

Pleistocene Changes in the Fauna and Flora of South America

Present speciation patterns of the South American biota resulted from Pleistocene climatic changes.

Beryl Simpson Vuilleumier

The significant biological changes, including drastic distributional shifts, wholesale extinction, and rapid speciation, that occurred in the floras and faunas of Eurasia and North America during the Quaternary are well known and have been thoroughly documented (1-2). All of these phenomena have been related, either directly or indirectly, to Pleistocene climatic events that are believed to have been worldwide (1-2). However, the lack of geological and biological data has discouraged, until recently, reconstructions of the Pleistocene biotic histories of continents in the Southern Hemisphere. Instead, biologists have tended to accept speculations about Pleistocene conditions in tropical and austral continents, based on knowledge of the Northern Hemisphere (3). These postulations were made from a few localities in low latitudes of the Northern Hemisphere. Unfortunately, these localities suggested that tropical and southern latitudes suffered little during the Pleistocene, thus giving rise to a widespread belief that these areas remained relatively "stable" during the Quaternary (4). Within the last 10 years, this idea has begun to give way. Both biological and geological investigations in situ have increasingly revealed that Quaternary climatic events actually played a significant role in the evolution of the biotas of Africa

(5), Australia (6), and South America (7-21).

Moreau's work on the vicissitudes of the African biota (5) was the first to demonstrate how the flora and fauna of an austral continent were affected by Pleistocene climatic events. His conclusions immediately raised the suspicion that other southern land masses had undergone similar modifications. This article provides evidence that the present biotic patterns in South America have, indeed, been determined by Quaternary paleoecological changes. The evidence supporting this conclusion is derived from two sources: analyses of speciation patterns of the flora and fauna throughout the continent, and geological and paleobotanical studies that document the requisite climatic events.

In using speciation patterns as clues to the evolutionary history of a group of organisms, it is necessary to locate areas of secondary contact between distinguishable forms. These are recognized as stepped clines, hybridization belts, places with character displacement, or areas with narrow sympatry of closely related taxa. In most sexually reproducing, outcrossing organisms, differentiation can occur only if populations are isolated from one another (reduced gene flow). Consequently we can assume that an area in which we now

find overlapping of differentiated forms indicates where the two forms had previously been separated. If the modern contact zone coincides with a discernible physiographic feature (mountain range, river, and so on), it is probable that the feature is, and was, a geographical barrier to gene flow. If the present area of overlap does not coincide with any visible physical or ecological feature, it can be postulated that a barrier existed in the past, but is no longer operative.

Although much can be inferred from this type of analysis, supportive evidence is necessary to provide a convincing argument for the existence of former, ecologically distinct, isolating barriers. Reconstructions of past environmental conditions can be made from geological and paleobotanical studies, and they have been used here to supply additional evidence for the presence of former barrier zones. These reconstructions are based on two assumptions. First, geological processes that operated in the past to produce a given landform (U-shaped valley, pediment, and so on) were analogous to those now producing the same type of landform (glacial action, arid climatic regime, and so on). The second assumption, used primarily in paleobotanical and paleontological work, is that fossil organisms lived under ecological conditions similar to those under which their closest modern relatives now live.

The speciation patterns presented here include those from work on the paramo-puna (7-14) and *Nothofagus* forest (7, 8, 15) flora and fauna, combined with other studies on the tropical montane and lowland forest faunas (14, 16-21). These patterns are divided, for discussion, into the following geographical regions, each of which circumscribes a more or less coherent biota and appears to be (and, therefore, was also in the past) under a distinct climatic regime: the southern

The author is an assistant curator at the Gray Herbarium of Harvard University, Cambridge, Massachusetts 02138. She has spent a period of 7 years, much of it in the field, working on the flora of South America.

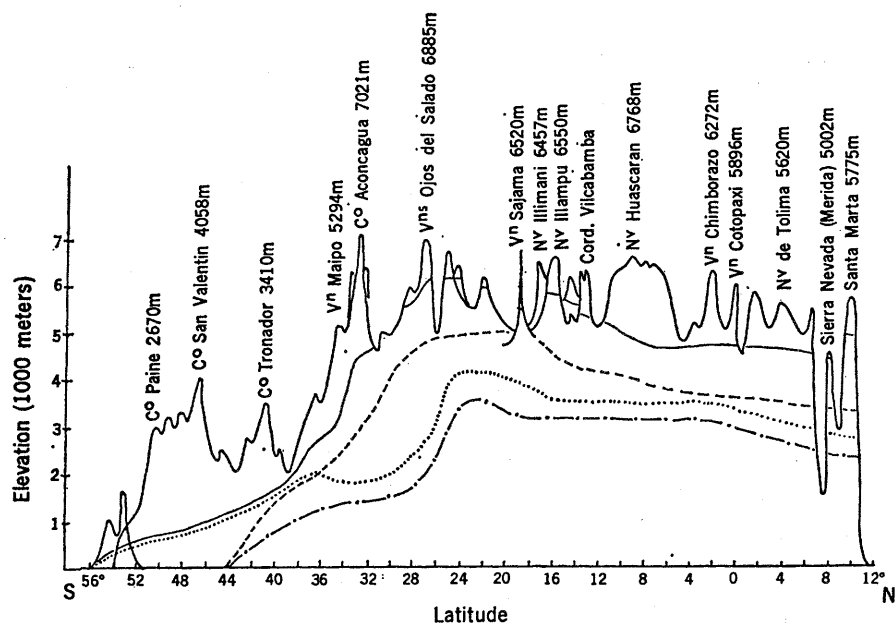


Fig. 1. A longitudinal transect of the Andes from Venezuela to Tierra del Fuego, showing present snowline (solid line), Würm snowline (dashed line), present treeline (dotted line), and Würm treeline (broken line) along the western slope. Compiled from numerous sources (see Table 1). [Abbreviations: cerro (C°), volcano (V°), cordillera (Cord.), nevado (N°).]

Andes, Patagonia, the central and northern Andes, the lower montane slopes, and the tropical lowlands. Because the geological and paleobotanical data are considered vital as supportive evidence, and because they are so poorly known, I include a brief summary of them in an appendix that parallels the biological discussions.

Southern Andes

The only area of South America that has been well studied from the point of view of Pleistocene speciation patterns is the southern Andes of Argentina and Chile. Over 50 years ago, European geologists, struck by the resemblances between glacial landforms of southern South America and northern Europe, initiated a series of investigations on the Quaternary of Fuego-Patagonia. The parallels they uncovered in glacial history (Appendix, 1, 2; Table 1) prompted biologists to wonder whether the Pleistocene glaciations had also affected the biotas in similar ways. In the Northern Hemisphere, climatic changes were known to have caused expansion of the tundra, retreat of the forests, elimination of species, fragmentation of ranges, and isolation into refugia. In order to pursue the apparent parallels in historical development, biologists first looked at the distributions of plant taxa to see if

they could best be explained in terms of glacial events.

