

## Pleistocene changes in the flora of the high tropical Andes

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*Abstract.*—Geological data show that high Andean habitats have been available for plant colonization only since the end of the Tertiary. The manner in which plant species moved into these habitats, the times during which, and the methods by which they differentiated during the Pleistocene varied altitudinally and latitudinally along the tropical Andes. The process of speciation in all areas, however, was the same as that in temperate environments, namely, geographic isolation and subsequent divergence. Except on the Altiplano, most plant species expanded their ranges during glacial periods when vegetation zones were lowered. In the northern paramos at elevations above treeline, colonization was greatest during glacial periods but has always occurred in a manner similar to that of oceanic islands. At lower elevations in the northern Andes, and along the Eastern Cordillera, direct migration was possible in glacial times because of increased contiguity of upper montane forest habitats. On the upper slopes of the west coast of Perú, glacial-age plant migrations were fostered more by changes in precipitation than by the lowering of vegetation belts. In all of these areas, interglacial periods were, and are, times of isolation and differentiation. Across the Altiplano in contrast, glacial periods were times of population fragmentation accompanied by differentiation and/or speciation.

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### Introduction

When we try to explain the floristic diversity of tropical regions such as the tropical Andes, we must take into account two components: the ancestral origins and processes by which the wealth of species arrived and developed, and the ecological factors which now permit the particularly high number of taxa to co-exist. One component deals with the origins of diversity and the other with its maintenance. The persistent enigma of tropical species diversity has frequently been approached either by trying to determine if speciation of tropical plants differs from that of temperate organisms (cf. Federov 1966) or by trying to uncover some unique ecological properties of tropical species or environments (cf. Ashton 1969). Explanations based solely on one approach have, in general, been unsuccessful. Part of the failure of past hypotheses to account for tropical species diversity stems from the fact that we do not as yet have a good understanding of the biology of tropical plants. Another, more fundamental, problem with these explanations is that the authors started with the assumption that the tropics were geo-

logically and climatically stable over time and therefore thought that processes of species formation in the tropics must be unique.

We are now, however, in a position to say something about historical events in the tropics and dispel the notion that low latitudes have always provided a benign and uniform environment. While gross geologic and climatic changes can not be considered the only factors responsible for the wealth of tropical species, it is probable that such processes were major factors in determining the directions and methods of colonization and subsequent speciation of a large part of the South American tropical flora.

This paper is intended to show how Pleistocene events led to substantial amounts of colonization, speciation, and extinction in the flora of the high tropical Andes at elevations above 3000 m. Included in this upper region are four principal vegetation types: the paramos of the northern Andes, the upper Andean forests of the eastern and some of the western slopes of the mountains, the puna of the Altiplano and surrounding regions, and

