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GEOMORFOLOGIA E HERANÇAS BIOGEOGRÁFICAS: UMA VISÃO INTERDISCIPLINAR COM BASE NA TEORIA DOS REFÚGIOS DE AZIZ AB'SABER

GEOMORPHOLOGY AND BIOGEOGRAPHICAL LEGACIES: AN INTERDISCIPLINARY VIEW BASED ON AZIZ AB'SÁBER'S REFUGE THEORY

GÉOMORPHOLOGIE ET HÉRITAGES BIOGÉOGRAPHIQUES: UNE VISION INTERDISCIPLINAIRE BASÉE SUR LA THÉORIE DES REFUGES D'AZIZ AB'SÁBER

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1. INTRODUÇÃO

A busca pela reconstituição das paisagens na superfície terrestre tem sido uma tarefa hercúlea para diversos pesquisadores das geociências. Compreender quais etapas são mais importantes que outras é um verdadeiro quebra-cabeça científico. Quase sempre nos deparamos com processos complexos na evolução e manutenção dos sistemas ambientais, em verdadeiro equilíbrio entre ecossistemas e geossistemas.

Se hoje a incumbência é árdua, no passado recente era ainda mais. Nesse contexto, cabe ressaltar o trabalho do Professor Aziz Ab'Saber, que durante muitos anos trabalhou no desenvolvimento e aplicação da Teoria dos Refúgios e seus desdobramentos para a ciência geográfica. O artigo intitulado *Ice-Age Forest Refuges And Evolution In The Neotropics: Correlation Of Paleoclimatological, Geomorphological And Pedological Data With Modern Biological Endemism*, de autoria dos Professores Keith S. Brown Jr. e Aziz Nacib Ab'Sáber, revela caminhos para a compreensão e possibilidades de aplicação da referida teoria em diversas áreas do conhecimento.

Os autores apresentam a Teoria dos Refúgios, com breve revisão bibliográfica e mapas que têm por objetivo identificar as áreas que serviram de verdadeiros santuários para a fauna e flora em períodos de clima seco, com expansão da semiaridez e diminuição significativa das precipitações pluviométricas em tempos recentes da nossa história geológica.

Essa fase marca um período importante na trajetória do planeta, caracterizado pelas variações climáticas do Quaternário, ou seja, os últimos 2,58 milhões de anos, momento em que o gelo e a neve desempenharam papel de destaque nas alterações da paisagem. As glaciações, com períodos em torno de 100 mil anos de duração, alternavam-se com fases mais quentes e mais curtas, em torno de 20 mil anos, os interglaciais.

Nas fases glaciais, destaca-se o último grande registro, conhecido como fase Würm-

Wisconsin superior (entre 23 e 13 mil anos antes do presente), quando o nível do oceano estava cerca de 100 metros abaixo do nível atual. Nesse cenário, as condições de semiaridez predominavam sobre grande parte do continente sul-americano, com retração das florestas e diminuição progressiva da oferta de alimentos e umidade. Momento propício para a expansão da caatinga e retração das florestas pluviais. Ainda assim, algumas áreas resistiam às condições desfavoráveis e mantinham parte da vegetação de grande porte, formando "ilhas" que se tornaram verdadeiros refúgios para a biodiversidade.

Nos períodos interglaciais, as condições de pluviosidade favoráveis retornavam e as florestas voltavam a se expandir, com a consequente coalescência dessas áreas. Essa alternância provocava uma explosão de vida, com aumento da biodiversidade nas áreas de florestas. Esses registros foram estudados com base em espécies de aves, borboletas e répteis, como abordado no artigo.

Essa breve descrição, que pode ser apreciada em detalhes com a leitura do texto, mostra a riqueza na interpretação e os impactos que a paisagem do território sul-americano conheceu durante o Quaternário. Embora haja atualização dos dados e técnicas recentes de datação e melhor conhecimento desse período, o tema ainda abre importante debate na comunidade científica. De forma breve, gostaria de tecer comentários relativos à importância para a geomorfologia e biogeografia.

2. DA GEOMORFOLOGIA A BIOGEOGRAFIA: PERSPECTIVAS PARA A INTERDISCIPLINARIDADE

Sem entrar nas condições de fragilidade da discussão e do modelo proposto pelos autores, é importante compreender o impacto no desenvolvimento e aprimoramento do conhecimento sobre a superfície terrestre.

Do ponto de vista geomorfológico, a compreensão da paisagem por interferência de elementos de maior ou menor aridez é fundamental. Embora o foco seja a expansão e retração da cobertura vegetal, os processos erosivos são desencadeados por essas variações. Processos lineares e areolares dependem dessas interferências nos sistemas de erosão.

A importância da leitura da paisagem através das *stonelines* e essas primeiras interpretações foi fundamental para o desenvolvimento da geomorfologia, inicialmente voltada para os estudos do Quaternário.

Autores como Jean Tricart, além do próprio Aziz Ab'Saber, desenvolveram estudos que deram suporte para uma geomorfologia básica e aplicada, em diferentes naturezas e escalas. Foram trabalhos pioneiros na consolidação da geomorfologia enquanto ramo de destaque na Geografia Física. Não é por acaso que hoje a geomorfologia é um importante eixo e guia para a delimitação e estudos de análise ambiental, fundamentais para subsidiar trabalhos de planejamento e gestão ambiental.

Hoje, com a diversidade de estudos na geomorfologia, muitas pesquisas procuram desvendar não apenas se houve ou não processos erosivos em determinado período, isso já sabemos! Mas questões como: qual a intensidade? Quanto tempo durou? Qual foi a capacidade de incisão fluvial naquele intervalo de tempo? Quanto material foi transportado? Perguntas que enriquecem uma geomorfologia de base que procura reconstituir paisagens pretéritas. São esses trabalhos que dão suporte para os estudos de análise ambiental, com diferentes aplicações para a sociedade.

Outro aspecto relevante é a referência aos estudos dos elementos abióticos que deram suporte à interpretação dos refúgios na floresta amazônica, base para a espacialização dessas áreas. Mesmo com recursos tecnológicos limitados à época, os autores apresentaram mapas fundamentais para a sociedade. A interpretação com base em variáveis como geologia, geomorfologia e solos foi basilar para a correlação com os dados de flora e fauna.

O casamento entre Biologia e Geografia tem potencial para gerar frutos de grande valia para a população. Vale mencionar o esforço do Professor Adriano Figueiró na consolidação de uma Biogeografia ampla e aplicada na ciência geográfica. Geodiversidade e Biodiversidade, quando estudadas em conjunto, com métodos de integração e equipes interdisciplinares, geram grande potencial de resultados.

A importância que os estudos de geodiversidade têm desempenhado na geografia é animadora. Novas formas de compreender o significado abiótico têm gerado diversos artigos e maneiras de entender a paisagem. Ainda acredito que a biogeografia, com viés sistêmico, seja um caminho que pode gerar resultados ainda mais aplicáveis e com respostas mais efetivas à sociedade. O Professor Aziz Ab'Saber nos mostra esse esforço em diversos trabalhos.

Uma das contribuições dos estudos sobre refúgios que poderia ter desempenhado papel crucial durante os últimos trinta anos refere-se à criação de Unidades de Conservação. Embora o foco dos autores seja na floresta amazônica, não é difícil compreender a importância da biodiversidade presente nos diferentes biomas brasileiros.

Um bom exemplo é o bioma caatinga, que dentro de sua grande extensão apresenta enorme diversidade em relação à flora quando analisada em seus diferentes compartimentos geomorfológicos. Variáveis como topografia e solos podem mudar sensivelmente as espécies de uma área para outra. Assim, os sertões podem desempenhar um papel de riqueza da biodiversidade ainda pouco conhecido. O que aparentemente é uma grande área com traços de semiaridez, na verdade se mostra como um mosaico de sistemas ambientais com diferentes níveis de integração entre seus elementos.

A superfície terrestre é um conjunto de paisagens que carregam marcas de um passado recente e/ou antigo. Hoje já é possível compreender que essas heranças são do Quaternário, mas também podem ser de tempos mais antigos (Mesozoico, Paleozoico ou Proterozoico).

Entender a gênese desses espaços é um excelente primeiro passo para melhor preservar e manter bancos de biodiversidade no território brasileiro. Os espaços urbanos e os diferentes tipos de uso e ocupação do solo já interferem nessa dinâmica. Estamos preparados para enfrentar esses desafios?

3. CONSIDERAÇÕES FINAIS

O artigo analisado desempenha importante contribuição para os estudos integrados de análise da paisagem, mas nos lembra da importância da interpretação geomorfológica como subsídio para a compreensão da diversidade na superfície terrestre.

Assim, estudos de biogeografia em conjunto com a geomorfologia têm potencial para o melhor entendimento e intervenções voltadas à dinâmica ambiental em áreas de maior fragilidade. A extinção de espécies da fauna e flora tem nos tirado importantes fontes de estudos, além da possibilidade de preservação de espaços que têm sofrido com pressões sobre seus recursos naturais.

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ICE AGE FOREST REFUGES AND EVOLUTION IN THE NEOTROPICS: CORRELATION OF PALEOCLIMATOLOGICAL, GEOMORPHOLOGICAL AND PEDOLOGICAL DATA WITH MODERN BIOLOGICAL ENDEMISM

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This paper, which represents both a summary review and a presentation of new data, is dedicated to the Fifth International Symposium of the Association for Tropical Biology, February 8-13, 1979. It is hoped that the broad data-sets which are summarized and correlated here may be amply debated at the Symposium, and may come to be useful in different fields of biological and geographical research, and their application in landuse planning.

The action of paleoecological forest refuges in the Neotropics was suggested as early as 19481, in analogy with northern hemisphere studies2 to help explain the paradoxically complex geographical patterns of evolution discovered within the superficially homogeneous Neotropical forest biome. Especially since the publica- tion of Haffer's paper analyzing speciation in Amazonian forest birds3, many biologists have turned their attention to the correlation of present-day distribution patterns of forest organisms with postulated past "refugia" in the Neotropics4. It has become fashionable to refer to one of the various available "refuge" models in any biogeo- graphically oriented systematic revision, genetic study, or evolutionary discussion involving forest organ- isms occurring in tropical America. These "refuge" models have in some cases been derived, wholly or in part, from modern biological data (species and subspecies endemism, or even species rich- ness). Paleoecological forest refuges, however, were largely determined by climate, substrate, and other geoscientific factors. An independent model for biological correlation needs to be derived from geoscientific data, especially paleoclimate, geo- morphology and pedology.

In this paper, we bring together new and published data which lead to the mapping of (1) probable areas of paleoecological forest refuges during the most recent glacial period (three geo- scientific data-sets, Figs 1, 3 and 4); and (2) de- fined areas of high biotic endemism today (four biogeographical data-sets, two as quantitative iso- line maps of concentrations of endemic taxa, Figs 7-9). The maps show a high degree of congruence (Figs 10-11); this implies a reasonable correlation between past climatic variations and present-day distribution patterns of differentiated plants and animals, without however proving causality. Both the isolated maps and the correlations should be useful in modern research and land planning in the Neotropics.