Skottsberg (22), Reiche (23), Loo-ser (24), and Auer (25) all provided examples of plant ranges which indicated that the Chilean *Nothofagus* forests retreated northward (toward the equator) in a manner similar to the southern migration of the Eurasian forests. Relict, disjunct patches of woodland such as Fray Jorge (Provincia Coquimbo, Chile, around 30°S) are depauperate remnants indicating the northern extension of the forests in glacial times (23–25).

Within the forest belt along the Chilean slopes, numerous plant taxa were found to have distributional limits, or areas of secondary contact, at the latitudes of the Río Maule (36°S) or the Río Bío Bío (37° to 38°S), or both (7, 8, 23). In both of these areas, glacial tongues reaching out from the Andes into the central valley (26) seem to have acted as barriers, interrupting gene flow sufficiently to have allowed differentiation of populations to the north and south of these tongues.

South of 44° to 45°S, all of the land west of the Andes was covered by ice (see Appendix, 2; Figs. 1 and 2) and would thus seem to have precluded any life. However, the number of plant species with disjunct populations, or slightly differentiated, closely related taxa, south of this latitude (7, 22–25) indicates that a few areas within the

zone of maximum glaciation must have served as refugia for floristic elements. In contrast to the plants, the vertebrate fauna of the *Nothofagus* forests seems to have been little affected by local events during glacial periods (15). The major mode of speciation of some frog, and most avian, taxa indigenous to the forest has been slow phyletic change, without speciation by splitting (7, 15). For montane forest elements of the southern Andes, therefore, Quaternary glaciations acted primarily to reduce their total distributional ranges, shift them slightly northward, and, in the case of some plant taxa, allow differentiation during isolation in refugia or by the interposition of local ice barriers.

The high altitude "alpine" elements of the southern Andes were affected differently from, and perhaps more dramatically than, the forest elements. During the time of glacial advance, plants and animals of this zone expanded their ranges as vegetation belts were lowered (7–9). During interglacial periods, they were restricted to the tops of individual, high mountains. Repeated episodes of migration and isolation, corresponding to the successive glacial-interglacial cycles, contributed to the rapid proliferation of some high-altitude genera (7, 9). A similar history of cyclical speciation has been proposed for plants of the high mountains of northern Europe (27).

Patagonia

Exactly how the Pleistocene climatic changes affected the Patagonian Tableland is not understood. The questions of the amount of ice (if any) present on the plateau and the changes in precipitation are currently under debate and need more study (Appendix, 3). It is known that a huge area of the Argentine continental shelf was exposed in glacial times (Appendix, 3; Fig. 2). During these periods of exposure, the land surface available for colonization in southern Argentina almost doubled, and this factor must have facilitated dispersal from the mainland to the Falkland Islands (7, 9, 25). The presence of slightly differentiated avian and plant populations on the islands suggests that they may have served as a refugia for some taxa when glacial ice covered a great part of Fuego-Patagonia (8, 15, 22).

On the eastern side of the southern Andes, the limit of glaciation seems to

have coincided with the base of the mountains (Fig. 2). The narrow band of forest now present on parts of the eastern slopes was apparently pushed slightly eastward in front of the ice. Yet, despite the increased coolness and humidity that occurred on the Patagonia plateau during glacial periods (25), the forest never seemed able to spread across the tableland (25). Instead, the forest underwent, at the base of the Andes, a complex and confusing series of minor advances and retreats which did not correspond in time to either glacial maxima or minima. The major part of Patagonia appears to have been a bogland (25) dissected by outwash streams and lakes from glacial meltwaters that presumably isolated some peripheral populations and caused the differentiation now visible in numerous plant species across the Patagonian steppe (7).

High Central Andes

The central Andes consist of several parallel mountain chains that begin in northern Perú, and the broad, flat altiplano into which they merge. This plateau, at a high altitude and flanked by high ranges, covers southern Perú, western Bolivia, northwestern Argentina, and adjacent Chile. Geological studies throughout this area have shown that the glacial climates lowered both the snowline and the timberline (Appendix, 4; Fig. 1). A parallel downward and outward spread of the puna grassland along the Pacific and Amazonian facing slopes would have increased the opportunities for organisms that exist in high altitudes to migrate from mountain to mountain along a north-south axis (7-11). At the same time, however, the large glacial systems that formed in some areas, such as the Nudo de Vilcanota, seem to have acted as effective barriers to gene flow in some organisms (8, 11).

Examination of the speciation patterns of avian and plant taxa has revealed several zones of secondary contact (with hybridization or narrow sympatry) that do not correspond to any present-day (interglacial) ecological barrier (7-10, 17). One such area has been found in the Andes east of Lago Titicaca, Bolivia, where diglossid finches (10, 11) and species of the genus *Perezia* (Compositae) (8) exhibit complex patterns of hybridization and introgression. This area is known

to have been particularly heavily glaciated, and it is probable that glaciers or tongues of ice created enough of a gap in the puna vegetation to have caused divergence of populations on either side of it (7-11).

Other barriers separating populations during glacial periods may have been the immense systems of glacial lakes that formed in northern and central Bolivia (Fig. 2) (7-11). In a few cases, these bodies of water may have effectively isolated populations on the

eastern and western sides of the altiplano.

During interglacial periods such as the present, climatic conditions were drier, and the puna grasslands were restricted to high elevations of various mountains and ranges. During these periods, intermontane valleys that lie in rain shadows act as barriers to those puna organisms that cannot live in such hot and arid environments. Table 2 lists the most important of these ecological, interglacial barriers.