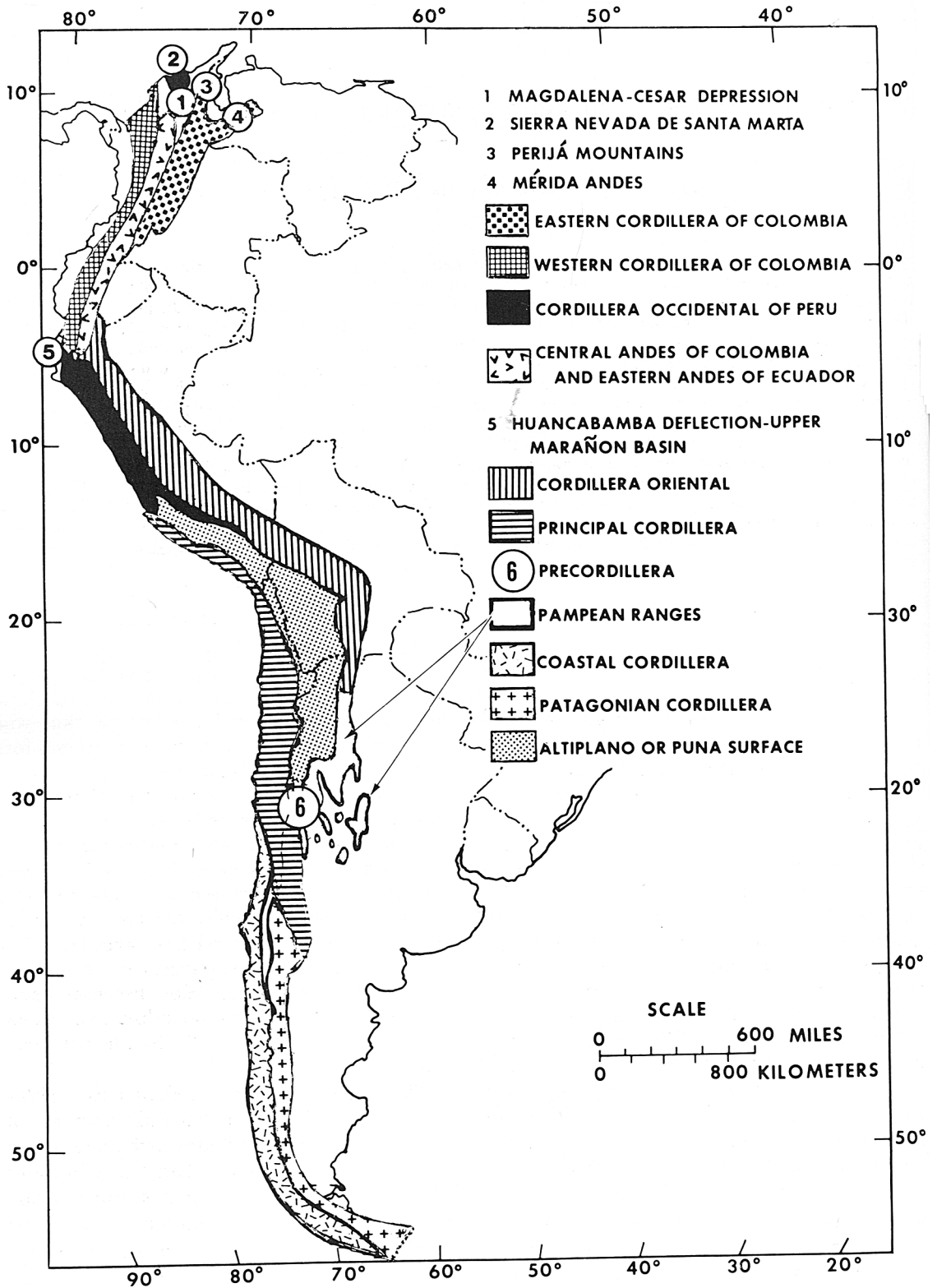


FIGURE 1. The major structural units of the Andes (schematic). Note that boundaries of these geological units often coincide with topographic discontinuities such as the Magdalena and Patía River valleys in Co-

the dry desert scrub of high intermontane valleys and parts of the western slopes of Perú. Discussion will be restricted to the first three, as the desert flora has been treated elsewhere (Sarmiento 1975; Solbrig 1975).

First, we will see that the habitats of the high tropical Andes and consequently the flora with which we are dealing are, for the most part, no older than the end of the Pliocene and that most subsequent evolution must have occurred in the Pleistocene. Second, we will examine the speciation patterns of selected taxa of three principal habitats: the paramos of the northern Andes, the uppermost Andean forests, and the puna of the Altiplano. For the production of the patterns, plant taxa were chosen for which there were complete systematic treatments. For each species in these groups, the precise locality and habitat of every specimen cited in the various revisions were determined. If necessary, the original author's exsiccatae lists were supplemented with later herbarium records (at the Gray Herbarium and U. S. National Herbarium). Maps shown in Figures 4 to 19 were constructed from both these sources of data. Analyses of the resultant distribution patterns, combined with field observations, provide the basis from which conclusions are drawn about the times and pathways of speciation. When possible, these patterns are compared with those of other organisms in the same region and examined in the light of earlier theories of speciation. Finally, we will examine the known Pleistocene history of each area to show what historical and climatic changes contributed to the evolution of the flora in each habitat.

