is, in a cladistic system—taxonomic rank of the group) and age of vicariant events. For example, sister species pairs of carabids in the Nearctic Region probably date to a late Pleistocene vicariance event (Ball 1964; Whitehead 1972; Ashworth 1979; Matthews 1979). Two “sister” genera, however, probably date to an older event, perhaps mid-Tertiary (Erwin 1970; Noonan 1973; Ball 1975).

Vicariance events coincident with historic events such as subsidence patterns, rifting, flooding cycles, glaciation, desert formation, etc., in the history of carabids were (are) probably the same as those affecting many other flying insects. There is no evidence yet that genetic switching or host alternation exists, so at present we can only deal with the traditional “allopatric” speciation model and see how it applies to observed patterns.

Taxon pulses. In 1976 Erwin (1979b) expanded the “taxon cycle” concept introduced by Darlington (1943) and named by Wilson (1961) into a model for carabid beetles which accounts for habitat shifts along certain pathways away from the complex of tropical wetland habitats.
Taxon pulses flow unidirectionally along these pathways toward forest canopies, high latitudes, grasslands, deserts, caves, and up mountains (both tropical and temperate). Progression is along a sequence of habitats in one direction only; reverse pulses have not been observed, and it was suggested (Erwin 1979b) that they do not occur. A taxon pulse (fig. 19.6) is defined as a taxon's adaptive shift from one habitat into another along such pathways as mentioned above. For carabids, the shift initially takes place as a tropical wetland evolutionary generalist (pleisiotype) radiates into a biotic zone away from the waterside surface and becomes an evolutionary specialist (apotype). Further along the pathway evolutionary superspecialists (superapotypes) evolve. Replacement of wetland pleisiotypic taxa takes place, but these groups are long persistent. Pleisiotypes may generate several pulses before replacement; these pulses overtake previous pulses and replace them along the pathways. Pulse members usually show sequential relict patterns toward the termini of the pathways because of high extinction rates and replacement by succeeding waves of taxa. The driving forces behind the pulses are various and change through time (fig. 19.7). It is these driving forces, acting on the wetland pleisiotypes, that keep major carabid pulses flowing and account for the incredible diversity and persistence of the family through time (probably since the Permian; Ponamarenko 1979).

Use of this model (fig. 19.5) for phylo-

(fig. 19.5); this model was called "taxon pulses."

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**Figure 19.5** Evolutionary direction of carabid beetle taxon pulses or pathways to extinction. Dagger (†) indicates ultimate end to radiation above the species level.

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Figure 19.6  Status of life styles by fauna and area. Tropical Wetlands-Generalists, some specialists (Fossorial, ectoparasitoids); Tropical Forest Floor. Temperate Wetlands. Temperate Forest Floor. Tropical Mountains-Specialists (seasonally adapted): Tropical Undercanopy and Canopy. Temperate Canopy-Specialists and superspecialists (seasonally adapted, climbing, special life histories, special prey); Temperate Grasslands, Deserts-Specialists and superspecialists (seasonally adapted, life histories, feeding habits, water retention); Temperate Mountains, Tundra, Cold Temperate Forests-Specialists and superspecialists (seasonally adapted, cold adapted). From Erwin (1979).

Figure 19.7  Representation of evolutionary driving forces that greatly affected carabid beetles.
genetic and zoogeographic studies was outlined by Ball (1978). Taxa may be categorized into sets which reflect how far they have departed from the evolutionary generalist stage. Sister group relationships between taxa of sequential habitats can be discovered, the pleisiotype at the base, same level, or lower down the sequential scale than the apotype, as in any transformation series. Correlation of habitat sequences with behavioral and structural characteristics adds power to phylogenetic and zoogeographic analysis (e.g., see Ball 1978; Allan & Ball 1980). Habitat vicariance is simply geographic vicariance at a much finer resolution.

The mechanism by which this process occurs can be thought of as habitat cosmopolitanism. A wetland evolutionary generalist spends part of its time living at the edge of the adjacent drier forest or savanna and through time becomes adapted to both habitats, or even more broadly adapted. Competition or predation pressure increases in the wetland habitat, but not in the drier adjacent habitat, and the wetland form becomes rarer and finally extinct. Selection is toward those that live only in the drier habitat and these survive. This adaptive shift is a pulse. In species that occupy larger ranges, perhaps the wetland form survives locally where competition and predation were less or did not occur. Sister pairs are established between wetland-dryland (pleisiotype) survivors and dryland-only isolates (apotype). Allopatric isolation of different elements of these population sets the stage for differential selection, and subsequent speciation or extinction.