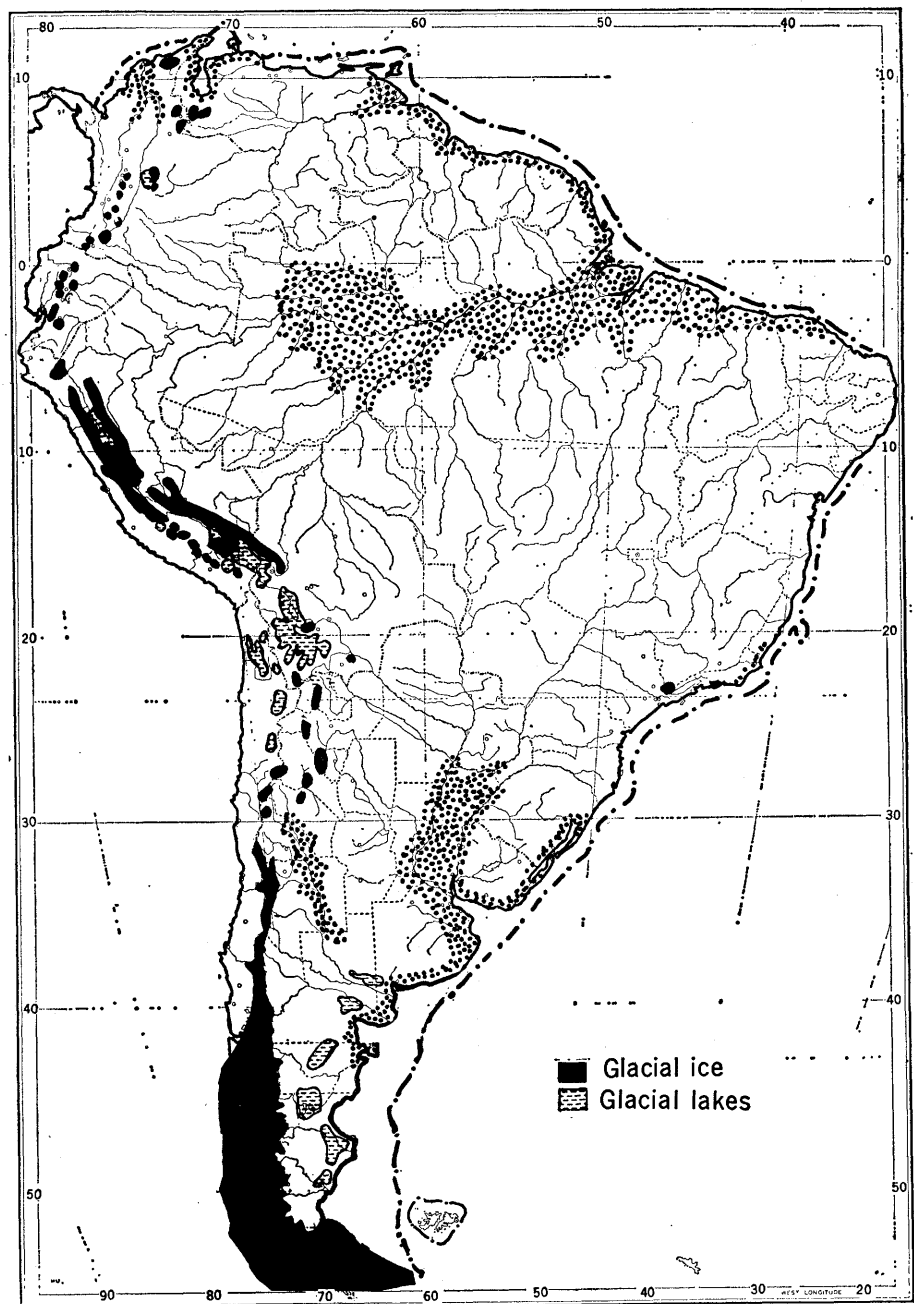


Fig. 2. Features of the Würm glaciation and an interglacial episode (26, 28, 30, 31, 41, 44, 45, 49, 59). Black areas represent glacial ice, dashed areas indicate glacial lakes, and the broken line that follows the 100-meter-depth line illustrates the probable glacial coastline. Dotted areas show the locations of interglacial sea transgressions and the large, inland, freshwater lake in western Argentina (1, 51, 59).

Table 1. Summary of Pleistocene glacial events in South America.

Localities	Glacia- tions (No.)	Age of glaciations, relative to Euro- pean sequence	Present snowline (m)	Glacial snowline (m)	Glacial climate (°C)	Interglacial climate (°C)	Glacial lakes and their localities	Interglacial lakes and sea transgressions	Tectonics
Mérida, Perija	1 or 2	Würm or Riss and Würm	4800-4900	2700-3300	Venezuela (28)		Over 100 in mountains	Coastal flooding	Andean uplift, Orinoco Basin, subsided
Perija, Santa Marta, Central Cordillera of Colombia; Ecuador, volcanos above 4500 m	Variable; 1 to 3	Mindel to Würm	4200-4500	700-100; lower than present	Colombia and Ecuador (17, 28, 31) Lowered; 4-11 wet raised 2-3		Lago Humboldt (Sabana de Bogota)		Andean uplift
All high peaks, most extensive in Cordil- lera Blanca	3	Mindel to Würm	5800 in west; 5000 in east	4500 in west; 4200 in east	Perú (44, 45) Lowered 7 wet		Lago Markill (Cuzco Valley), Lago Yana- hura (Huanuco Basin), Lago Chinchicocha (now called Lago Junin)	Coastal flooding	Coastal movements, volcanic activity, Andean uplift
All northeast ranges, high peaks in south- east, few peaks in southwest	3 or 4	Günz or Mindel to Würm	5900 in west; around 5300 in east	5000-5300 in west; 4600- 5000 in east	Bolivia (44, 48) Lowered 6 wet		Lago Ballivian (Titi- caca to Oruro); Lago Minchin (Lago Poopo, Salares)		Uplift in northeast, volcanic activity
Few peaks between 30° to 42°S; south of 42°, all land to west and to the base of Patagonian Cordillera in the east	3 or 4	Günz or Mindel to Würm	Variable; above 5900 in north to 800 in Tierra del Fuego	500 at Santi- ago; sea level at 45°S	Chile and Andean Argentina (25, 26, 41) Wet		Numerous, small in north; fiord-like in south	Coastal flooding; in northern Ar- gentina, from meltwater	Differential coastal movements, volcanism
Only Tierra del Fuego	3 or 4	Günz or Mindel to Würm	None	Glacial ice to base of mountains	Patagonia (25, 27, 28) Colder than pres- ent; dry alter- nating with wet present		Numerous across plateau	Large lake on plateau west of San Jorge	
None				Paraguay-Paraná Basin (30, 37, 50, 52, 53) Cool, dry	Humid, warm			Huge area of Para- guay-Parana Basin	
Mount Itatiaia	1 or 2	Würm or Riss and Würm	None	2300	Brazil (36, 51)			Large part of Amazon Basin	

Northern Andes

The presence of glacial advances and their positive influence in the modification of plant and animal distributions in the southern and, to a lesser degree, the central Andes, have been acknowledged for some time. Yet, an appreciation of the effects of glaciation on the flora and fauna of the northern Andes is only beginning to develop. This disregard of Pleistocene climatic events is surprising, in view of the fact that all of the biotic patterns of the high northern Andes must have developed since the end of the Tertiary (8, 11, 17). From Venezuela to Ecuador, the area above the timberline and below the zone of permanent snow is now covered by paramo (humid grassland). This kind of habitat could have developed only after the Andes had reached their present height at the Plio-Pleistocene boundary (28).