We have been stimulated to bring together these data-sets and to emphasize their correlation, by the intensity of the current debate about Neotropical forest "refuges". Some of this debate is based on misunderstandings about the geoscien- tific and biological data-sets, or on exaggerated use of limited data; some derives from improper use of important terms, including "refuge" itself, which we try to define below. Further debate revolves around theoretical aspects related to past and present in- fluences on the evolution of biological communi- ties; we will adopt a synthetic position here. Our analysis of available data indicates that some as- pects (such as biotic endemism) seem to correlate better with past climatic changes, while others (such as species richness) are better correlated to present ecological conditions.

Some biogeographers such as Croizat5 have adopted a skeptical position towards any action of Quaternary refuges in evolution, preferring to re- late the majority of geographical patterns in biotas ("generalized tracks") to tectonic changes in the earth's surface in the more distant past. Recent cli- matic changes would thus play a very minor role, mostly differentiations at the population level. At the other extreme, population biologists6 and systematists7 correctly noting that species differentiation can take place without the strict allopatry which is a premise of the "refuge model" have also questioned the relevance of paleoecological refuges to modern biological patterns. They suggest that the patterns of differentiation observed in plants and animals could be accounted for by simple se- lection gradients along presently observable eco- logical clines, related to habitat topographical, or edaphic barriers, local disruptive selection by biotic elements, or gradual modifications of climate and biotic communities. The superficial homogeneity of many continental Neotropical forests belies a bewildering array of soil mosaics8, microclimates9, coevolved subsystems of closely associated organ- isms10, and selective pressures on individual populations. These conditions could be sufficiently variable through time and space to explain the subdivision of species into geographical differentiates, correlated across taxomonic groups. The data analyzed here indicate that many present-day patterns may indeed be related to verifiable geographic variation in modern environments.

DEFINITION AND ACTION OF ECOLOGICAL REFUGES

One current concept of Neotropical refuges is that they were homogeneous islands of dense humid forest, isolated by broad expanses of scrub and savanna. This idea is refuted by the presently observed very fine mosaics of soils and vegetation in the continental Neotropics. We believe that a statistical definition is necessary11. We regard an ecological refuge in any time, past or present, as a region in which there exists sufficient continuity of favorable climate, soils, topography and vegetation to maintain the integration of formerly more widespread landscapes and biotas. This makes the preservation of organisms associated with these conditions more probable than their extinction. In an ecological refuge, populations are permitted to evolve under diverse environmental pressures and in accord with their respective genetic plasticities. This may lead to divergence of theses populations from others, formerly contiguous but now effec- tively separated by regions in which disintegration and discontinuity characterize the physical and bi- otic environments. In these interrefugial regions, extinction is a more probable fate than preserva- tion for the majority of the same populations12 .

The evidence for the existence of forest refuges of this sort in the Neotropics during the late Pleistocene is abundant, in rocks, soils, climate, geomorphology13, and palynology (study of fossil- ized pollen in geological strata)14. In essence, the debate revolves around their location, character- istics, and especially their effects (if any) on the presently observed parallel patterns of evolution in plants and animals.

Independent biological data-sets, collected for forest organisms with fundamentally different regimes of selection on the characters used in their taxonomy, have suggested very similar areas as important in recent differentiation15. However, this does not distinguish whether the plants and animals were in fact all confined together in forest refuges in the past, or are intimately tied up in present-day ecological units, evolving in harmony as a result of similar, though often imperceptible barriers to random gene exchange16. Both of these alternatives are probably valid in the different cases which have been studied, and they are not mutu- ally exclusive.

It might be possible to investigate the influ- ence of past refuges on present distributions by ex- amination of the coincidence of the presumed posi- tions of paleoecological forest refuges (determined exclusively by paleoclimatological, geological, geomorphological, pedological and palynological studies) with present regions of strongly differen- tiated biotic communities. If indeed the refuges acted in a preponderant fashion in the evolution of these viscous biotas17, a large percentage of their less dispersive members (deep-forest plants and sedentary animals) should still be found today in characteristic and taxonomically distinct associa- tions in the general regions in which they evolved in the past. Indeed, this is what has led biologists to propose "refuges" based in large part on modern species distributions. Such proposals should not be confused with paleoecological refuges based on geoscientific data. We suggest that biologists use terms such as "center of endemism" and "center of species diversity" to describe their data, since even "center of evolution" implies processes which elude direct scientific investigation. It seems best to re- strict the term "refuge" to proposals derived from geoscientific investigation and inference.

It seems clear that the fundamental bio- logical stocks during the late Pleistocene were not greatly different than those of today, or even those which reigned still farther into the past. Many species and genera (especially of plants, invertebrates, and smaller vertebrates) known from Tertiary fossils are very close in morphology and ecological associations to surviving modern equivalents18. However, the geo- graphical arrangement and dimensions, and the fine structure of functional ecological communities, must have been greatly modified during the expansion of semi-arid climates, setting the stage for divergent evolution of entire forest bi- otas as can be observed today in non-forest biotas isolated into patches by expanded humid forests19. The rapidity of species and system evolution observable in modern ecological refuges open vegetation islands within the Amazon forest20, humid pockets in dryer climate21 or man-made islands of primitive habitat22 implies that geographical isolation is indeed a strong promotor of biological diversification, which can even lead to speciation or dramatic morphological differen- tiation in the course of relatively few generations, depending upon intrinsic, populational, and en- vironmental factors for each species in each lo- cality.

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LOCATION OF PALEOECOLOGICAL FOREST REFUGES

Climatic patterns have changed, sometimes rapidly a]nd usually unpredictably, in historical times23. Just as these changes have repeatedly caught man off his guard and caused massive famine, migrations, or cultural evolutions24, so they also must have had profound and similar ef- fects on plants and animals in prehistoric times. The harsh cold, dry spell between 13,000 and 20,000 years B.P., which terminated the Würm- Wisconsin glacial period25 and plunged much of the northern hemisphere into icebox conditions, had great effects on tropical humid forests as well. This period has recently been defined by data from palynology26, geomorphology27, and deep-sea sedi- ments28. The CLIMAP team's determination of boundary conditions for 18,000 years ago and the resulting simulation of the global climate for July-August in that period29, together with work in Brazil30 provide an adequate picture of the basic weather patterns and ocean currents in the Neotropics during this rigorous time for tropical forest organism. The summary of these conditions, shown in Figure 1, represents the driving force for the formation of ecological refuges of humid forest in the Neotropics, resulting from reduced rainfall and greatly lowered continental temperatures.

The ecological effects of this climate were mediated by the complex compartmentalization of the terrain in Tropical America. To a first order of approximation, the relief of the South American continent then was probably very similar to that of today; minor changes due to neotectonics, epeiro- genesis and continental flexion are probably much less important than the 90 m difference in sea level31 in determination of the relations between the paleospaces and today's landscapes. Figure 1 thus reflects a coastline determined by the lowered sea-level, and shows rainfall as suggested by the prevailing currents, winds and temperatures at that past time, interacting with present-day topography. It represents a qualitative paleoclimatological data- set, which may be used in the identification of fa- vorable areas for the maintenance of integrated tropical forest landscapes and biotas.

Comparison of the rainfall patterns sug- gested in Figure 1 with the present precipitation (Figure 2)32 shows that, while rain is more generally distributed today (especially in the northwestern Andes and the Amazon Basin), there also exist areas with a dryer climate today than in the regres- sive phase 18,000 years ago, in many cases linked to the shift of prevailing winds to more easterly (as in northern Venezuela and southeastern Pará). This implies that regions which show degraded forest or dryer climate in the present, were maintained in humid forest during the rigorous climatic episode an observation already made by Journaux33.

In regions where the forest was extensively compromised during the long dry spell, dramatic modifications in morphogenetic processes led to new factors in the evolution of the landscape. The traces of theses forces are easily observed today, as stone-lines in soils (gravel to boulder layers in sub-surface horizons), paleosols (laterites, paleopavements and other concretions in the subsoil), de- tritus fragments of previous laterites (including in piedmont regions) and truncated soil horizons. A wealth of geomorphological data, collected over the past twenty-two years34, has shown the presence of these signs of past semi-aridity in a wide variety of localities in tropical America, presently forested or not. These localities are concentrated in lower or flatter regions (depressions and plateaus), which represented exposed areas and corridors for the penetration or dryer climatic regimes. Three broad routes for the expansion of semi-aridity, indicated by geomorphological studies as well as observation of superficial formations and relict dry-adapted vegetation patches in presently forest-dominated habitats (Figure 3), were (1) the southeastern coast of Brazil, the Paraguay river valley, and the Bolivian piedmont region (extension of the Argentinian "monte"; (2) the Brazilian central plateau and much of the southern part of the Amazon Basin (extension of the northeastern "caatinga"); and (3) the northern Amazon and upper Orinoco Ba- sins (extension of the Colombian and Venezuelan "llanos"). There is ample evidence in the geomor- phological data that these three semi-arid domains coalesced broadly in the Amazon Basin35, Andean foothills, and Brazilian and Guianan shield areas, leaving moisture-dependent formations dramati- cally reduced in their extent (Figure 3). Even in the humid parts of the Amazon Basin, cerrado-like formations (today existing only as scattered relicts36) must have predominated in regions of poorer soils, leading to further reduction of habitats available to deep-forest species.

The depression of temperature over the con- tinental land-mass37 encouraged replacement ofinterior tropical forests by subtropical and tem- perate systems; the Patagonian steppes invaded the south-central depressions, Araucaria and sub- tropical forests together with more open forma- tions penetrated the Brazilian coastal and interior highlands to near 18º S., and south Andean clouds forests were probably extensively substituted by rocky deserts.

On the other hand, the absence of stone- lines or paleosols, and presence of favorable topography encouraging continuous precipitation (Figure 1), indicates persistence of humid tropical forest in a number of limited areas during the cooler, dryer, climatic episode. In the topographically very complex Brazilian shield, such humid areas were favored only on steep slopes exposed to prevailing moisture-laden winds for most of the year. These conditions existed in much of northeastern Brazil, on the Atlantic coast as well as in mountainous areas of the interior which faced northeastward. In southeastern Brazil, only a few favored middle elevations (400-800 m) of the coastal and interior mountains, and subcoastal valleys surrounded by steep mountains north of 23º S., could have maintained continuous humid tropical forest. In central Amazonia, a few salient though low areas of polyconvex slopes apparently intercepted enough moisture from the weakening sea breezes to en- hance the closely woven drainage system and conserve reasonable amounts of forest. Much of the ocean's evaporation would have condensed far to the west on the Andean foothills, from southern Colombia to northern Bolivia: but even these areas must have received far less pre- cipitation than today, as prevailing southerly dry winds38 would have greatly moderated the influ- ence of the moist northeasterly breezes. North of this region, extensive forests were maintained in the central Guianas and southeastern Venezuela, and in the coastal mountains of northern Vene- zuela, Trinidad and northern Colombia. The rain shadows created by each of these favored areas helped to enhance the dryness of their leeward depressions, and increase the distance between them and neighboring humid refuges.