Importance of Flooding Patterns

Most of us at this symposium, we believe, have interests transcending those of the forest refuge concepts. We think we are all after the answers to why there is such incredible species richness in the tropics. The forest refuge concept is doubtless one of those answers. But, it is necessary to deal with all the mechanisms bringing about geographical isolation. Therefore these were generally regarded as macrobarriers such as glacial lobes in the north, continental rifts, or even the sorting-out of refuge forests. But what of organisms or portions of biotas that have low powers of vagility? Perhaps microbarriers act equally as well for them. Evidence for their effectiveness is accumulating (e.g., primates as noted by Hershkovitz 1977; deep forest birds, Haffer 1974; and some plants, Prance 1973).

An explanation, then, of tropical species richness must involve several factors. The most important of these is time, but also, a multiplicity of geographical isolates, low vagility, and/or rapid speciation rates contribute. Therefore, in addition to climatic shifts and refuges, we offer the following scenario: that historical flooding cycles with formation of lakes, broadening of rivers, and reduction of land surface through subsidence may help to explain the postulated habitat isolates; that rapid speciation exists in tropical habitats due in part to climate mildness, (i.e., more generations per year) and to intense driving forces such as competition and predation during annual flooding cycles, and that tropical species generally possess low powers of vagility, making microbarriers important.

Flood Cycles

The forest systems along the banks of the Rio Negro and other large rivers in Central Amazonia and peripheral areas are annually inundated to a height of a few meters for 5 to 6 months. Three factors contribute to this flood cycle: 1) runoff waters from adjacent uplands, especially to the north and the more western Andes; 2) local rains along the length of the river or its tributaries; 3) continental watertable which is
dependent upon ocean level. All of these factors have been operative in the Amazon region since at least the late Laramide orogeny of the Andean Cordillera, which reached its present state in the late Miocene (summarized in Emsley 1965).

Runoff and local flooding are factors that depend on regional climatic conditions which vary and/or cycle through time. Historically alternating periods of tropical aridity and wetness have been coincident with the ebb and flow of ice fronts in the northern hemisphere (Moreau 1969; Vuilleumier 1971). Ocean level was directly influenced by ice sheet advances and retreats, hence was lower during glacial advance, higher during glacial retreat. Higher ocean level directly affects river and stream depths and forms lakes by raising the general watertable level. It seems apparent then that cyclical periods of wetness and dryness not only affected vegetation richness, but also determined land surface availability for faunal and floral occupation, and distance between blocks of land.

Evidence from Rio Tarumã Mirim near Manaus suggests alternation of two types of inundation in that area, flooding and watertable rise, over the last million years (Irion & Adis 1979). In the last 100,000 years, three major inundation cycles occurred, each 10 to 30,000 years in duration, (see also Absy 1979, for cycles less than 10,000 years). During periods of low watertable, terra firme vegetation spread extensively, replacing inundation forest vegetation (Ellenberg, pers. comm.). Conversely and by extension, during periods of high watertable, terra firme vegetation zones were reduced because water occupied more surface area, and igapó vegetation (dependent on annual flooding) was reduced, limited in extent, and shifted up minor tributaries (which still had annual flooding) because larger water bodies are less affected by annual flooding than rivers, and water rise would be smaller. These larger water bodies were formed at the mouths of several major tributaries of Central Amazonia (Irion & Absy, MS). Moreau (1969) reports that similar lake formation events occurred in Africa.

The results of this alternation of wetness and dryness through time was the development of a mosaic of biotypes. During the wet end of the wet-dry gradient, vegetated "continental" islands and peninsulas were established, separated by varying widths and types of water bodies. It was within the confines of these islands and peninsulas during maximum wet periods that species populations may have accumulated divergent characteristics. The degree of divergence, of course, determines the outcome upon renewed contact with sister populations when the wet-dry gradient reverses and the islands again become contiguous. Full or partial speciation, hybridization, character displacement, swamping, extinctions, and coexistence are all possibilities. Results depend upon time, degree of isolation, and speciation.