As shown in Fig. 3, these high paramos are isolated from one another by expanses of lowland or montane forest, in a way that is reminiscent of islands in a sea of water. An analysis of the avifauna of these paramo "islands" has shown that it is primarily derived from birds of the high central Andes, and not from birds of the montane forest or Central America. Consequently, if these paramo islands were not affected by historical climatic changes, their endemic flora and fauna should have arrived by way of long-distance dispersal from high altitudes to the south. The present biotic distribution patterns should be the result of straightforward colonization, and the number of species on each paramo should be consistent with the number predicted by the model of island biogeography (29). Inherent in this theory is the assumption that rates of immigration and extinction have remained constant. In other words, the paramo islands are assumed not to have varied in size or in spatial relation to one another and to the source area.

It is therefore possible to determine on a priori grounds whether the paramo islands were modified during the Pleistocene by comparing the number of species actually present on each paramo with the number predicted, assuming constant rates of immigration and extinction. F. Vuilleumier (12) has conducted such an analysis with the indigenous avifauna of the Andean paramos. Table 3 gives the number of bird species actually breeding on each paramo (island numbers correspond to

Table 2. Major interglacial barriers to dispersal of paramo-puna and upper montane forest elements in the north and central Andes.

Barrier	Ecology	Areas effectively separated
<i>Venezuela</i>		
Paria Valley	Dry lowland	Cordillera de Paria and Cordillera de Caripe (17)
Unare Depression	Dry, low area	Cordillera de Caripe and the coastal and central Venezuelan Andes (10, 17)
Torbes or Cristobal Valley	Arid slopes	Andes of Mérida and eastern Colombian Andes (11, 12, 17)
Llanos	Low, flat, dry grassland	Andes and Venezuelan tablelands (17)
<i>Colombia</i>		
Cesar Depression	Low, dry valley	Perija Mountains and Nevada de Santa Marta (11, 17)
Magdalena Valley	Low, dry valley	Eastern and Central cordilleras of Colombia (11, 12, 17)
Cauca-Patía valleys	Inter-Andean, dry valley	Western and Central cordilleras of Colombia (10, 12, 17)
Patía Canyon	Inter-Andean, dry valley	Western Andes of Colombia and western Andes of Ecuador (10)
<i>Perú</i>		
Upper Marañon Valley and northern Perú lowland	Dry valley and low mountains	Andes of Ecuador and Andes of Perú; Eastern and Western Cordilleras of Perú (10, 11, 17)
Huallaga Valley	Dry valley	Andes of Huancavelica from those in Apurimac, Perú (8, 11)
Apurimac-Pampas Valley	Dry valley	Vilcabamba and Vilcanota ranges from the central Peruvian Andes (8, 10, 12)
<i>Argentina-Chile</i>		
Andes of northwestern Argentina	High, snow-covered peaks and foothills—both without rocky plains	Altiplano and Patagonian steppe (10, 11)
Chaco	Dry, low scrubland	Andes and planalto-southeastern highlands of Brazil (8, 34, 35)

those in Fig. 3), compared with the number predicted under the model of island biogeography. There is considerable agreement between the two sets of values, but noteworthy discrepancies do occur (in islands 2 and 12).

The differences between the predicted and observed values could be due to rigid assumptions about the constancy of the paramo islands. If the rates of immigration and extinction had been altered during the Pleistocene, the number of species actually breeding on various paramos would tend to deviate from the theoretical number. Such a change in the rate of immigration could have been caused by shifts in the paramos because of glacial events.

It is, in fact, known that glaciations did occur in the northern Andes (Appendix, 5) (28, 30–32). Within the last 10 years, van der Hammen and his associates have documented the influence of glacial periods on the high mountain vegetation zones of Colombia (32). Van der Hammen's data, based on palynological remains in glacial lacustrine sediments, indicated a lowering of the treeline to an elevation of about 2000 meters during glacial maxima. Figure 3 (dashed line) reconstructs the areas which would then, presumably, be covered by paramo vegetation. It is obvious that, under such climatic conditions, the paramo islands changed shape, size, and relative distance from one another. In essence, they came "closer together" and allowed freer exchange of plants and animals between different paramos.

Haffer (17) has also illustrated the effect of lowered vegetation zones on

dispersal, and he has reconstructed the probable Pleistocene history of the upper montane forest avifauna in the northern Andes.

Organisms from high altitudes were thus allowed to disperse comparatively freely when vegetation zones were lowered, but were restricted in interglacial times, when warm climates prevailed. Temperatures during the Pleistocene interglacials were probably warmer than they are today (Appendix, 6) (30, 32). As a consequence, those barriers that are now operative (primarily ecological) acted more strongly at times during the Quaternary than they do at present. Detailed analyses of avian speciation patterns in the northern Andes (10, 11, 17) have pointed out a series of barrier zones that correspond today to such areas of unfavorable habitat as montane or lowland rainforest, or intermontane, arid valleys. The most significant of these regions, their locations, and their ecology are given in Table 2.

Highlands of Venezuela and Southeastern Brazil

The relations of the faunas and floras of the Venezuelan highlands and the tablelands of southeastern Brazil to those of the Andes were noticed long ago (17, 33), but how these organisms migrated from the Andes across the intervening, inhospitable areas of lowland rainforest or savanna has remained open to speculation. Haffer (17) has proposed, and convincingly documented, that, during cool, humid

glacial maxima, the lowering of vegetation zones had the effect of increasing the lateral surface of montane forest along the Andes and around the Venezuelan mountain masses. Moreover, the temperature depression also permitted subtropical forests to develop on mountains that are now covered only by tropical elements. The combined effect of the reduction of unfavorable habitat between montane areas and the interposition of new patches of montane forest, which acted as stepping-stones, allowed Andean plants and animals to spread eastward more easily (17).

Similar periods of increased opportunity for dispersal in glacial times are believed to have led to some of the disjunct distributions of organisms in the Andes and in the planalto of southeastern Brazil (8, 34, 35). Documentation of a Pleistocene glacier on Mount Itatiaia, Brazil (Appendix, 7), and evidence of periglacial climates (36) are indications that highland vegetation zones must have been lowered and, consequently, that they increased in horizontal distribution during glacial maxima. In this case, however, the ecology of the lowland area between the Andes and the uplands seems itself to have been altered by changes in climate (Appendix, 8). Increases in humidity across northeastern Argentina and southern Paraguay and Uruguay probably allowed the southward extension of organisms from more mesic habitats, thus adding the factor of a more amenable migration route eastward for montane plants and animals (8, 34–37) (also see Fig. 4).