Rivers arising from the Andean slopes and northern escarpments of the Brazilian shield, flowing rapidly to a lowered Atlantic ocean, would have conserved broad gallery forests in many parts of central Amazonia, important in the preserva- tion and dispersal of smaller forest organisms, though possibly not of entire systems39. North- western Peru, western Ecuador and western Co- lombia, Darién, and eastern Costa Rica probably maintained a warm humid climate very similar to that in the present, influenced by the warm equa- torial countercurrent.

The combined conclusions from the above paleoclimatological and geomorphological argu- ments are presented in Figure 340. The natural do- mains in this map, representing predominant and characteristic vegetation formations 13,000-18,000 years ago, are a more quantitative data-set giving evidence for the location of integrated systems in the past. Tropical forest areas on this map, as de- termined both by exclusion from dry or semi-arid domains and by evidence for higher precipitation, represent defined paleoecological refuges, as far as present data can establish their location and size.

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CONTRIBUTION OF EXPLORATORY SOIL MAPS

Tropical forest cover, independent of its taxonomic nature, combines with topography and climate to slowly produce and effectively conserve characteristic soils. In more level terrain, these are usually classified as fine-textured,mesotrophic lato- sols (FAO/UNESCO Ferralsols, USDA Oxisols), while in folded terrain they tend to be classified as structured or podzolized soils (FAO/UNESCO Orthic Acrisols and Luvisols USDA Ultisols and Alfisols) or Terra Roxa Estruturada (FAO/ UNESCO Nitosols). In contrast, sparse vegetation cover usually inhibits the formation of fertile, fine- textured deep soils, and leads to the degradation of such soils when formed by previous forest cover. Rapid removal of clay and nutrients gives coarse, infertile substrates; the prolonged action of wind and rain often leads to formation of pavements, or gravelly or pebbly surfaces, under more open veg- etation. The presence of remains of these surfaces as stone-lines in presently forest-covered latosols or podzolic soils is thus an excellent sign of the ab- sence of forest in such localities at some past time, often the last ice age41. Some types of presently forest-covered soils are too young to evaluate, in terms of continuous forest cover over many thousands of years (volcanic and alluvial soils, or shallow cam- bisols and lithosols). Fertile, fine-textured latosols and podzolized soils, however, may be regarded as good signs of long-term forest cover in the past, in the absence of stone-lines or other contraindica- tions.

Thereby, a further geoscientific represen- tation, complementary to that in Figure 3, can be derived by interpretation of exploratory soil maps of central and South America42. These maps were prepared with the aid of extensive ground work generalized to images obtained with remote sensing methods, correlating topography and veg- etation with characteristic soil types. They have a minimum contribution of biological data (only gross vegetation formations). Their possible disad- vantage resulting from imperfect soil/vegetation correspondence over small areas is compensated by their precision in representing integrated systems. The soil units on these maps, like the ecological refuges which they may indicate and probably helped to determine, are actually very fine mosaics, with sufficient dominance of particular soil types to permit integration of the accompanying vegeta- tion formation which in turn represent the integrated ecological systems.

In the interpretation, a strong elimina- tion was first applied. All regions where the maps showed dominant soil which are young (alluvial or recently volcanic), saline or allic, very sandy, organic, hidromorphic or plinthic, petric or stony, lateritic concretionary, strongly dystrophic, or char- acteristic of high altitudes, cold or dry climates, or open prairie, were considered as generally unfavor- able to an hypothesis of continuous tropical forest cover over the past 20,000 years. While this may have eliminated some areas in which forest could indeed have persisted, it permitted a dramatic reduction of the soil maps with definitive exclu- sion of most areas where tropical forest is or was strongly discouraged by physical factors, especially of the substrate. The next step was the inclusion of richer fine-textured tropical soils derived from parent rock with a chemical composition giving high natural fertility, independent of climatic con- ditions (diabase, besalts, some diorites and lime- stones), and of soils formed slowly on relatively stable surfaces under warm, humid conditions and subject to rapid degradation under sparse vegeta- tion (fine-textured and fertile latosols and pod- zolic soils). These soils are mapped in black on Figure 443. Closely related but less fertile soils, supporting a rich tropical forest on polyconvex slopes today, were then identified, and included as hatched in Figure 4. Also hatched are younger eu- trophic soils (cambisol and some lithosol mosaics) which are covered by tropical forest today; these probably supported continuous, even if small and renewing forest patches in the past, and continue to represent islands of rich forest biota today.

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LOCATION OF NEOTROPICAL FOREST CENTERS OF ENDEMISM

Henry walter Bates recognized the existence of many differentiated endemic biotas in the Am- azon forest, over 120 years ago44. He commented especially on the parallel variation in mimetic color-pattern of forest butterflies, as he went from area to area within the Amazon Basin. Modern studies, especially in interfluvial regions, have placed his observations on a quantitative base, and also permitted their generalization to many elemets of the Neotropical forest biota.

Two relatively well-known groups, birds and butterflies, have been investigated in depth in the search for Neotropical forest centers of endemism (concentrations of characteristic taxa in a limited geographical region). In one group, aposematic (warningly colored) mimetic butter- flies in the tribe Heliconiini and in the subfamily Ithomiinae45, a series of favorable circumstances has now permitted "topographical mapping" of isolines for endemism over the entire neotropical region. In these common and easily sampled spe- cies, the characters used in taxonomic description correspond to those selected in nature for protec- tion against predation on adults (size, color and

Details of the soil subunits judged as favorable, neutral, or un- favorable to the hypothesis of continuous forest cover in the past, on the basis of these criteria, are available from the authors, who are grateful for orientation and criticisms received from Igo Lepsch, A. Küpper, and D. Gifford. As our criteria were being developed, applied and mapped, D. Gifford independently observed that the same soil subunits identified as favorable or unfavorable by us were, in fact, conserving patches of forest or not, under a progressively less favorable climate regime in central Brazil.

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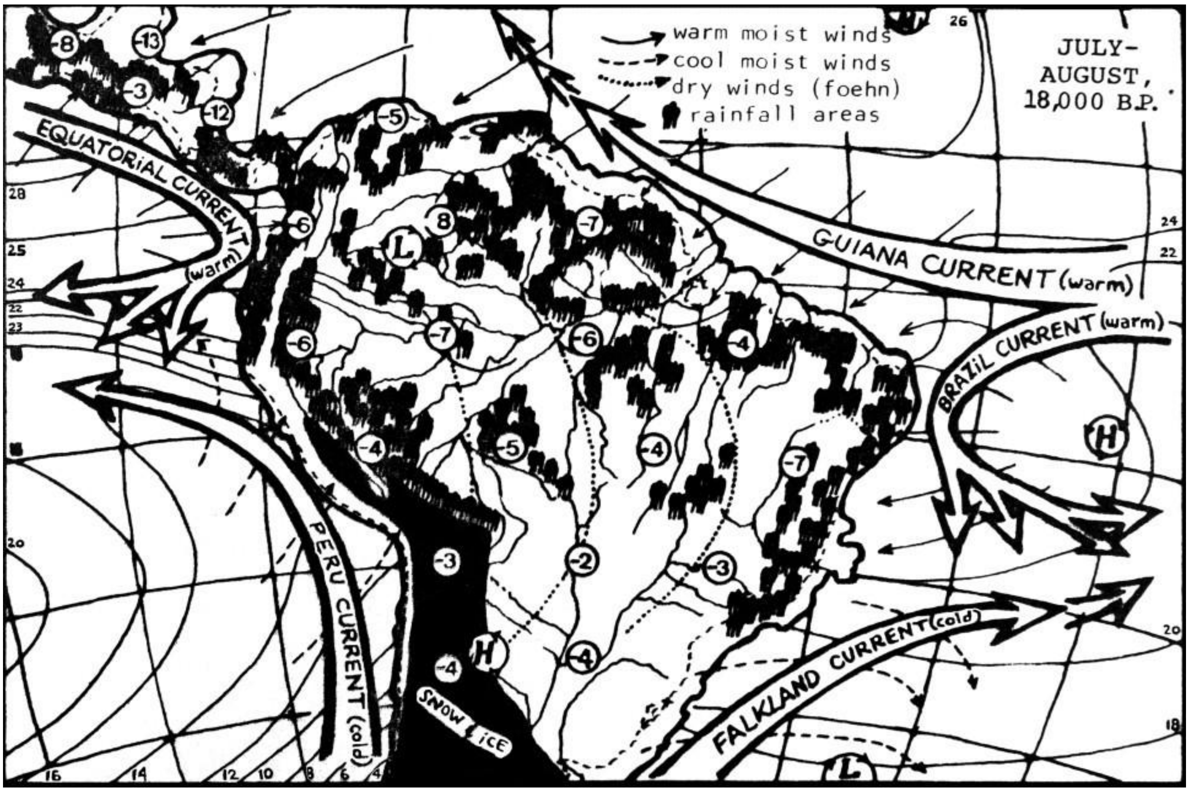

Figure 1. Predominant ocean currents, sea surface isotherms, pressure cells, dominant winds and continental temperature depressions (in na 8º x 10º grid) for July and August conditions during the peak of the last gla- cial episode, 18,000 yrs, B.P.1, and probable continental rainfall patterns resulting from interaction of these weather conditions with present-day topography. Continental outlines are determined by a 90 m lowering of sea level in relation to the present.

pattern behavior, habitat, choice of food-plant, and mimetic association). The organisms are readily located, evaluated and correlated with close relatives; they can also be tied into entire forest, subsystems of plants and animals with which they have coevolved[46]. The race diferences are determined by few genes, which in some species have been reasonably well studied[47], facilitating the linkage of ecological and evolutionary processes in the analysis. The systematics of the groups are difficult but not impossible, and recent revisions have placed the identification of conphyletic units (subspecies or species of recent common ancestry) on a

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Figure 2. Present-day isohyets (total annual precipitation) in the Neotropics1.