Speciation Rate

This depends upon inherent genetic plasticity and external driving forces such as predation, competition, climatic changes, and population size. Flooding cycles have dramatic impact on inundation forest faunas. This is especially important when two kinds of flood patterns manifest themselves through time. In the greater Amazon region these flooding patterns may affect the biota in several ways. During high watertable and maximum wetness annual flooding would be minimized because the larger water bodies would be essentially lakes that buffer flooding, major shore lines would be more stable, and the associated flora and fauna would be selected toward species without flood response, while flood-response species would shift up smaller streams. During periods of medium wetness, annual flooding would raise river levels, change shore lines dramatically, and force selection of a biota which responds in some way to elimination or submersion of the soil. During periods of low water-
table and maximum aridity, flooding would again decrease due to lack of water at tributaries and again the biota would be composed of species that are nonresponsive to flooding. Since dramatic climatic changes, which would account for flooding patterns, can come about within a few hundred years (as shown by Absy in this volume), stabilize, then last several thousand years, there would be periods that would favor lakeshore species, then inundation forest species, then riparian species. Critical here is that the biota must change its balance often as a result of these perturbations. Van der Hammen's observation (this volume) of a dry period 20,000 years ago matches that of Irion and Adis for a Rio Negro site. If we liberally expand Absy's minor short cycles with major long cycles, which seems to be the pattern of the Pleistocene in the north, we perhaps can deduce, for purposes of this scenario, major and minor flooding patterns through time with associated faunal and floral shifts.

But what about annual flooding and its effect on the biota? What alternatives are available to terrestrial organisms when flooding occurs 5 to 6 months a year? Organisms may either 1) acquire adaptations for remaining in flooded terrestrial areas, 2) disperse to dry terrestrial areas, 3) disperse to dry canopy areas, or 4) do a combination of these things. Adis (1977, 1979) and Beck (1976) showed that the flightless terrestrial arthropod fauna of the igapó compensates for loss of terrestrial habitat in two ways: 1) dispersion toward the canopy at onset of high water or early rainy season with severe population losses, then recolonization of the soil and reproductive cycles during low water; 2) dormancy in the inundated soil in adult or egg stage with development and/or reproduction during the low water season. Additional evidence gathered by Beck (1972, 1976) and Irmmler (1976, 1978) showed that no horizontal mass migration of flightless arthropods takes place prior to inundation, but they did not show that flying forms such as carabid beetles do not move to the terra firme forests through the air. There is evidence that movement away from waterside into dryer habitats does occur in the north, with hibernation or aestivation occurring away from waterside. It is very probable that tropical forms can do the same, and it is known that carabids of wetlands are very active fliers.

At high water there is an increased number of species found in the subcanopy, and this increase lasts for several months (Adis 1979). This may also be true of adjacent terra firme forests or other biotypes. Additional data will soon be forthcoming from a program of seasonal fogging of Amazonian forest canopies to sample the entire arthropod fauna. This has already been done in Panama (Erwin & Scott 1980).

The terrestrial fauna of carabid beetles which are forced into the canopy or into the soil during high water are less adapted than the native species and thus may be at a disadvantage (see Erwin 1978, 1979b for a discussion of arboreal adaptations). It seems to us that this forcing together of terrestrial and canopy faunas would result in intense competition and predation and, through time, evolution of terrestrial species toward arboreal existence would occur. Of course, other species would be eliminated.

Annual flooding cycles with induced species-mixing overlain by major climatic/flooding perturbations perhaps every 10-30,000 years, which reduce flooding but dissect the available biotopes, must put tremendous pressures on the biota through time. In fact, it seems that long-term stability of local biotopes is not possible except perhaps those at standing water margins. Other biotopes would be in constant expansion/contraction and shifting from one place to another or being replaced by other climate-controlled vegetative types.

Provided with continually disturbed habitats (in a geologic time frame) and isolation of populations for cycles of 10-30,000 years, species with multivoltine or short-term breeding cycles may achieve suf-
sufficient interpopulational divergence that speciation may occur before renewed contact. Haffer (1969, 1974) suggested rapid reproductive rates for avian species. Certain birds appear to have speciated in less than 30,000 years. Certain groups of carabid beetles appear to exhibit the same phenomenon judging from the numerous and closely related species (Demetrida in New Guinea, Darlington 1968; Agra in the Neotropics, Erwin 1978; and possibly Paratychys, Platynus, and Lebia). Paarmann (1977) showed that carabids in "permanently humid biotopes" such as tropical wetlands have nondormant gonads, indicating that they are continuous breeders, or at least have that potential.