Montane Slopes of Central and Northern Andes

Numerous speciation patterns of organisms in montane forests cannot be easily explained in terms of ice barriers or increased migration routes along lowered vegetation zones. For example, the Koepckes (38) have discovered and described, along the Pacific slopes of the Western Cordillera, north of Lima, Perú, a series of isolated pockets of evergreen montane forest, sequestered in humid canyons. The small patches of vegetation, some quite lush in aspect, are essentially depauperate representatives of the montane (ceja) forest of the Eastern Cordillera. Yet some differentiation has been reached (at the level of subspecies or species pairs) between related taxa of the isolated woodlands and their counterparts

across the mountains. The small forest fragments on the western slopes of central Perú have never been in direct contact with (at least since the final uplift of the Andes), nor were ever extensions of, the true ceja forest, because the Andes in this area are too high to allow trees to grow at the level of the east-west passes. It is, therefore, impossible that the woodlands are relicts of a recent, continuous forest across the mountains. Moreover, the lack of close biotic relationships in an east-west direction also indicates that the western patches of forest were not colonized at different points by propagules from across the Andes.

In the provinces of Amazonas and Cajamarca in northern Perú, the Andes are lower and, in a few areas, are completely covered by forest. It is possible that organisms from the ceja crossed

the Andes in this area and migrated down the western slopes of the Peruvian Cordillera. This dispersal down the Pacific slopes could have occurred either stepwise, with propagules hopping from one favorable area to another, or in a more continuous fashion. Under the present climatic regime, a more continuous band of forest cannot exist. If Pleistocene climatic events did not affect this area, the woodlands must have been colonized by means of short-to long-distance dispersal from the north. If this were the case, the individual patches of woodlands should differ slightly from one another in species composition (due to chance arrival of different species), and individuals of a given species should vary greatly between populations (founder effect and local selection pressures). Upon examination, the woodlands are found to be very homogeneous in respect to flora and fauna.

An explanation for the existence of the woodlands and their lack of inter-differentiation is that they are recent relicts of a more or less continuous band of forest along the western slope. A relative increase in the humidity would have allowed such an increase in the distribution of the forest. Geomorphological and anthropological studies (Appendix, 9) at localities along the Western Cordillera have indicated that there were cycles during the Pleistocene, when the humidity was higher than it is now. The distribution pattern of the genus *Polylepis* (Rosaceae) (which forms unique woodlands at higher elevations than those described by the Koepckes) and its constituent avifauna also suggests a sequence of humid-arid changes in climate along the central Andean slopes (39).

Within the past year, Vanzolini and Williams (19) have completed an analysis of the morphological variation of the lizard *Anolis chrysolepis* in eastern tropical South America. One large population of this species occurs fairly continuously down the eastern Andean slopes from Colombia to Perú. Yet, despite the apparent uniformity of habitat throughout the range of this population, an analysis of variation in morphological characters revealed a sharp discontinuous pattern (stepped clines). Vanzolini and Williams interpreted this abrupt variation from north to south as evidence of recent contact between populations. Since the slopes are now covered by montane forest, smaller populations of *A. chrysolepis* could

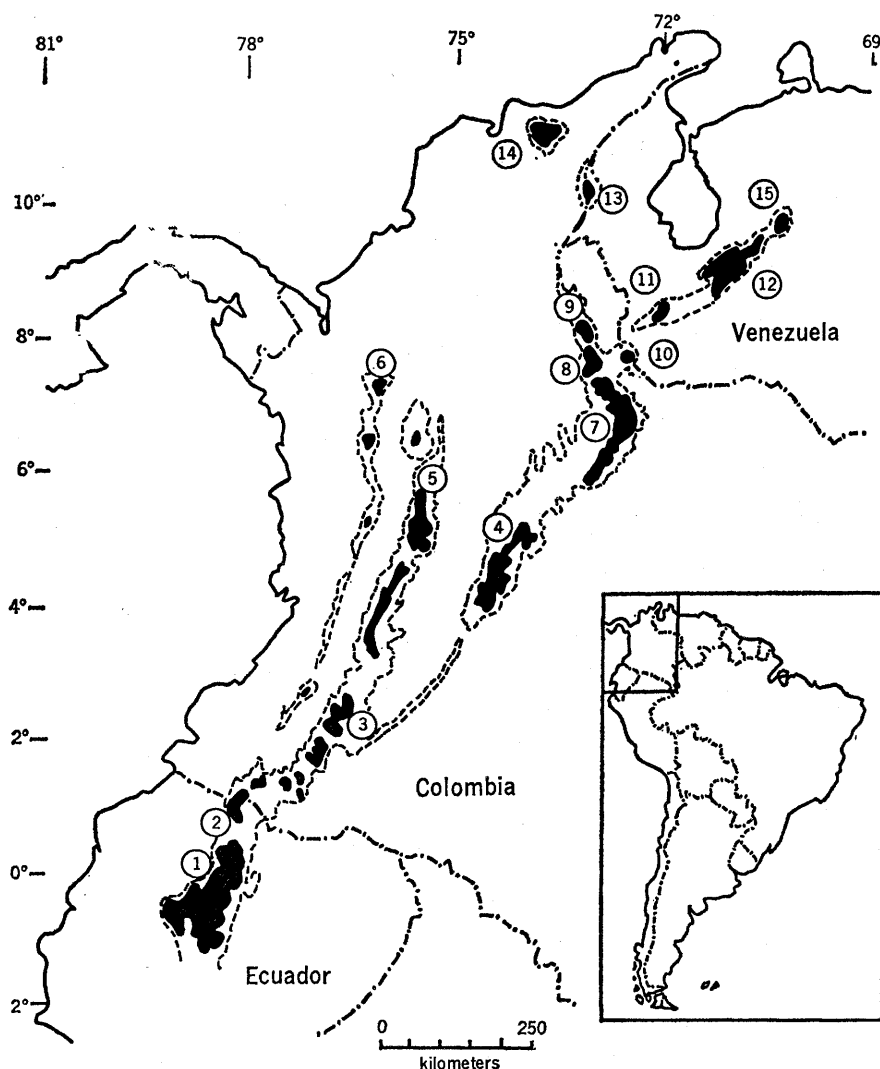


Fig. 3. The present distribution of land above the treeline (paramo and glaciers) in northern South America (black), showing its archipelago-like arrangement. The dashed line indicates the lowest elevation reached by paramo grassland in times of glacial maxima (assumed to have been at an elevation of 2000 to 5000 meters). Arabic numerals indicate paramo "islands" (see Table 3). [Modified from (12)]

have been isolated in the past only if an arid cycle had occurred, causing fragmentation of the forest.