### Andean Geology

The principal structural units of the Andes are shown in Figure 1 and their tectonic histories shown schematically in Figure 2. However, in order to determine more precisely the ages of the high tropical Andean habitats and the time span during which the high elevation flora developed, it is necessary to examine in detail the geological history of each of the

TECTONIC HISTORY OF THE TROPICAL ANDES (SCHEMATIC)

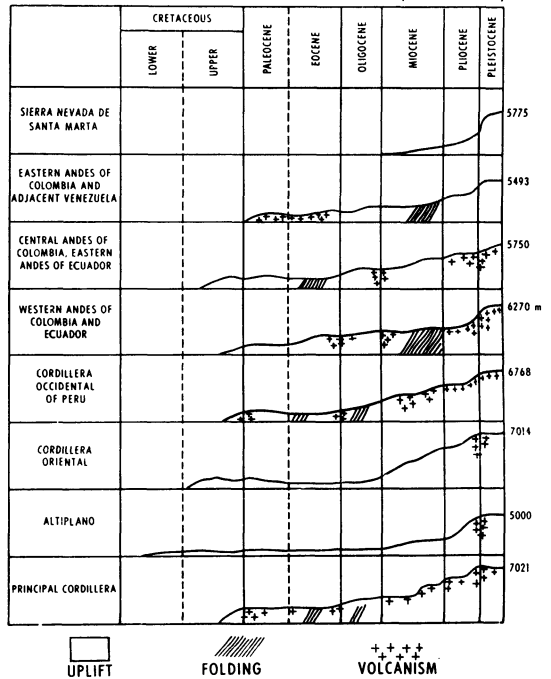


FIGURE 2. Schematic summary of the tectonic and volcanic history of the tropical Andes. The location and extent of the structural units listed on the left are shown in Figure 1. Although uplift began in most cases in the late Cretaceous, the final uplift throughout all the Andes was at the end of the Pliocene or during the Pleistocene.

units shown in Figure 1. Since the development of each of these units has been more or less independent of that of the others, we will discuss them in turn going from north to south along the Andean chain.

*Sierra Nevada de Santa Marta.*—Rising high above the surrounding area, the Sierra Nevada de Santa Marta is the most northern and isolated mass that is commonly considered part of the Andes. The area occupied by this massif was under water until the mid-Tertiary. Uplift began in the late Miocene and continued through the Pleistocene. The principal uplift, probably in the early Pleistocene, block-lifted the Sierra vertically 2000 to 3000 m (Gansser 1955). This late uplift has been inferred because there are traces of only one glacial episode on the summit.

←

lombia, the Marañon River valley in northern Perú, and the Huancabamba Deflection (low area) in northern Perú. Redrawn and modified from Harrington (1956).

*Eastern Cordillera of Colombia.*—The cordillera of eastern Colombia and adjacent Venezuela, which includes the Perijá mountains and the Mérida Andes in Venezuela, began to be uplifted in the Upper Cretaceous but rose above the surrounding areas only in the Paleocene (van der Hammen 1961). Stronger tectonic movement occurred in the mid and upper Oligocene; extensive folding took place in the Miocene; and the entire mass heaved upward in the Pliocene (van der Hammen 1961). The Perijá and Mérida Cordilleras lagged somewhat behind the principal chain to the south and became increasingly separated from one another during the Tertiary as the Maracaibo Depression sank between them (Mencher 1963).

*Central Andes of Colombia and Eastern Andes of Ecuador.*—Although the Central Andes of Colombia and the Eastern Andes of Ecuador are often treated independently, Sauer (1971) decided from their structural similarities that they should be considered as a single unit. In the northern part, the Central Cordillera of Colombia is separated from the eastern Colombian Andes by the César-Magdalena Depression and from the Western Cordillera by the Cauca and Patía valleys. In Ecuador, the mountains descend to the lowlands on the east and are separated from the western ranges by a series of high valleys. The mountains have a general north to south orientation from north-central Colombia to the Huancabamba Deflection (Figure 1) in northern Perú. Uplift began in the late Cretaceous and reached a peak during the mid-Eocene, followed by later Tertiary erosion. In the late Cenozoic, volcanism broke out, reaching its highest level in the late Pliocene and early Pleistocene. This volcanic activity produced the beautiful snow-capped cones of Antisana, Cotopaxi, Chimborazo, etc. which now dot the Central Valley of Ecuador.