Vagility

Few appropriate data have been gathered on vagility of tropical organisms. Some birds (Haffer 1974) are known not to leave the deep forest and fly across rivers. The carabid genus Agra (fig. 19.8) which is a highly diverse canopy group with perhaps 1,000+ species in the neotropical region (Erwin 1978) has species confined to very small geographical areas even though these beetles are excellent fliers. No species are cosmopolitan and very few have ranges more than a few 10s or 100s of kilometers. In comparison with many other carabid species whose members are highly vagile dispersants, (Erwin 1979a) these Agra species appear to be restricted in their vagility.

In mammals, such as the Amazonian saddleback tamarin, races have their geographic boundaries limited to river systems and maintain differences even though distinct populations are within sight of each other across fairly narrow water bodies (Hershkovitz 1977). Whether this is due to low vagility, as it seems, or to other factors remains to be tested.

Given an ecosystem that is constantly shifting its floristic elements due to climate, and that these elements are being continuously dissected by floodwaters of varying widths, it would seem that species vagility is a crucial factor in sorting out and isolating gene pools. Thus small barriers may be highly disruptive to populations of individuals with low vagility. The maintenance of these barriers long enough for rapidly evolving species may be the key to tropical species richness. It is necessary now to determine vagility of Amazonian species, extent of historical flood patterns in the area and their persistence, and breeding cycles as an indicator of potential speciation rate.

Summary

In summary, flooding cycles, both annual and long-term working simultaneously, have rendered the Amazon basin riverine system a giant "disturbed" habitat. Alterna-
tion of riverside habitats on a 10–30,000 year cycle, sequencing from lake shore to inundation forest to riparian biotopes and back again, provides a driving force that promotes intense selection on riverine biotas which never become stabilized. The biota responds to the disturbance by active speciation, vicariant relationships being established among elements on “continental islands.” The intense dissection of the basin by water bodies establishes barriers, over which the majority of the biota members cannot cross (especially at high water table and maximum wetness) because of low powers of vagility. Climate mildness at low water table and intense competition and predation promotes rapid speciation, especially along the igapó and várzea where flooding mixes terrestrial and canopy biotas together during half the year. This mixing mechanism may explain why and how carabid beetles became adapted to canopy life in the tropics; dispersion due to flooding is the driving force which initiates canopy-oriented and forest-oriented taxon pulses (see below).

What is needed now to test these ideas are 1) data on patterns of flooding during the last several million years; 2) data on species vagility and speciation rates; 3) examination of vicariance patterns within the biota; and 4) examination of adaptation of various lineages regarding flood response. In addition, data are needed to determine the long-term stability of standing water habitats. As mentioned at the outset, we have just begun to look at the Amazonian carabid fauna in detail; there are many lines of investigation yet to be pursued.

The methods employed will be twofold. We already mentioned the genus *Agra* which has more than 1,000 species (fig. 19.8). A systematic and biogeographic study should provide a standard refuge data base of the type so well documented by many others for birds, plants, butterflies, etc. The advantage of looking at *Agra* is that these beetles are absolutely confined to forest canopies, where they are predaceous leaf runners, appear to have low powers of vagility, are incredibly diverse, are large enough to work with easily, and can be collected at lights or by fogging.

The second approach will be systematic fogging with pyrethrin of forest canopies of several types in different seasons and different flood stages to test the importance of mixing of biotas. This would be done concurrently with sampling the terrestrial faunas or in areas where terrestrial faunas are known already (Adis 1979). We will also look at life history strategies of the carabid biotas which mix to gain perspective on what happens under competition.

The carabid component of the canopy samples is the focus group because of their diversity in structure (which parallels the taxon pulse gradient mentioned earlier) their diversity in powers of vagility, and the fact that there are several thousand species now living in the Amazon basin, the majority of which are in the riverine and wetland biotopes.

The expectations of theory color perception to such a degree that new notions seldom arise from facts collected under the influence of old pictures of the world. New pictures must cast their influence before facts can be seen in different perspective.


References


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