Vanzolini and Williams's conclusions about the eastern slopes are analogous to those of the Koepckes (38) about the Pacific slopes, but they indicate that climatic conditions on the two sides of the Andes are out of phase. Geomorphological data (Appendix, 9) confirm not only that wet-dry cycles existed in both of these areas, but also that, at any time during the Pleistocene, the climatic processes on one side of the Andes were the reverse of those found on the other.

Tropical Lowlands

Although the humid, lowland tropical areas of South America have traditionally been conceived of as having remained unchanged throughout most of the Tertiary and the Quaternary (4), the presumed climatic and ecological stability of these areas during this period appears to be a complete misconception (Appendix, 10, 11). Investigations of several avian taxa (14, 16) and members of the lizard genus *Anolis* (19-21) have demonstrated that many areas of disjunction, hybridization, secondary sympatry, and introgression exist in the Amazon Basin. Since these areas of secondary contact do not correspond to any modern, observable, physical or ecological barriers, they must, therefore, be the result of historical causes.

Haffer's work on the Cracidae, tucanets, parrots, cotingids, and manakins of lowland northern South America (16) revealed a striking coincidence in the location of areas of secondary contact in these unrelated groups of birds. Less detailed examinations of several other avian genera indicated that they, too, had contact zones in the same areas as the cracids, tucanets, and so on. As a result of these studies, Haffer proposed the theory that Pleistocene climatic oscillations in the lowland tropical areas of South America resulted in an alternating series of restrictions and reexpansions of the rainforest and its fauna. During dry phases, he postulated, the forest covered only small, disjunct areas that were humid enough to allow its persistence. These isolated regions of forest would have acted as refuges for organisms from tropical forests. Over extended periods of time, local selection pressures would have allowed differentiation among

populations of a species inhabiting different forest refugia. In humid phases the forests reexpanded and, where previously isolated populations remet, they formed the present complex patterns typical of zones of secondary contact. Figure 4 shows the areas in which Haffer felt such refuges might have occurred.

The correlation in time of the humid-arid cycles with South American glacial events remains controversial, but Haffer (16) illustrated the interglacial sea transgressions up the Amazon Valley on the same map as the forest refuges of the arid phase.

Conclusions similar to those of Haffer have emerged from the study of Vanzolini and Williams (19) on *A. chrysolepis*. A statistical analysis of the variation of morphological characters throughout the Amazon Basin populations of this species brought out that in certain areas large blocks of characters were correlated with one another and varied geographically in the same direction. In other regions, the characters showed little or no intercorrelation, and trends were apparently nondirectional

in a manner suggesting hybridization or introgression, or both. Vanzolini and Williams considered the areas of correlated characters to be "core" areas, or regions in which populations had evolved as a unit over a long period of time. Complex character variation appears to occur now in places where differentiated forms had come into secondary contact after a period of isolation.

Since all of the area across Amazonia in which these patterns are found is now covered by an apparently uniform habitat, Vanzolini and Williams (19) also postulated that there must have been, during the Pleistocene, changes in climate that caused fragmentation and reexpansion of the forest. These changes in climate were presumably synchronous with those that affected the montane forests on the eastern slopes of the Andes. Figure 4 compares the refugia of Vanzolini and Williams with those of Haffer. Despite the differences in approach and in organisms investigated, the two studies agree in their principal conclusions; together they provide convincing biological evi-

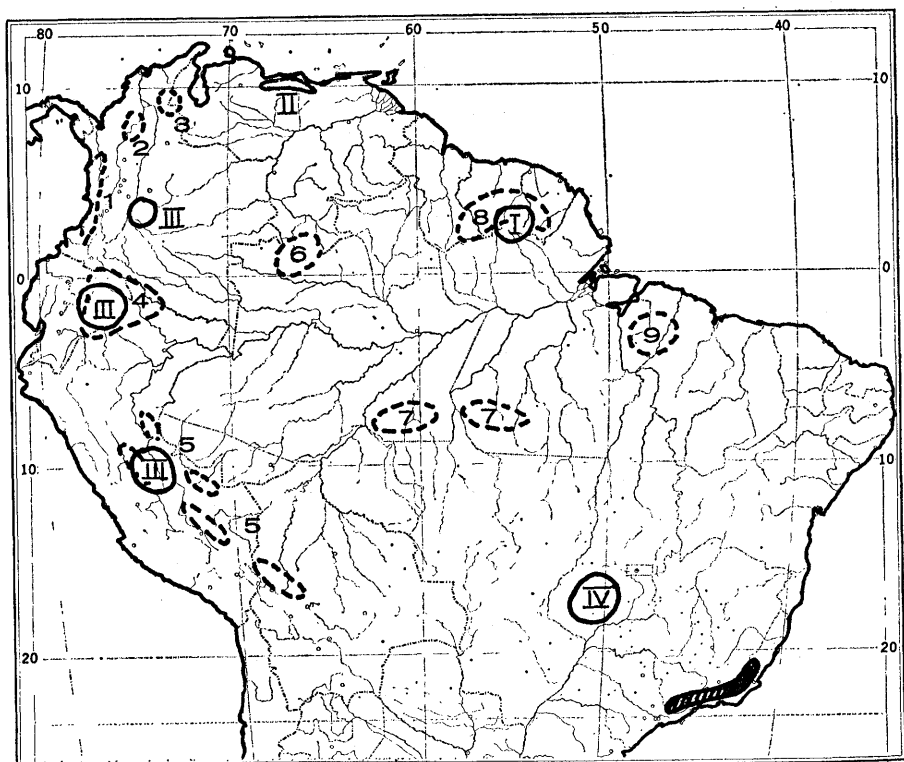


Fig. 4. Areas of forest during an arid climatic phase (16, 19-21, 35). The dashed lines and Arabic numerals refer to Haffer's refugia (16): 1, Chocó; 2, Nechí; 3, Cataumbo; 4, Napo; 5, eastern Perú; 6, Imiri; 7, Madeira-Tapajoz; 8, Guyana; and 9, Belem. The solid lines and Roman numerals indicate the refugia of Vanzolini and Williams (19): I, Serra do Tumuc Humac; II, Cordillera de la Costa, Venezuela [see also Garner (56)]; III, lower eastern slopes of the Andes; and IV, southern escarpments of the central planalto, especially the Mato Grosso de Goiás. The shaded area refers to the Serra do Mar refugium of Müller (35).

Table 3. The endemic avian taxa in the paramo islands of northern South America illustrated in Fig. 3 (12).