Sauer (1971), on the basis of plant and animal fossil evidence, fossil soils, and glacial geology, surmised that the last uplift of both the Cordilleras of Ecuador occurred in the Pleistocene and raised the mountains at least 2500 m. Van der Hammen, however, concluded that the final uplift was at the end of the Pliocene (1972a).

*Western Cordillera of Colombia and Ecuador.*—The Western Cordillera of Colombia

and Ecuador extends from northwestern Colombia southward through Ecuador almost to the Peruvian border. Movements of this unit began in the Cretaceous although the coastal section emerged later in the Paleocene. The first appreciable uplift occurred in the Eocene (van der Hammen 1961) and reached a climax at the end of that period. Some activity took place in the mid-Oligocene but the most recent, and still continuing uplift, began in the Miocene. The most significant phase of this uplift (at least in the Ecuadorian sector) was at the end of the Pliocene and/or beginning of the Pleistocene (Sauer 1971).

*Cordillera Occidental of Perú.*—The Cordillera Occidental of Perú, composed of a series of ranges, begins south of the Huancabamba Deflection at about 5° S latitude where it parallels the Pacific Ocean and continues south until it abuts against the Altiplano at about 14° S. Included in this structural unit are the Cordilleras Blanca and Nigra which are separated from the eastern Cordillera by the deep upper Marañón River Valley. Uplift in northwestern Perú began in late Cretaceous times when the present cordillera was outlined (Jenks 1956b; Petersen 1958). In the Miocene, there was volcanic activity in the south and central parts which initiated a Pliocene orogeny. The final uplift seems to have occurred between the first and second major Pleistocene ice advances (Jenks 1956b).

*Cordillera Oriental.*—The Cordillera Oriental, like the Cordillera Occidental, is composed of a series of ranges, but it is arranged in a more complex fashion than those along the Pacific coast and stretches from northern Perú around the eastern rim of the altiplano and into Argentina. It includes the Cordilleras de Ausangate, Oriental, Central and Vilcabamba in Perú, and Postosí, Los Frailes, Tres Cruces, Oriental, Real and Apolobamba in Bolivia.

There seem to have been three major times of activity in the history of these mountains; the first was in the Cretaceous (Jenks 1956b; Ham and Herrera 1963; Lohmann 1970; James 1971). Sandstone deposits indicate that, before the Miocene, this area was lower than land to the west of it. In the Miocene strong folding occurred but more important movement took place in the Pliocene with overthrusting (Ahlfeld 1970). It was during the Pleistocene, however, that the Cordillera Ori-

ental was forcefully jammed against the Altiplano, producing the modern jagged narrow ridges (Lohmann 1970).

**Altiplano.**—The Altiplano is a broad, relatively flat high altitude plateau stretching from southern Perú to northern Argentina. The area was first permanently raised above the sea in the Cretaceous but throughout much of the Tertiary remained low, receiving sediments from the higher areas of the Western Cordillera (Turner 1970). In the Miocene it was further uplifted due to compression and thrusting of the Eastern and Western Cordilleras (Lohmann 1970). However, significant uplift occurred only post mid-Pliocene (Ahlfeld 1970) and possibly as late as the Pleistocene (Ahlfeld and Braniša 1960). The deep deposits which now cover the surface of the Altiplano are not from early erosion but from lacustrine sedimentation which Lohmann (1970) states could have been deposited during the Pleistocene when the surface had an extensive lake system (Figure 20). The present deep valley of the La Paz River is a very recent product of intense, presumably glacial, erosion (Ahlfeld and Braniša 1960).