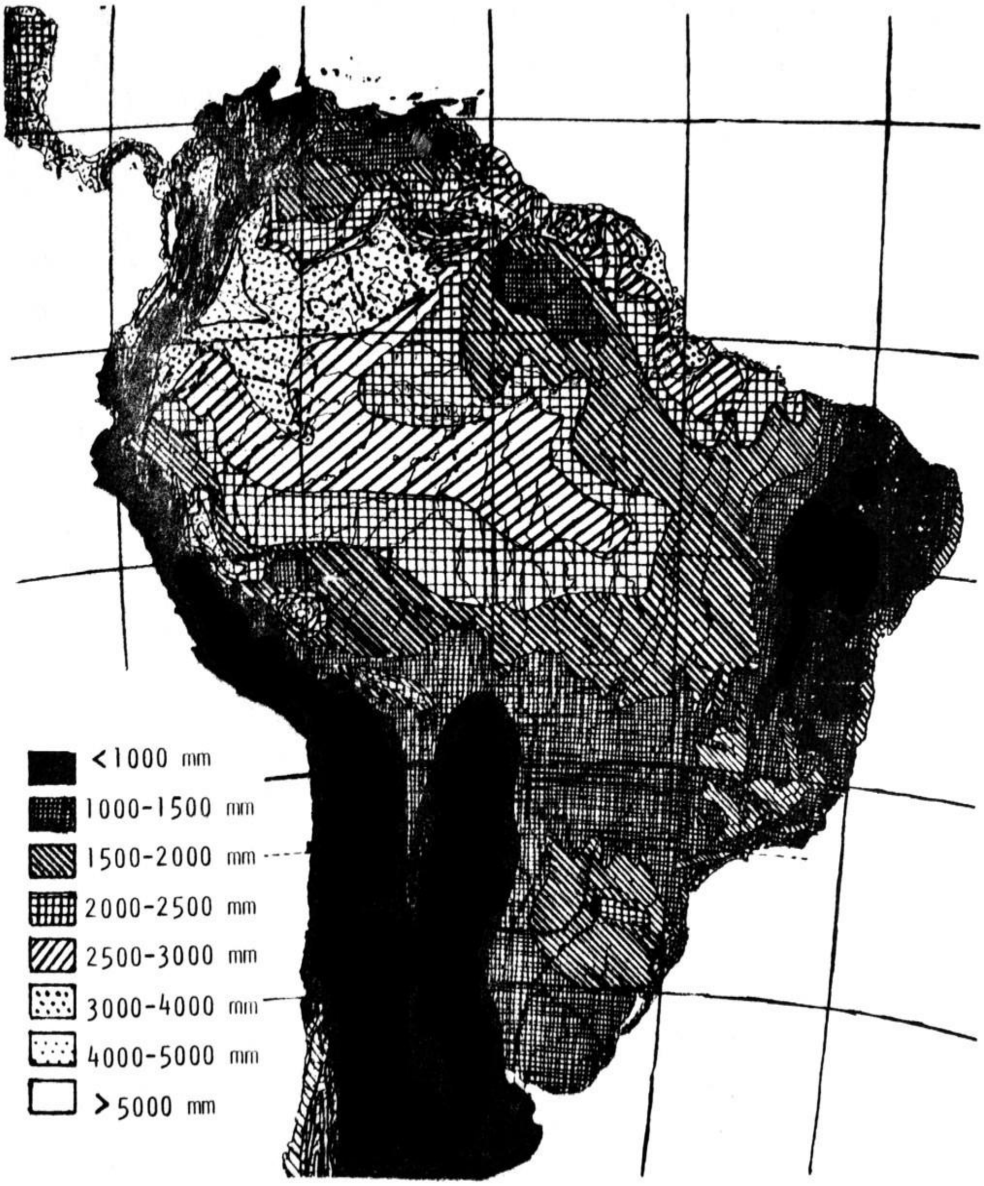


Figure 3. Natural domains, in which climate and morphological factors favored predominance of character- istic vegetation types, 13,000-18,000 years B.P.1.

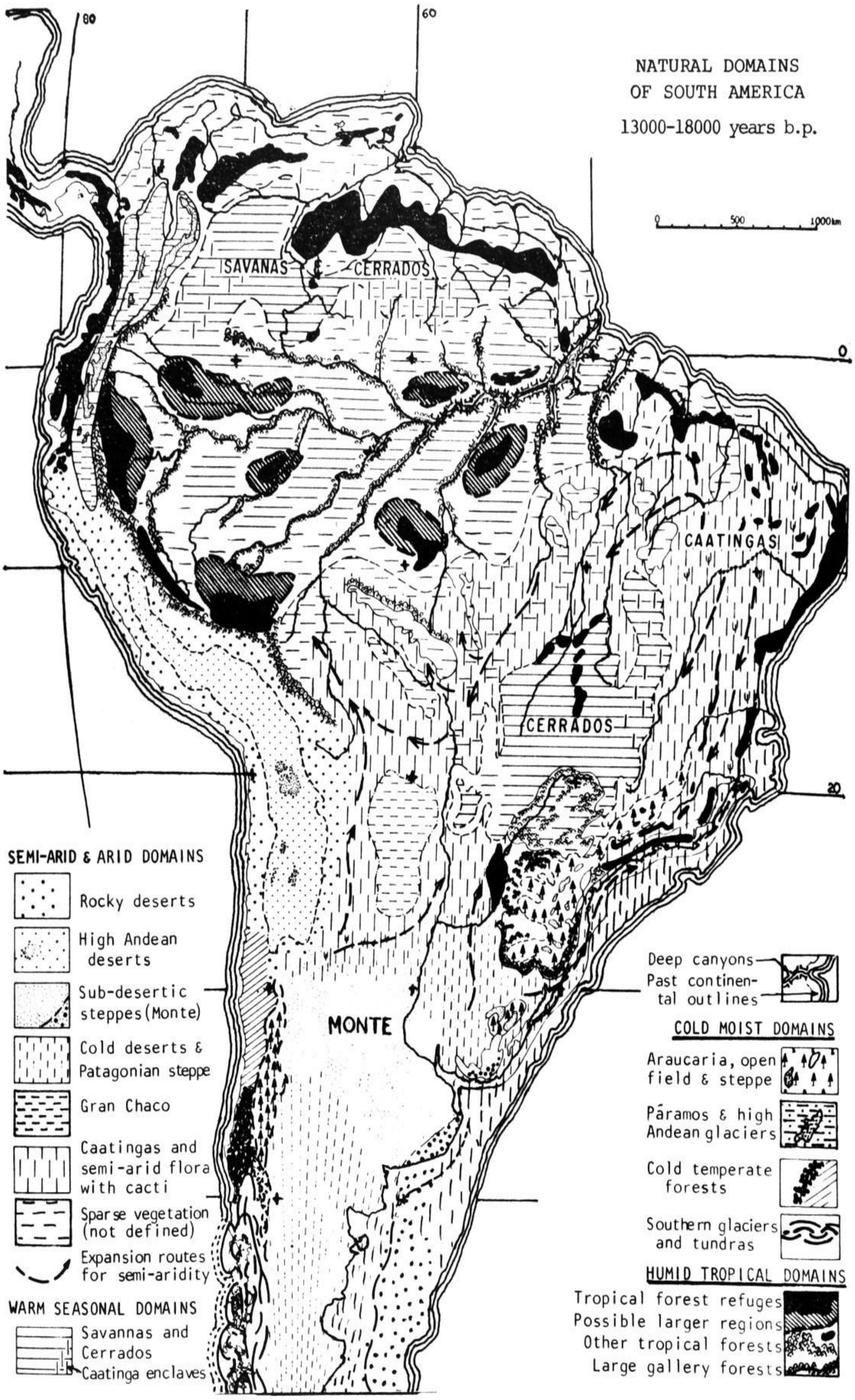
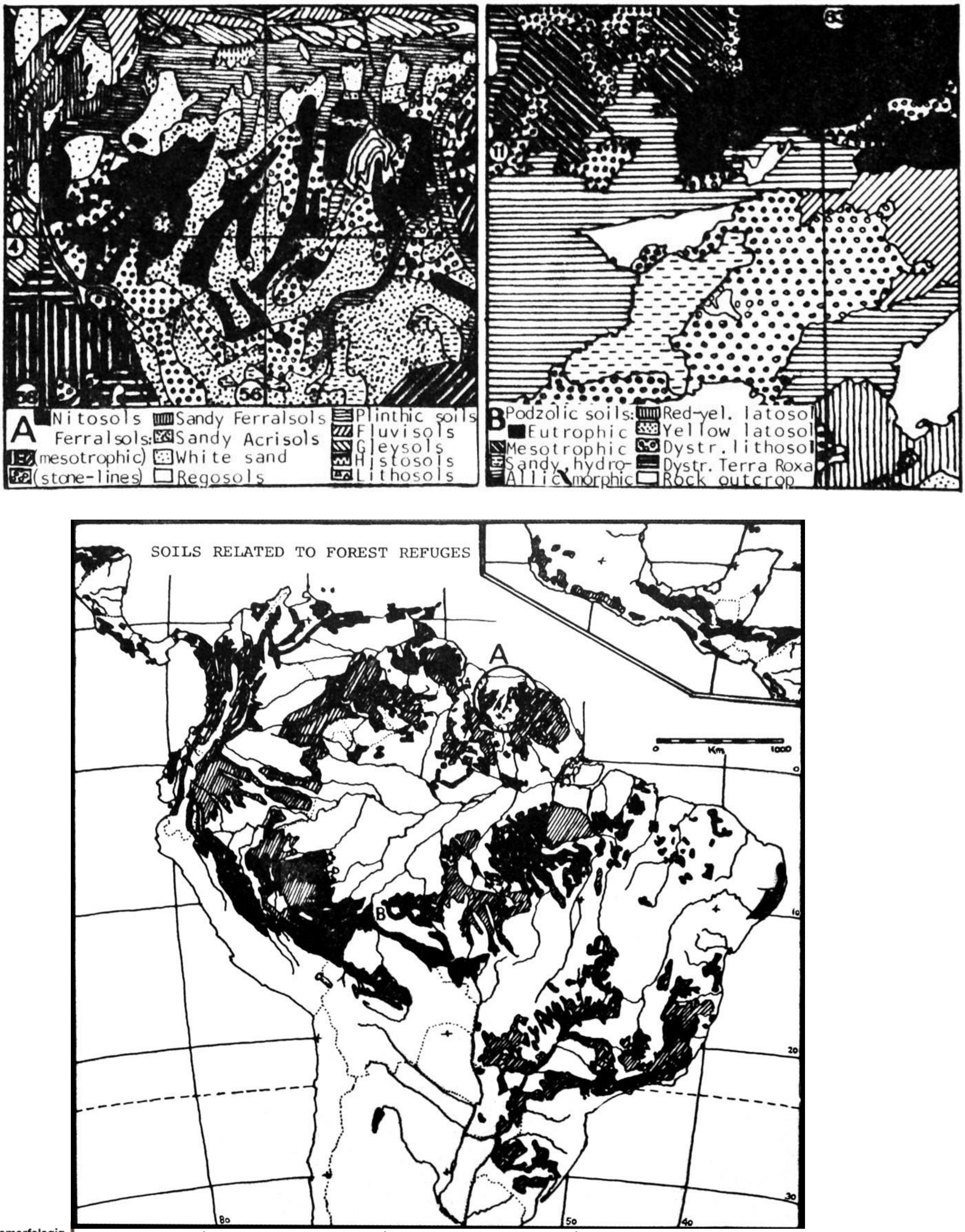


Figure 4 (previous page). Present-day soils of central and South America, classified as favorable (black) or acceptable (hatched) to an hypothesis of continuous forest cover over the last 20,000 years1. At bottom are shown details of encircled areas, A (Suriname)2 and B



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who are grateful for orientation and criticisms received from Igo Lepsch, A. Küpper, and D. Gifford. As our criteria were being developed, applied and mapped,

D. Gifford independently observed that the same soil subunits identified as favorable or unfavorable by us were, in fact, conserving patches of forest or not, under a progressively less favorable climate regime in central Brazil..

FAO/UNESCO, Mapa Mundial de Suelos (World Map of Soils), vol. 3 - México y America Central (UNESCO, Paris, 1976) and vol. 4 - America del Sur (UNESCO, Paris, 1971).