Number	Paramo island		Species observed (No.)	Species predicted (No.)
	Name			
1	Páramo 1 (northern Ecuador)		65	66
2	Chiles		36	32
3	Las Papas-Coconuco		30	30
4	Sumapaz		37	38
5	Tolima-Quindía		35	32
6	Paramillo		11	14
7	Cocuy		21	25
8	Pamplona		11	12
9	Cachirá		13	15
10	Tamá		17	20
11	Batallón		13	13
12	Mérida		29	23
13	Períja		4	3
14	Santa Marta		18	20
15	Cendé		15	12

dence for the theory of recent ecological changes in the tropical lowlands of South America.

There is, unfortunately, little geological research to confirm definitely the hypothesis of fluctuations in the climate of the Amazonian lowlands during the Pleistocene. However, geomorphological studies of the coasts of Brazil and the Guyanas and of the eastern part of the northern Andes, as well as preliminary aerial surveys of landforms in central Brazil, indicate that such changes did occur and that future geological work will document them (Appendix, 10).

Summary

In recent years, the view that Pleistocene climatic events played a major role in the evolution of the biotas of southern, primarily tropical continents has begun to displace the previously held conviction that these areas remained relatively stable during the Quaternary.

Studies of speciation patterns of high Andean plant and avian taxa (7-14) have led to the conclusion that Pleistocene climatic events were the factors that ultimately shaped the patterns now observed in the paramo-puna and the related Patagonian flora and fauna. The final uplift of the Andes at the end of the Tertiary automatically limits the age of the high Andean habitats and their biotas to the Quaternary. Within this period, the number of ecological fluctuations caused by the glaciations could easily have provided the mechanism behind the patterns now

present in these habitats (Appendix, 1; Figs. 1 and 2; Table 1). In glacial periods, when vegetation belts were lowered, organisms in the paramo-puna habitat were allowed to expand their ranges. In interglacial periods, these taxa were isolated on disjunct peaks, where differentiation could occur. At times of ice expansion, glacial tongues and lakes provided local barriers to gene exchange, whereas in warm, interglacial times, dry river valleys were a major deterrent to the interbreeding of populations on different mountains (Fig. 2; Table 2).

A preliminary analysis of about 10 to 12 percent of the total South American avifauna (14), subsequent to the study of the high Andean biota, suggested that the birds of all the major habitats of the continent possess, with about equal frequency, similar stages of speciation. This correspondence in levels of evolution indicated that the avifauna of vegetation zones which were thought to have been more stable (for example, tropical rainforests) are as actively speciating as are those of the more recent paramo-puna habitats.

More intensive work on lowland tropical taxa (16, 19-21) and recent work on montane forest elements (40) now justify the conclusion that the floras and faunas of these areas were also greatly affected by Pleistocene climatic shifts. In the broad region of South America that lies within the tropics, a series of humid-arid cycles (Appendix, 6, 8-10) drastically and repeatedly altered vegetation patterns during the Quaternary. Both montane and lowland rainforests were fragmented during dry periods and were able to reexpand during humid phases. Speciation of forest elements was initiated—and sometimes completed—in isolated patches of the fragmented forest. Secondary contact, with hybridization or reunion of populations that did not become reproductively isolated, occurred in periods of reexpansion.

These biological data, combined with supportive geological evidence (Appendix, 1-11), show that climatic events during the last million or so years have affected the biota of South America as much as the Pleistocene glacial changes affected the biotas of Eurasia and North America.

Since most of South America lies within tropical latitudes, it is suggested here that part of the diversity of species in the tropical areas of this continent is due to two historical factors: the lack of wholesale elimination of spe-

cies (compared with northern and high latitudes), and ample opportunity for speciation in successive periods of ecological isolation. The apparent paradox of the wealth of species in the "stable tropics" is partially explained by the fact that the tropics have probably been quite unstable, from the point of view of their biotas, during the Pleistocene and perhaps part of the Tertiary.

Appendix

1. Glacial advances occurred throughout the Andes, but the number of glacial-interglacial cycles varied from one area to another. Figure 1 gives a schematic representation of present and Würm snowlines on the eastern Andean slopes, and Fig. 2 illustrates the major South American glacial and interglacial features, respectively. Table 1 summarizes the glacial history of the Andes and Patagonia and attempts to provide correlations of events in different latitudes.

2. In southern South America, three or four glacial periods, usually correlated with the last three, or all four, European glaciations (25, 26, 41, 42), have been recorded. In Chile, between the latitudes of 33° to 34°S and 45°S, the glacial snowline paralleled, at lower elevations, that of the present (Fig. 1) (26). South of 45°S, almost all land west of the Andes (Fig. 2) and Tierra del Fuego was covered with glacial ice (26). As the glaciers flowed downward into the sea, they dug deep channels and basins that are now high-altitude lakes and fjord-like inlets (25, 26) reminiscent of Scandinavian glacial landforms.

3. Many geologists contend that, on the Argentine side of the southern Andes (Patagonia), there were no glaciers extending beyond the foot of the Patagonian Cordillera (41). Yet some authors maintain that Piedmont glaciers existed at least on the Somoncuro Tableland and possibly elsewhere (42). There is agreement that several glacial episodes occurred and that during them glacioeustatic lowering of sea level exposed enormous areas of the Argentine continental shelf (25, 41, 42) (Fig. 2), across which inland lakes and bogs formed (25). The Falkland Islands were not extensively glaciated, but because of the lowering of sea level, were separated from continental South America by less water than at present (Fig. 2) (25, 43).

4. In the central Andes from Ecuador to northwestern Argentina and adjacent Chile (to a latitude of around 30° to 33°S), at least three glacial episodes left discernible remains (44, 45). Glacial periods throughout the area corresponded to pluvial periods [as defined by Flint (46)]. The extent of glaciation and elevation of glacial snowline varied greatly from one mountain to another (44, 45, 47). The greatest actual accumulation of ice was in the Cordillera Blanca of northwestern Perú—despite the fact that, in general, the snowline was depressed more in the east. A glacial moraine has been

found at 1300 meters [the present snowline is about 4000 meters (see Fig. 1)] in the Champara Valley on the western slopes of this cordillera (47). Estimates of temperature depression in the Peruvian Andes (at 3000 to 4000 meters) during glacial maxima are around 7°C (48). Throughout the intermontane areas of northern Perú and across the altiplano, water accumulated into large glacial lakes (Fig. 2; Table 1) (44, 48).

5. The northern Andes of Mérida, Venezuela; the central Andes of Colombia; and the Ecuadorian Andes experienced at least two, and perhaps three, glacial episodes (28). The mountains of Períja on the Colombia-Venezuela border and the Sierra Nevada de Santa Marta, Venezuela, in contrast, were uplifted so late in the Pleistocene that they were affected by only the last glaciation (28). During times of major glacial advance, the snowline was lowered about 1000 meters (Fig. 1) (28, 32). In both Colombia and Venezuela, hundreds of lakes were formed at high altitudes in low areas and depressions dug by ice. Pollen studies of lacustrine sediments of one of these lakes, which covers the Sabana de Bogotá, have provided documentation for the lowering of high montane vegetation zones during glacial periods (32) and have indicated temperature depressions of 11°C during the Riss and 7° to 8°C during the Würm glaciations (at an elevation of 2000 to 3000 meters) (32). One of the few pieces of evidence that definitely supports the contention that glaciations in South America were synchronous with those in North America is the correlation between segments of the cores from this lake and several from North America, all of which have been dated at 14,000 years before the present.