**Principal Cordillera.**—The Principal Cordillera that forms the western edge of the Altiplano begins in southern Perú and continues southward to central Chile and northwestern Argentina. Until the Cretaceous, it was lower than areas to the east of it, but at the close of the Mesozoic several episodes began that gradually raised it to its present altitude of over 6000 m (Brüggén 1950). These uplifts included a slight Oligocene rise, a major Miocene upthrust, a weak displacement (especially in the Frontal Cordillera of Argentina) in the Pliocene, and a final major Pliocene uplift (Harrington 1956; Ahlfeld and Braniša 1960; Herrero-Ducloux 1963). Petersen (1958) concluded that Pliocene and Quaternary uplifts amounted to 3000 to 4000 m.

This brief summary of the geological history of the tropical Andes reveals several important facts for an analysis of the evolution of the high altitude flora. First, the tropical Andes (see Figures 1 and 2) are actually composed of several independent structural units. Second, although all of these units had a somewhat unique geologic development, all of them, except Santa Marta, were initially uplifted in the Cretaceous or Paleocene. Third,

even though the Andes rose gradually throughout the Tertiary, the last, and in most cases the major, uplift of all the tropical ranges occurred near the end of the Pliocene or even during the Pleistocene. This late final uplift of as much as 1000 to 3000 m means that a study of the evolution of the high Andean flora is, in fact, a study of Pleistocene events. Finally, we can predict that the low valleys which separate the structural units and which became more pronounced as the mountains were progressively raised in the Tertiary have been, and still are, important barriers to dispersal of high altitude elements.

With these points in mind, we can turn to an examination of the vegetation types and distribution patterns of various plant taxa that now inhabit these high elevation habitats.

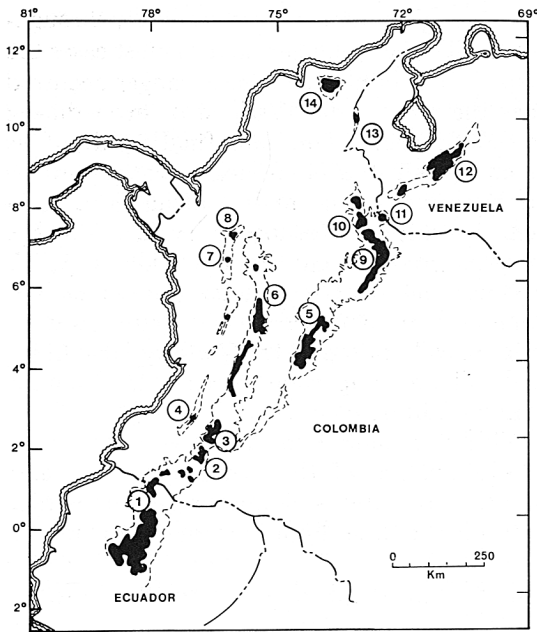
## The Paramos of the Northern Andes

Above treeline, the mountains of Colombia, Venezuela and parts of Ecuador and Perú are covered by a low vegetation known as paramo (Cuatrecasas 1957). The dominant plants of these cold, humid, sometimes boggy meadows are grasses, principally *Calamagrostis* and Compositae mixed with herbaceous gentians, lupines, buttercups and St. John's-wort.

Some of the most characteristic genera of the paramos have radiated within the high northern Andes. For example, *Baccharis* has 37 high altitude Colombian species (Cuatrecasas 1967), *Diplostephium* has 50 species in the same areas (Cuatrecasas 1969) and *Espeletia*, the most distinctive paramo genus, has about 90 species restricted to supra-forest habitats of Ecuador, Colombia and Venezuela (Cuatrecasas, pers. comm.).

Because of the relief of the northern Andes, the paramos are distributed in variously sized patches separated from one another by a "sea" of montane forest covering the intervening low areas (Figure 3). Seen from above, the paramo patches resemble islands of an archipelago (Figure 3).

Three theories, those of Chardon (1938)/Chapman (1917), F. Vuilleumier (1970), and van der Hammen (1972 a, b) have previously been proposed to explain the origin and development of the paramo biota. These hypotheses are briefly outlined below and the patterns of the modern flora are examined in the light of each.