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Figure 5. Neotropical area coverage, providing data used in plotting quantitative isolines for endemism in forest butterflies (to november 1978).

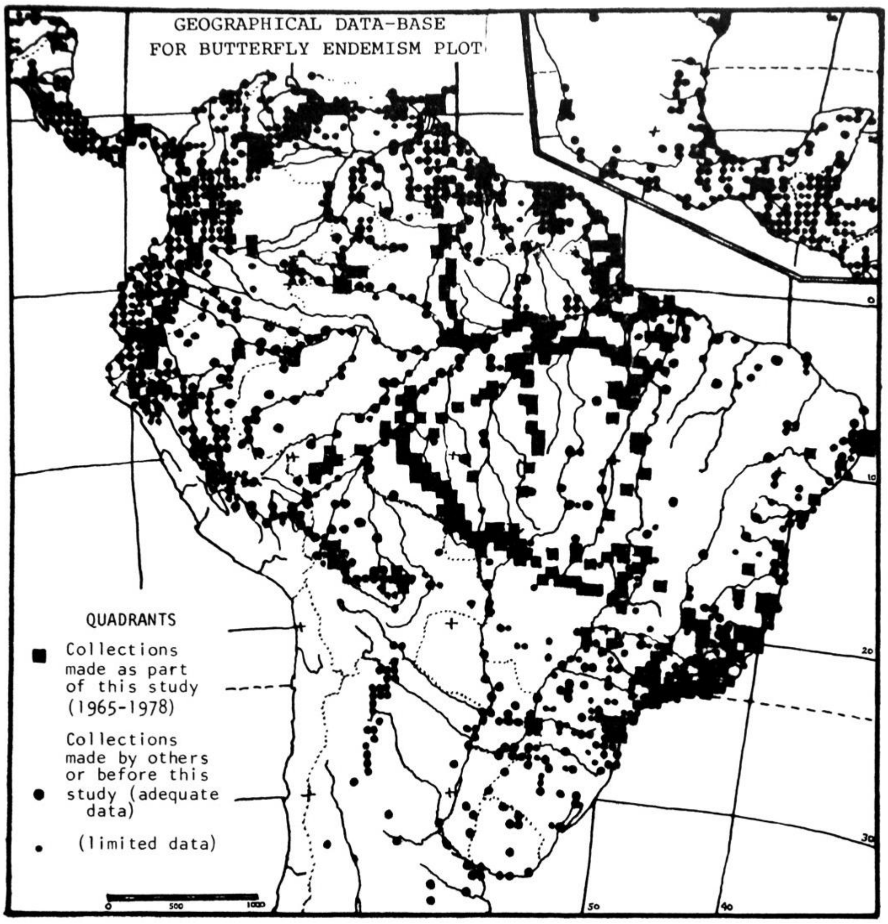
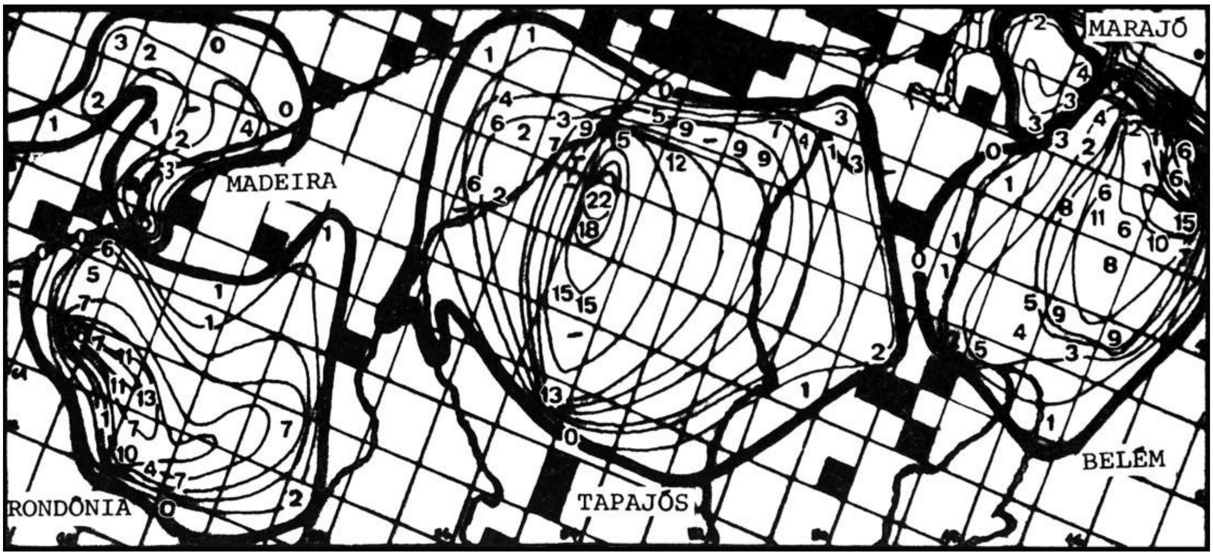


Figure 6. Representative isoline determination of five endemic centers in the Brazilian Amazon, from data on two groups of Neotropical forest butterflies.



Firm footing48; abundant biological information is also available49. The basic prerequisites for proper biogeo- graphical analysis (detailed taxonomic information, abundant geographical data, ecological knowledge)50, may thus be considered as satisfied for these butterflies (only fossils are still lacking).

During the past twelve years, extensive data on the biogeography and ecology of these forest insects has been obtained, in trips to all parts of tropical South America. Together with abundant museum data and literature reports, the biogeographical data-base (Figure 5) represents over a million individual records and 3,500 localities, in 1,500 of the 4,500 existing quadrants (30' x 30' of latitude and longitude51) of tropical forest between southern Texas and central Argentina. In the transformation of these data into a quantitative

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[66] 51, 76 (1975); 53, 104 (1977); , Biotropica, 10, 77 (1978); L.M. Cook, E. W. Thomason and A.M. Young, J. Anim. Ecol., 45: 851 (1976); A. Muyshondt, A. Young and A. Muyshondt Jr., J. N. Y. Ent. Soc., 81, 137 (1973); P. R. Ehrlich and L. E. Gilbert, Biotropica, 5, 69 (1973); H. Dunlap-Pianka, C. L. Boggs and

[67] L. E. Gilbert, Science, 197, 487 (1977); C. Papageorgis, Amer. Scient., 63, 522 (1975); T.E. Pliske, Environm. Entom., 4, 455 (1975); 4, 474 (l975); , Ann. Ent. Soc. Amer., 68, 935 (1975); J. A. Edgar, C. C. J. Culvenor and T. E. Pliske, J. Chem. Ecol., 2, 263 (1976); T.E. Pliske, J.A. Edgar and C. C. J. Culvenor, ibid., 2, 255 (1976); K.S. Brown, Jr. and J. Vasconcellos Neto, Biotropica, 8, 136 (1976).

[68] J. Haffer, Avian Speciation in South America (Publ. Nuttall Ornithol. Club n° 14, Cambridge, Mass., 1974).

[69] Vanzolini and N. Papavero, Índice dos Topônimos Contidos na Carta do Brasil 1: 1.000.000 do IBGE (FAPESP, Sao Paulo, 1968). This unit of about 3.000 Km² is not only convenient for mapping, but also congruent with the average dispersal characteristics of the organisms studied in this case.

Figure 7. Summary of isoline determinations of endemic centers for Neotropical forest butterflies (Heli- coniini and Ithomiinae; 119 species, 773 subspecies).

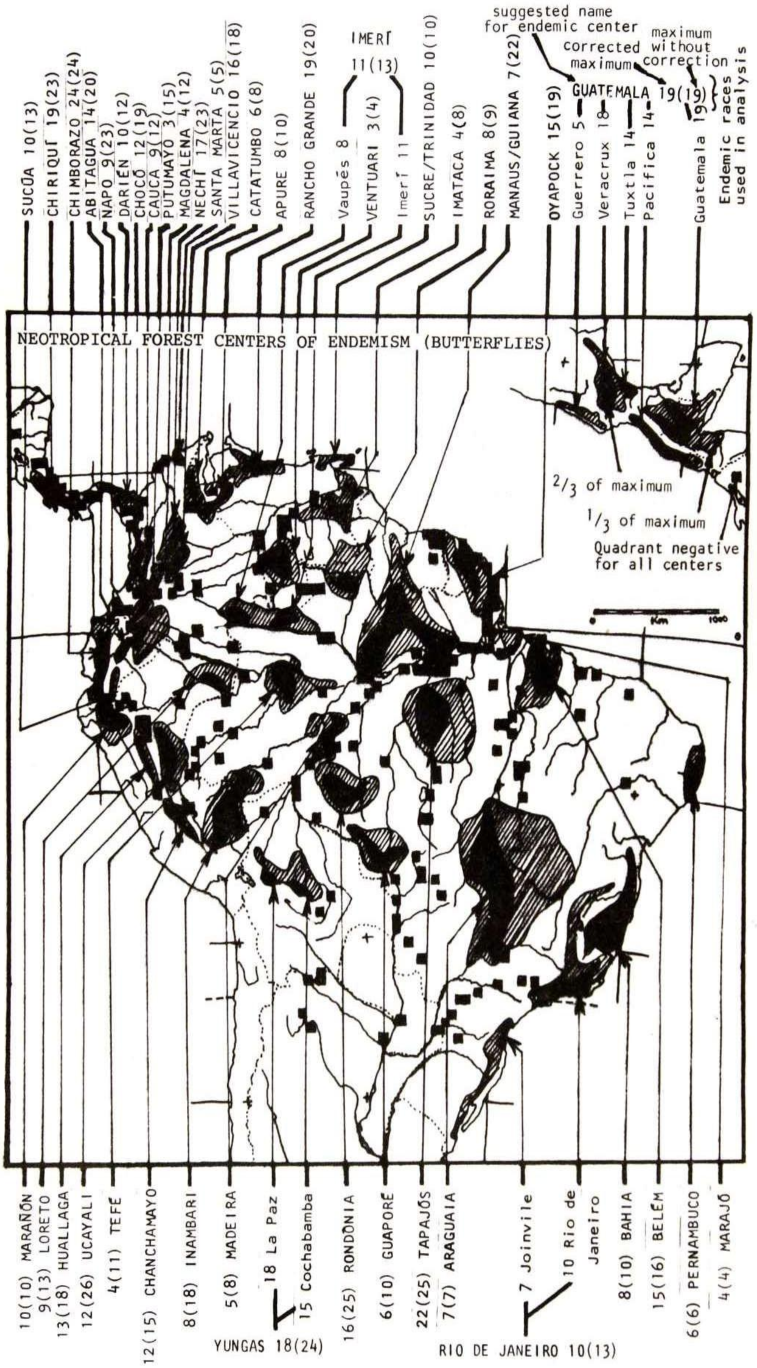
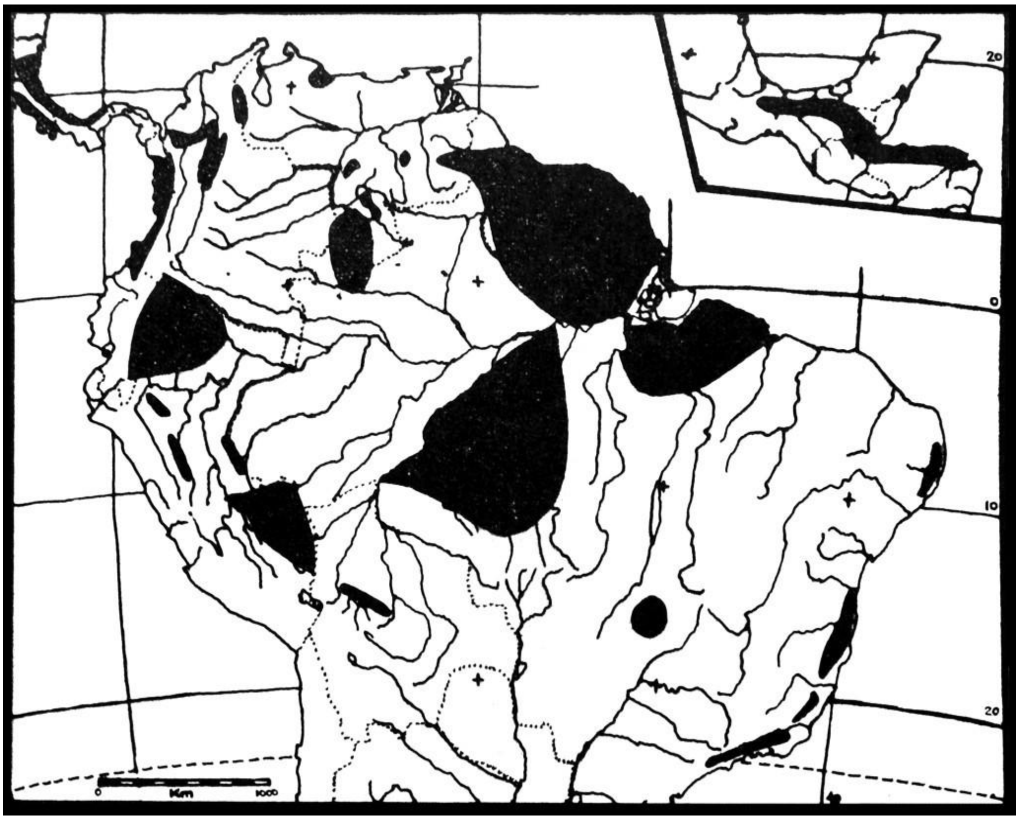