6. Interglacial periods seem to have been warmer than present climates in all parts of the continent. In Colombia, interglacial temperatures were estimated to have been 2° to 3°C above the present yearly average (32). In Patagonia, interglacial climates have been characterized as "more amenable" than those of the current regime (25).

Sea levels rose in interglacial periods to 10 to 50 meters above the present level (1, 49) and inundated such low-lying coastal areas of the continent as the Amazon Basin (16, 50), the area of the Paraguay-Paraná river systems (50), and the lower Orinoco delta (16) (Fig. 2). A large freshwater lake that was formed by glacial meltwater covered vast areas of La Rioja, Mendoza, and San Juan, Argentina (Fig. 2) (50).

7. Extra-Andean glaciation has been proved beyond doubt only on Mount Itatiaia in southeastern Brazil (36, 51). There glacial moraines have been located at an elevation of 2300 meters. At present, this mountain does not even support permanent snow.

8. Throughout the Pleistocene, loess deposits built up in northern Argentina and southern Uruguay. Although much of the loess is now known to be of volcanic rather than glacial origin (52), it was probably deposited most heavily in cool, dry periods (the end of glacial episodes), when the vegetation cover was reduced

and the force of the winds from the Andes was strongest (30, 50, 53). Fossil wood fragments found within the pampas indicate that, at times during the Pleistocene, this region was more humid than it is now, allowing woodlands from the north to extend further south (37).

9. Along the western slopes of the southern Peruvian Andes near Arequipa (15° to 17°S) (54-56) and the eastern slopes of the central Peruvian Andes in the Cordillera de Vilcabamba (10° to 15°S) (55, 56), geomorphological studies have revealed the presence of superimposed landforms that Fenner (55) and Garner (56) have convincingly argued were produced by a succession of arid-humid climates. Because the present climatic regimes on the eastern and western slopes of Perú are antipodal, Garner (56) postulated that they were so throughout the Pleistocene. His theory of a correlation in time between the dry periods of the Cordillera Occidental and the glacial maxima in southern South America (and conversely, dry periods in the Cordillera Oriental with southern interglacial periods) needs more substantiation. Archaeological studies along the coastal desert of northern Perú suggest that this area also experienced cycles of more humid climate earlier in the Pleistocene (57). Landform morphology of the western slopes of the Andes in northern Ecuador, and the slopes of the Venezuelan mountains facing the Caribbean implies that these regions either did not experience Pleistocene arid-humid climatic changes, or that all traces of earlier climates have been eradicated by a long period of humid, tropical climate (55, 56).

10. Investigations of several series of pediments along most of the coast of Brazil and part of the Guyanas have led to their being interpreted as "fossil" formations that were produced during several successive arid cycles separated by humid periods (58). Interpretive correlations of these pediments with times of low sea level (presumably caused by glacioeustatic forces) led to the hypothesis that the arid cycles were synchronous with glacial periods (58). Paleobotanical analyses of deep-sea oceanic cores off the coast of Argentina and Brazil have shown that xerophytic plants grew along these areas during times when the sea was cold (estimated from carbonate content) (59).

11. Geomorphologists who have made reconnaissance flights over central Brazil have intimated that landforms characteristic of arid areas are present in regions that are now humid (60). Further study should document Pleistocene ecological changes within the Amazon Basin.

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Radiation Exposure in Air Travel

Levels of ionizing radiation at high altitudes do not significantly increase the population dose.

Hermann J. Schaefer

The prospect of present-day, large-scale passenger operations shifting from jet aircraft, flying at subsonic speed and at altitudes in the region of 25,000 to 40,000 feet (approximately 7.6 to 12.2 kilometers), to supersonic transports (SST), flying at two to three times the speed of sound and at altitudes of 60,000 to 65,000 feet, has raised the question of what harmful effects the substantially higher levels of environmental radiation could have on crew members and passengers. In connection with these developments, an evaluation and comparison of the environmental radiation levels at conventional jet and at SST altitudes appears necessary.

The author is head of the biophysics division at the Naval Aerospace Medical Research Laboratory in Pensacola, Florida 32512, and conducts operational and experimental radiation monitoring on high altitude flights and space missions. Opinions stated in this article are exclusively those of the author and do not necessarily reflect the view of the Navy Department.

Solar Proton Beams

In discussions of radiation hazards at high altitudes, interest usually centers on solar particle beams produced by flares. Inevitably, the giant solar flare of 23 February 1956 is cited as an event that is estimated to have created, during the first hour, radiation levels well in excess of 100 millirems per hour at an altitude as low as 35,000 feet. At that time, commercial passenger jets were in all likelihood at an altitude that exposed passengers to radiation levels which, in terrestrial installations, would have called for a number of precautionary measures. It must be pointed out, however, that forecasting solar flares has become a routine matter and is now conducted continuously, with a global network of observation stations. It is therefore extremely unlikely that an SST could continue at cruising altitude without knowing that a major flare was in

progress, even if its radiation monitoring instruments were malfunctioning.

The hazard that solar flares create for high-flying aircraft is further alleviated by the infrequent occurrence of the kind of flare that would produce a substantial increase in the level of galactic radiation at an altitude of only 65,000 feet. During solar cycle 19, which lasted from 1954 to 1965, seven such flares occurred. During the smaller maximum of cycle 20, in 1968 to 1969, only a few flares, creating insignificant to moderate increases in the galactic radiation level at SST altitudes, have been observed.

Because large solar flares occur infrequently and the peak of the radiation surge at SST altitude does not last longer than 1 hour at the most, the larger part of the total dose would accrue from galactic radiation—even when exposure at SST altitude is continuous during the period of maximum solar activity. Although complete protection from flare radiation by the avoidance of exposure requires a number of elaborate provisions, such provisions are entirely feasible and would merely entail very infrequent curtailments of SST service. On the other hand, the increased level of galactic radiation at conventional flight altitudes, and all the more at SST altitudes, is an ever-present phenomenon from which no means of protection exists. (The resulting exposure has to be accepted as the price of progress, as is the population's exposure to radiation from medical x-rays or from the use of atomic power.) Thus, the public health aspects of exposure to radiation at high altitudes center on galactic radiation.