**FIGURE 3.** The distribution of paramo "islands" in the northern Andes. The outline of the "islands" was determined by tracing the 3500 m contour line (except for Tamá, Perijá, and Farallones for which the 3000 m contour line was used). The dark area in many cases includes both the mountain top glaciers and the paramo vegetation zone. The names of the numbered paramos used in the analysis are listed in Table 1. The dotted line is drawn at about the 2500 m contour line and indicates a possible tree line during glacial times. The glacial "islands" outlined by the dotted line are those included in Table 4 and used in the second analysis (Table 5).

*Chardon/Chapman's hypotheses.*—Chardon's work (1938), while shown to be partially incorrect for some groups (notably birds, Haffer 1970b) still stands as one of the most comprehensive theories of the development of the Colombian high altitude fauna and flora. Chardon concluded that various components of the biotas were derived via three major pathways: vertical evolution, that is, the gradual development of species from low elevation stocks as the mountains were uplifted (*most higher plants, parasitic fungi, and insects*); "land" migration from the southern South American lowlands (birds and some other vertebrates); or by passive aerial transport (fungi and ferns). Chardon predicted that groups arriving via the first pathway would have increasing endemism with increasing altitude, and he predicted that taxa following the second pathway of land migration or

short distance "hopping" or the third pathway would show less endemism with increasing altitude.

In the light of recent data, Chardon's interpretation of the origin of the high altitude flora does not seem to pertain. For example, an important group of higher plants, including many dominants, are not derived from low elevation Neotropical ancestors but from species found at high elevations elsewhere in South and/or Central America, or from groups characteristic of cool temperate climates. Such important genera include *Sisyrinchium* (Iridaceae), *Bomarea* (Alstroemeriaceae), *Cerastium* (Caryophyllaceae), *Ranunculus* (Ranunculaceae), *Draba* (Cruciferae), *Lupinus* (Leguminosae), *Gentiana* and *Halenia* (Gentianaceae), *Bartsia* (Scrophulariaceae), *Lysipomia* (Campanulaceae), and *Erigeron*, *Lucilia*, *Senecio* and *Werneria* (Compositae), all of which occur primarily in cold montane or higher latitude regions. Other important genera such as *Jamesonia*, *Espeletia*, and *Diplostephium* are exclusively Neotropical, but authors who have studied these groups (Tryon 1962; Smith and Koch 1935; Cuatrecasas, pers. comm. and in prep.) agree that, while ancient ancestral stocks may have grown at lower elevations, the radiations of these genera have been primarily horizontal within high elevation habitats.

A third group of paramo genera, notably members of the Ericaceae, Vacciniaceae, Melastomataceae, and Rubiaceae, also of Neotropical origin, do contain species related to, and derived from, taxa of low elevations. Species in this group alone could have evolved vertically as envisioned by Chardon (1938).

Chardon (and subsequent authors, e.g., Murillo 1951) realized that the distribution of the paramos resembles islands, but he drew no parallels with patterns of evolution on oceanic islands. He also knew that the Andes had been increasingly uplifted during the Tertiary and that glacial episodes lowered vegetation zones. Yet, he mentioned migrations during glacial periods as having been important only in the case of *Espeletia*.

Recent studies which have taken into account both dynamic colonization and glacial migrations have led to differing, but not mutually exclusive, explanations of the origin of the paramo biota.

*Vuilleumier's study of the origin of the*

*paramo avifauna*.—In 1970, F. Vuilleumier ascribed the origin of the modern paramo avifauna to immigration and extinction processes known to be important for the biota of oceanic islands (MacArthur and Wilson 1967). In making this analogy, Vuilleumier (1970) had to assume that species numbers on continental paramo “islands” are in equilibrium. The concept of predictable island species diversity begins with the assumption that the islands involved have remained constant in size and relative distance from one another (and/or a source area) over a long enough period of time for an equilibrium of species numbers to have been reached. Under such conditions, the model further assumes that colonization is from constant source areas, that rates of immigration from these areas are uniform, and that rates of extinction do not vary on a specific island. Given the constancy of these parameters, the number of species expected on any island can be derived from an equation with the area of the island and its distance from source areas as the principal independent variables.