Figure 8. Endemic areas and additional refuges for Neotropical forest birds1.

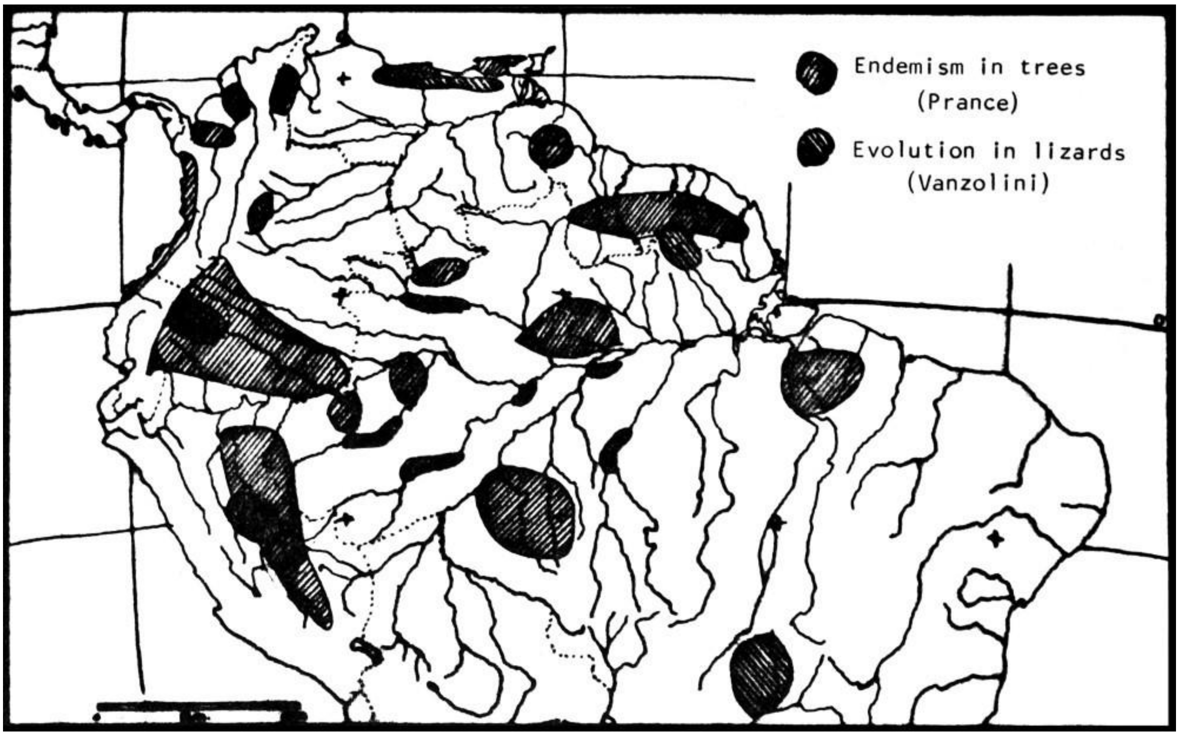


Map of centers of endemism, the species list for each quadrant was evaluated for organisms endemic to each geographical region (Rx) represented in the list. The "home endemic region" for each butterfly taxon, and general areas for endemism of many taxa, were determined by superimposition of range maps for the 119 species and 773 recognized subspecies used in the quantitative analysis. Presence of any signs of hybridiza- tion in the populations in the quadrant, involving subspecies or semi-species from different geographical regions, was indicated for all species. A quantitative estimate for relative degree of endemism, Ex, was then determined for each region represented on the quadrant list, by the expression.

$$Ex = \sum SRx - 2\sum HRy$$

Where SRx represents a taxon present and associated with the endemic region Rx, while HRy represents a taxon present, associated with another area of endemism Ry, and substituted in Rx by a conspecific race or closely related semi-species. Taxa associated with other regions (Ry) but not substituted by very close rela- tives in the fauna endemic to Rx were assigned a value of zero (neither adding to nor subtracting from the endemic value). Thereby, when hybridized populations or taxonomically very close entities from other re- gions (HRy) were present for more than half of the locally endemic taxa (SRx) on the quadrant list, the value

Figure 9. “Refuges” determined principally from biological data, representing endemic centers for four fami- lies of large forest trees1 and forest lizards2.



For endemism fell below zero. Maximum values (about 25) usually occurred in areas of minimum hybridiza- tion or mixing of taxa. The robustness of this program for endemism in these species was demonstrated by the virtual absence of quadrants positive for more than one region of endemism, and by the minimal change in calculated values for quadrants including representatives from several regions, upon addition of further records beyond a small workable number (usually a third to a half of the 20-30 species present)52.

The results of the plotting of quantitative endemic values for these butterflies are shown in Figure 6 (a detailed partial map) and 7 (a summary map for the entire Neotropical forest region)53. As with the paleoecological forest refuges (Figure 3), the centers of endemism shown in Figures 6 and 7 are subject to minor revision as more data becomes available (especially in the northern and western Brazilian Amazon). They represent, however, a well integrated picture of discontinuous endemic biotas, at least the butterflies analyzed and other organism in close harmony or coevolved relationship with them in the humid tropical forests54.

Quadrants with very little hybridization (mostly at the peripheries of the Neotropics, or near strong ecological barriers) simply increase in value for the principal (and often only) center of endemism represented, as the list becomes more complete. One endemic center is not represented in Figure 7; de- noted "Andes", it contains 11 analyzed races (9 of which are mimetic dark orange and black) which occupy a nearly continuous band at medium elevations (600-1.800m) on the eastern slopes of the Andes from southern Colombia to northern Bolivia, with concentrations in certain high valleys (upper Pastaza and Huallaga, Chanchamayo area) and some discernible N-S differentiation. Because the range of these subspecies is today very narrow in flat maps, most of the quadrants positive for the center are also positive for the nearest foothill endemic center.

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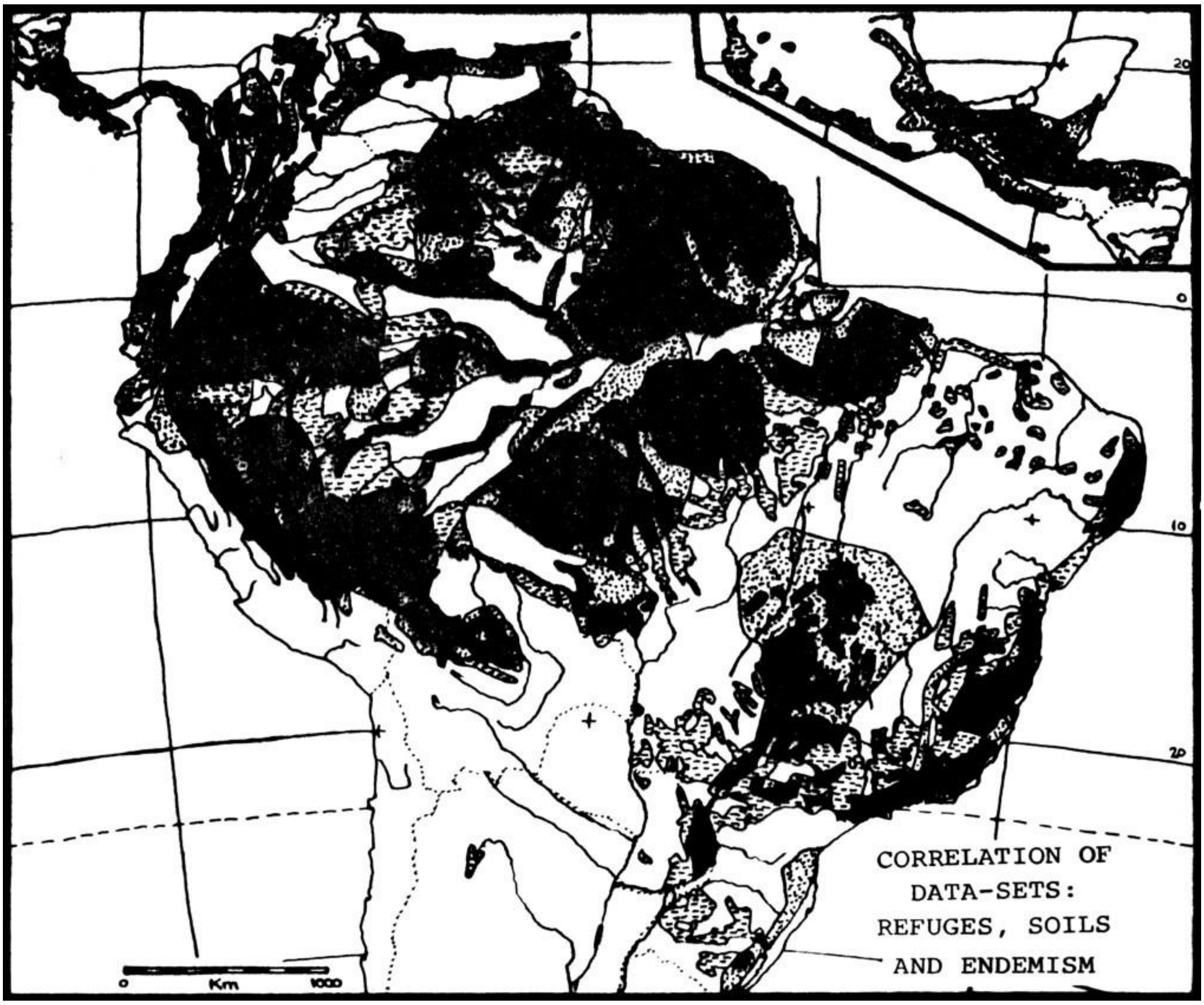
W.W.Benson, K.S.. Brown, Jr. and L.E. Gilbert, Evolution, 29, 659 (1976); L.E. Gilbert, Colloq. Intern, C.N.R.S., 265, 399 (1977); K.S. Brown, Jr., in Encontro Nacional sobre a Proteção da Fauna e Recursos Faunísticos, Brasília 1977 (IBDF, Brasília, 1978); W.W. Benson, Evolution, 32, 493-(1978); see also