For his analysis, Vuilleumier (1970) used the 83 species of birds breeding on the paramos, most of which, in his opinion, colonized from Ecuador, a southern source area (Figure 3). His results showed excellent correlations ( $R^2 = .97$ ) between the number of species predicted from an equation with area and distance from Ecuador as the principal independent variables and the number of species actually breeding on a given paramo. He therefore concluded that for the breeding birds, the paramos are an insular system colonized by dispersal across unacceptable habitats. A corollary would have been that in the time necessary for the equilibrium to have been reached, the paramo islands essentially remained constant in size and relative distance from one another. Mauriello and Roskoski (1974), using ridge traces, recently reanalyzed Vuilleumier’s data. Their work refined, but did not alter, his results.

In contrast to Chardon’s prediction about endemism of high elevation bird species, Vuilleumier (1970) found that the number of endemic taxa increased rather than decreased with increasing paramo elevations and that endemism was more highly correlated with

distance to the nearest large “island” than with altitude.

Vuilleumier was aware of Pleistocene climatic changes that occurred in the northern Andes and used them to explain, in part, discrepancies from perfect coincidence of the actual number of breeding bird species on a paramo and the predicted number. However, the close approximation of the actual and predicted values implies that the present situation is near equilibrium and that, for the avifauna, Pleistocene climatic effects were not of lasting importance.

The alternative hypothesis, that range extensions allowed by Pleistocene climatic changes have been the major factor in determining the distributions of the biota of the high northern mountains, has been stressed by van der Hammen (1972a) and Haffer (1970a, 1974).

*Van der Hammen’s studies of Pleistocene fossil microfloras*.—Van der Hammen (1972a), van der Hammen and Gonzales (1960), and Geel and van der Hammen (1973) have clearly documented, by means of paleobotanical studies, that during Pleistocene glacial periods temperatures at high elevations in Colombia were depressed and vegetation belts lowered, in some areas as much as 1500 m. A simple downward shift of existing belts would have caused an increase in the horizontal extent of upper elevation vegetation zones (Figure 3). At the same time, the isolation of paramo “islands” would have been reduced or eliminated. Consequently, plant and animal immigration or range extensions would have been greatly increased. If within the last 50,000 years rates of immigration, “island” areas, and inter-“island” distances fluctuated, the numbers of plant and some animal species on the paramos might not be in equilibrium. If the flora and fauna were in disequilibrium, one should see relatively poor correlations between the present size of the paramos, their respective distances from source areas, and the numbers of species inhabiting them. Situations of modern mountain areas with non-equilibrium numbers of mammal taxa have been found in the Great Basin Ranges of North America by Brown (1971) and in numbers of bird species on the Venezuelan tepuis by Cook (1974). We can, therefore, examine floristic elements of the

TABLE 1. Numbers of species and endemics of selected plant taxa and physical parameters of paramo islands.<sup>a</sup>