Figure 10. Neotropical areas showing no indication for either paleoecological forest refuges or modern biological endemism in forest organisms (blank), or only indication of forest refuges from one data-set in Figures 3 or 4 (dashed) or only indication for endemism ia a single group of organisms (dotted).



Very recently, Haffer has published similar maps of quantitative isolines for endemism in birds, cov- ering five Colombian and Central American ("transandean") and six Amazonian centers55. He has also published maps of refuges for these organisms, incorporating geoscientific as well as biological data56. The central regions (>67%) of Haffer's endemic centers for forest birds, and his other refuges not yet published as isoline centers, are shown in Figure 8. A proposal for South American endemic centers ("as refuges") has also been advanced by Prance57 after analysis of differentiation in four families of slowly dispersedlarge forest trees58; these are shown in Figure 9, along with Vanzolini's "refuges"59 for quantitative differentiation

The families analyzed were Caryocaraceae, Chrysobalanaceae, Dichapetalaceae and lecythidaceae, all large forest trees, the last family including the very common Brazil Nut (Bertholletia excelsa), a tree which dominates (and thereby characterizes) many poorer-soil or marginal-climate parts of the Amazon Basin. A recent revision of the endemism map by Dr. Prance (personal communication), not yet published, gives only minor modifications when incorporated into the correlation (Figures 10 and 11), in all cases strengthening the level of superimposition of data-sets. This revision has been considered only in the area between the Tocantins and Xingu Rivers, which is eliminated in Figure 9 and in the correlation.

Figure 11. The results of summation by superimposition of data for the location of paleoecological forest refuges in the Neotropics (from Figures 3-4) and endemism in forest biotas today (from Figures 7-9). See explanation in text.

in lizards. While all three of these analyses represents smaller data-sets and fewer, more poorly differentiated species than is the case for the butterfly map, they derive from similar broad-scale geographical coverage, systematic revision, ecological knowledge of the organisms, and quantitative analysis of endemic patterns.

CORRELATION AND APPLICATION OF THE DATA

The data-sets mapped in Figure 3 and 4 (geoscientific evidence for paleoecological forest refuges) and 7, 8 and 9 (biological evidence for endemic plants and animals) may be regarded

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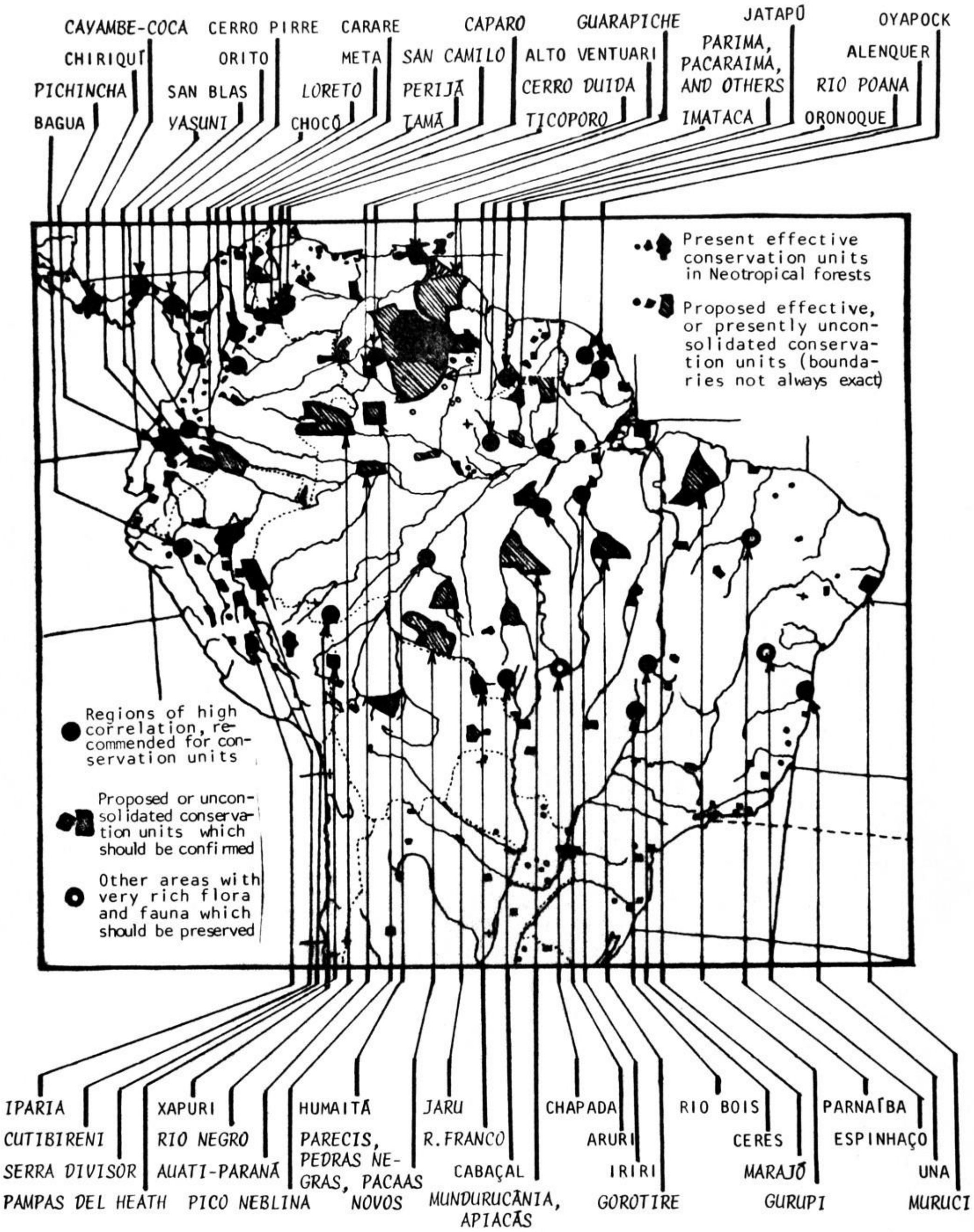
[70] P.E. Vanzolini and R. Rebouças-Spieker, Pap. Avulsos Zool., São Paulo, 29, 95 (1976).

[71] J. Haffer, Bonn. zool. Monogr., 7, pp. 42-64 (1975); , Bonn. zool.Beitr., 29, 38 (1978).

[72] See ref. 3 and J. Haffer, Avian Speciation in South America (Publ. Nuttall Ornithol. Club n° 14, Cambridge, Mass., 1974).See ref. 39

as reasonably in- dependent. They were not developed in collaboration, and they represent very different scientific disci- plines; on the biological side, they are derived from widely divergent groups of forest organisms (higher plants, invertebrates and vertebrates) with radically different ecological, evolutionary and dispersal pa- rameters. In an attempt to verify their level of correlation, all five figures were superimposed on a single map, using different-colored close shadings for the black areas in Figures 3, 4, 7 and 8, and open shadings for the hatched areas in figures 3, 4, 7 and 9, and the tree-symbol areas in Figure 3. The composite map led immediately to a definition of areas which received no consideration in any one of the seven data- sets; these occupy 38% of the 4,600 Neotropical quadrants (13,800,000 km²) which receive more than 1,000 mm of rain annually today (Figure 2). Although part of this 38% area is covered by dense tropical forest today, it possesses no known endemism in forest biotas, nor favorable substrate for tropical forest continuity, in periods of reduced precipitation. It is shown as white in Figure 10.

Figure 12. Present effective conservation units in the Neotropical forests (black), planned



Effective or pres- ently unconsolidated units (hatched); planned or unconsolidated areas which should be confirmed (hatched surrounded with heavy black, italicized names), and some suggested areas not presently included but merit- ing consideration on the basis of data in this paper (black circles, local names suggested). Three especially rich areas of transitional flora and fauna are also suggested areas not presently included but meriting con- sideration on the basis of data in this paper (black circles, local names suggested). Three especially rich areas of transitional flora and fauna are also suggested, as open circles.

A further 25% of the area appeared in only a single data-set (endemism in only one group of or- ganisms, dotted in Figure 10; or a single geoscien- tific evidence, dashed in Figure 10). This represents an over-all index of noncorrelation among the six data-sets. The noncorrelated area was divided by data-set and each part was compared with its total area. The part which "stood alone" averaged 19% varying between 2% (lizards) and 33% (soils). The vast majority of the noncorrelated soils are in areas which are subtropical or have a long dry season today; these may be regions in which climate and vegetation are less favorable to tropical forest organisms today than they were at some past time. Noncorrelated endemism data probably represent a part of the forest fauna which has been able to occupy more marginal habitats peripheral to the optimum centers (as in the Araguaia and Marañón regions).

The level of geographical correlation be- tween the data-sets was determined as follows: the black areas in Figures 3, 4, 7, 8 and 9 were assigned a value of 1, and hatched or tree-symbol areas, 0.5. Total possible sums were thereby 5 in South America (maximum possible 1 from each figure, since black and hatched areas are mutually exclu- sive); 4 in southern Central America (not covered in Fig. 9); and 3 in Mexico and Central America (absent also from Figure 3). India-ink was used to encircle areas on the multicolored composite map with more than 60% correlation (values of 3, 2.5 or 2, in relation to the maxima of 5, 4 and 3 in the three regions). These more highly correlated areas (appearing in at least three data-sets, virtually al- ways including both geoscientific and biological evidences) are shown in black on Figure 11. Additional areas with more than 40% correlation (values of 2, or 2.5; 1.5 or 2; and 1.5, respectively) were then discovered and encircled; these are shown as hatched in Figure 11.

The high overall degree of correlation which is apparent in Figures 10 and 11 suggests a strong geographical relationship between present-day endemic forest biotas and paleoecological forest refuges60. It does not prove that these biotas differentiated in such refuges. Nor does Figure 11 represent a universally applicable "refuge model" (perhaps Figure 3 is closer to this, for the partic- ular time period indicated). It might be called a "correlation model for biological differentiation in Neotropical forests". In this category, its predictive value (for presence of endemic plants and animals) has been extensively tested and in large part substantiated. Furthermore, both the data themselves and the correlation can be very useful in research and planning in the Neotropics.

In spite of the healthy diversity of concepts about recent Neotropical evolution which are cur- rently in debate, it is important, for a number of immediately applicable reasons, to establish an- swers to two key questions:

What are the geographical distributions of differentiated plant and animal gene-pools, within the relatively continuous modern Neotropical forests, and how much correlation exists across taxonomic groups ?

How well do these patterns of biological diversity correspond to the long-term consequences of present-day ecological processes, or alternatively to proposed past climatic changes which may reoccur someday ?

The first question might be placed within a practical context by the following reformulation: How much of the Neotropical forests must be pro- tected as "genetic banks" in order to guarantee the survival of the greater part of the diversity evolved over past millennia, for study, breeding, and other uses in the future; and where and how large must the preserves be in order to ensure continued inte- gration of their subsystems? A possible and prac- tical reformulation of the second question might be: Given the meager biological data available today to answer the first question, and the constant pressure to open up more and more areas of forest to coloni- zation and cultivation, how can one select now the areas of highest priority for protection and study? In 1976, the Brazilian Forestry Development institute (IBDF) accepted the possibility of using the refuge model to help answer these questions, in the elaboration of a National Park System Plan61; Brazil and six other countries are now using a combination of deductive (biological data) and inductive (biogeo- graphical theory and models) approaches in conser- vation planning in the Amazon, after an agreement on strategies was reached at a multinational confer- ence in Brasilia in mid-197762.

A definition of the positions and influ- ence of past forest refuges, and of concentrations of present-day endemic biotas, besides providing solid answers to the above urgent questions, could be useful in many other fields of research and planning. Plant and animal taxonomy could be appreciably refined by the generalizable aspects of a workable refuge model for endemism and evo- lution of forest biotas. More homozygous mate- rial for genetic experiments should be found in central areas of endemic regions, whereas greater heterozygosity would be expected in low-endemic (hybridization) zones. A careful definition of the distribution and evolutionary history of the tightly coevolved subsystems which dominate the Neo- tropical forest environment63 would be of cardinal importance in the comprehension of the diversity, dynamics, and structure of these much-admired but little-understood communities. The solid in- formation on the biological and evolutionary ef- fects of past weather changes on forests and on plant and animal populations would be very useful in the analysis of the consequences of man-made climate modifications in the tropics. Recognition of the patterns of compartmentalization of natural resources, such as game animal populations or me- dicinal plants, would be of use in the projections for their preservation and rational development. Areas of degenerated systems in the past would need a different and more careful agricultural or silvicul- tural management regime, and would be more apt for different cultures, than those which retained continuous humid forest, to help avoid irreversible degradation to relatively less usable systems.

An "Intergovernmental Technical Committee for the Protection, and Management of Amazon Flora and Fauna" (C. I. T.) was formed in Iquitos in June 1976. A summary of progress in planning and implementa- tion of this conservation program may be found in G.B. Wetterberg and M. T. Jorge Padua, "Preservação da Natureza na Amazônia Brasileira: Situação em 1978" (PRODEPEF Série Tecnica n°13, PNUD/FAO/ IBDF/BRA-76/027, Brasília, 1978).W.W.Benson, K.S.. Brown, Jr. and L.E. Gilbert, Evolution, 29, 659 (1976); L.E. Gilbert, Colloq. Intern, C.N.R.S., 265, 399 (1977); K.S.

Brown, Jr., in Encontro Nacional sobre a Proteção da Fauna e Recursos Faunísticos, Brasília 1977 (IBDF, Brasília, 1978); W.W. Benson, Evolu- For example, of the 42 regions of butterfly endemism (Figure 7), only three (Marajó, Cauca and Magdalena) fail to appear in the correlative map at the 40% level. They are all in areas of young soils, and may represent islands for modern evolution. A further six (Ventuari, Roraima, Loreto, Tefé, Madeira, and Guaporé) show 40% but not 60% correlation (the last is still almost unknown biologically). All nine regions below 60% correlation are relatively little studied as yet, poorly isolated from adjacent endemic centers, and represented by a small number of species in the maximum quadrant (average 5.8; for the other 33 centers, average 11.9) These will probably not turn up in many analyses of endemism, especially of larger, more vagile, or less adaptable organisms.

The data and correlations presented in Fig- ures 3-11 can provide approximate answers to the two original question raised, and thereby contribute to the various scientific endeavors which are inter- ested in these answers □ especially to conservation planning in the present. Apparently, the differen- tiated forest biotas have not moved around too much, although they may have expanded, become sutured on their edges, or occasionally divided fur- ther, since the last regressive climatic phase. The geographical resilience of these systems suggests that they will not be easy to transplant, even in part, to artificial parks, nor to preserve in part by concentration on population of their more salient vertebrate or arboreal components.

A sensible forest conservation policy, in light of the correlations shown in Figures 10 and 11, would seek to preserve large pieces (at least two quadrants of 3,000 km²) of as many of the endemic centers (Figures 7-9) as possible, to the extent that they still exist in natural form. Obviously, non- forest systems also need to be preserved, as do the complex and species-rich transition zones in which biotas meet and mix, which are valuable natural laboratories of ecological genetics and evolution. If a single conservation unit can include all of these, as well as areas of long-term forest stability (Figures 3 and 4), it could be all the more effective. Figure 12 shows the present and planned effectively pre- served areas within the Neotropical forest64, and a number of suggestions of regions which would be especially interesting to set aside as soon as pos- sible, in light of the correlations shown in Figures 10 and 11. It is encouraging to note that only six of the 42 endemic regions revealed in the but- terfly analysis (Darién, Chocó, Villavicencio, Oy- apock, Guaporé, and Madeira) apparently do not include any effective or proposed national park or biological reserve today. Many still unconsolidated reserves (hatched areas in Figure 12) must still be defined and confirmed, however, before it can be said that a reasonable part of the organic diversity evolved in Neotropical forests will be saved for the future.

SUGGESTIONS FOR FURTHER RESEARCH

The establishment of a basically correlative pattern (Figure 11) revealed a number of sugges- tive facets of relationship between the geoscien- tific and biological data, which point to important ecological and evolutionary processes that merit careful examination. In general, it was observed that quantitative endemism, especially lack of hybridization (Figures 7-9) was closely linked to paleoclimate (Figure 1), geomorphology (Figure 3), and stable forest soils (black in Figure 4), even in the absence of evident physiogeographic barriers, indicating that the fundamental evolu- tionary patterns being observed in these organ- isms may be closely related to paleoecological conditions. Species diversity and general richness of forest systems including highest endemic values in cases where physical barriers impede hybridization were strongly tied to present ecological conditions, however (Figure 2, younger soils in Figure 4), tending to appear in peripheral areas of endemic centers, with increased micro- heterogeneity of the environment65. This implies that "refuge" analysis and conservation planning based on species richness or even on high ende- mism must be carefully tempered by geological data, and should be complemented by abundant geographical sampling and careful study of ge- netic, ecological, and biosystematic aspects of the organisms. An interesting case is provided by separate areas in the Belém endemic center, which had very different rainfall patterns in the ice age (Figure 1) than at present (Figure 2). In the northeast near the coast, present high rainfall and a vegetational barrier to the east give high endemic values on relatively poor soils; a number of species are present which occur only around the peripheries of endemic centers66. In the dryer south, which has better soils and received much rain when the winds were more northeasterly in the past (Figures 1, 3 and 4), endemic values are low today (5-8), but there is no hybridization and no peripheral species are present. In the west (Tucuruí), where the soils are especially rich and rainfall is high today, species diversity is very high but hybridization is equally high, giving very low or negative values for endemism in an area of no- table richness in the forest system (see Figure 6 for details).

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[73] W.W.Benson, K.S.. Brown, Jr. and L.E. Gilbert, Evolution, 29, 659 (1976); L.E. Gilbert, Colloq. Intern, C.N.R.S., 265, 399 (1977); K.S.

[74] Brown, Jr., in Encontro Nacional sobre a Proteção da Fauna e Recursos Faunísticos, Brasília 1977 (IBDF,

Brasília, 1978); W.W. Benson, Evolu- tion, 32, 493-(1978); see also P.E. Vanzolini and R. Rebouças-Spieker, Pap. Avulsos Zool., São Paulo, 29, 95 (1976).

[75] K.S. Brown, Jr., Acta Amazonica, 7, 75 (1977); , in Biogeog- raphie et Evolution en Amérique Tropicale, H. Descimon, Ed. (Publ. Lab. Zool, Ecole Normale Sup., Paris, n° 9, 1977).

[76]

Belém is one of a number of endemic centers which seem to be peripheral to rather than coin- cident with favorable soils or refuge areas. Some others cases (Araguaia, Yungas) also show very dif- ferent prevailing winds in the past in relation to those today, giving large modifications in rainfall regimes. Several endemic centers show few charac- teristic species, mostly of smaller size, and may cor- respond to modern ecological islands or "miniref- uges" in steep areas (Cauca, Magdalena, Ventuari, Roraima, all on young lithosols) or gallery forests (Tefé and Madeira, along large rivers on alluvial soils). Such cases bear careful investigation of soil mosaics, climatic patterns, ecological barriers, and detailed distributions of endemic organisms. Like complex "tension zones", they may mark critical ecological areas where improper management could lead to rapid and irreversible disintegration of the landscape and species extinctions, due to cli- mate and soil degradation.

A few endemic centers cut broadly across areas which show poor soils and signs of low rain- fall and sparse vegetation in the past. Here, research may reveal unsuspected patterns of adaptation, competition, and colonization in forest organisms. Such processes are eminently interesting to agri- cultural man, who would ever adapt economic spe- cies to his progressively more degraded habitats.

Areas of microheterogeneity of soils, such as central Suriname and the Serra dos Parecis in western Mato Grosso, show different patterns of endemism in different organisms, and would be recommended for studies of modern evolution and differentiation, related to intrinsic population pa- rameters and dispersal abilities of the species and groups.

In all areas of high correlation (Figure 11), it would be interesting to conduct palynological studies with dated cores. In the long run, these la- borious but very important investigations should provide the most solid evidence for the true posi- tions of regions of long-term forest stability.

It is evident that much detail must still be organized and understood, before the complex re- cent reorganizations of the Neotropical landscapes can be fully elucidated, or their effects on biolog- ical endemism established. It is important to pre- serve immediately enough of this detail to permit further study on past changes and present species richness and endemism. Hopefully, this analysis will aid those who are striving to effectively con- serve as much as possible of the diversity still ex- isting in the Neotropical forests.

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