|                     | S                 | E                  | A                                    | ELE                        | DL   | DE                       | DS                                    | AVD  |
|---------------------|-------------------|--------------------|--------------------------------------|----------------------------|--|--------------------------|---------------------------------------|--|
|                     | Number of species | Number of endemics | Area (km <sup>2</sup> ) <sup>b</sup> | Elevation (m) <sup>d</sup> | Distance to nearest large Paramo (km) <sup>e</sup> | Distance to Ecuador (km) | Distance to nearest Paramo south (km) | Average distance of two closest Paramos (km) |
| PARAMO <sup>c</sup> |                   |                    |                                      |                            |  |                          |                                       |  |
| 1 Chiles            | 14                | 0                  | 412                                  | 1260                       | 36   | 31                       | 15                                    | 25   |
| 2 Pasto             | 19                | 1                  | 56                                   | 770                        | 25   | 112                      | 25                                    | 38   |
| 3 Puracé            | 38                | 3                  | 911                                  | 1170                       | 25   | 232                      | 10                                    | 17   |
| 4 Farallones        | 16                | 2                  | 45                                   | 1050                       | 100  | 345                      | 70                                    | 222  |
| 5 Sumapaz           | 42                | 4                  | 1856                                 | 1060                       | 166  | 540                      | 69                                    | 117  |
| 6 Quindío           | 34                | 4                  | 956                                  | 1900                       | 22   | 547                      | 22                                    | 104  |
| 7 Frontino          | 4                 | 1                  | 22                                   | 580                        | 142  | 705                      | 51                                    | 96   |
| 8 Paramillo         | 2                 | 1                  | 45                                   | 460                        | 51   | 772                      | 51                                    | 252  |
| 9 Cocuy             | 37                | 2                  | 2295                                 | 1995                       | 156  | 802                      | 10                                    | 83   |
| 10 Santurbán        | 26                | 5                  | 303                                  | 600                        | 10   | 945                      | 7                                     | 8  |
| 11 Tamá             | 16                | 3                  | 67                                   | 613                        | 38   | 990                      | 28                                    | 72   |
| 12 Mérida           | 21                | 3                  | 1901                                 | 1502                       | 81   | 1155                     | 81                                    | 66   |
| 13 Perijá           | 8                 | 5                  | 112                                  | 700                        | 249  | 1170                     | 91                                    | 45   |
| 14 Santa Marta      | 26                | 14                 | 472                                  | 2300                       | 91   | 1230                     | 91                                    | 500  |

<sup>a</sup> Data (148 species) from: Astereae, Cuatrecasas 1969 and Aristiguieta 1964 (97 sp.); *Puya*, Smith 1957, 1971 (21 sp.); *Loricaria* (Compositae) Cuatrecasas 1954 (5 sp.); *Niphogeton* (Umbelliferae), Mathias and Constance 1951, 1962 (10 sp.); *Jamesonia* (Gymnogrammeaceae) Tryon 1962 (15 sp.). Specific tabulation available upon request.

<sup>b</sup> Area calculated as in Vuilleumier, F. (1970).

<sup>c</sup> See Figure 4 for location of the Paramos.

<sup>d</sup> The base elevation = 3500 m for all paramos except Tamá, Perijá and the Farallones which = 3000 m. Elevation = the base elevation subtracted from the highest peak of the mountain.

<sup>e</sup> The nearest large island = the nearest paramo with an area  $\geq 200$  km<sup>2</sup>.

paramos to assess whether modern species numbers approach an equilibrium value.

*The origin of the paramo flora.*—In order to ascertain the magnitude of the correlations of the modern areas of the paramo “islands” and their distances from potential source areas with modern plant species numbers and numbers of endemic taxa on each, data for the presence or absence of 151 species (an important component of the total flora) were assembled (see Table 1 for sources). All of these species belong to genera not derived from taxa of lower elevations, or only distantly related to low elevation genera. The paramos used in the study are shown in Figure 3 and listed in Table 1. Many of these paramos are the same as those used by Vuilleumier (1970), except that Cachira, Batillon, Cende and northern Ecuador were excluded because each lacked sufficient data for plant species. However, three additional paramos for which there was good floristic data, Los Farallones, Frontino, and Pasto were added to this analysis.

In addition to the number of species and

endemic taxa, the following physical parameters were recorded for each paramo: area, elevation, distance from Ecuador, distance from the nearest paramo larger than 200 sq. km, distance to the nearest paramo to the south, and average distance from the nearest two paramos of any size in any direction. The upper right diagonal of the matrix in Table 2 gives all possible pair correlations of these variables and their logarithms.

These variables were then used in a program of stepwise multiple regression (BMD-02R; Dixon 1973) using three different models (linear, semi-log and log-log) to see which parameters would best predict the number of species and endemics on a given paramo. The results of these regressions are given in Table 3.

Basically, these results agree well with those of Vuilleumier (1970) on the paramo avifauna and with studies of plants on true islands (Johnson and Raven 1970, 1973).

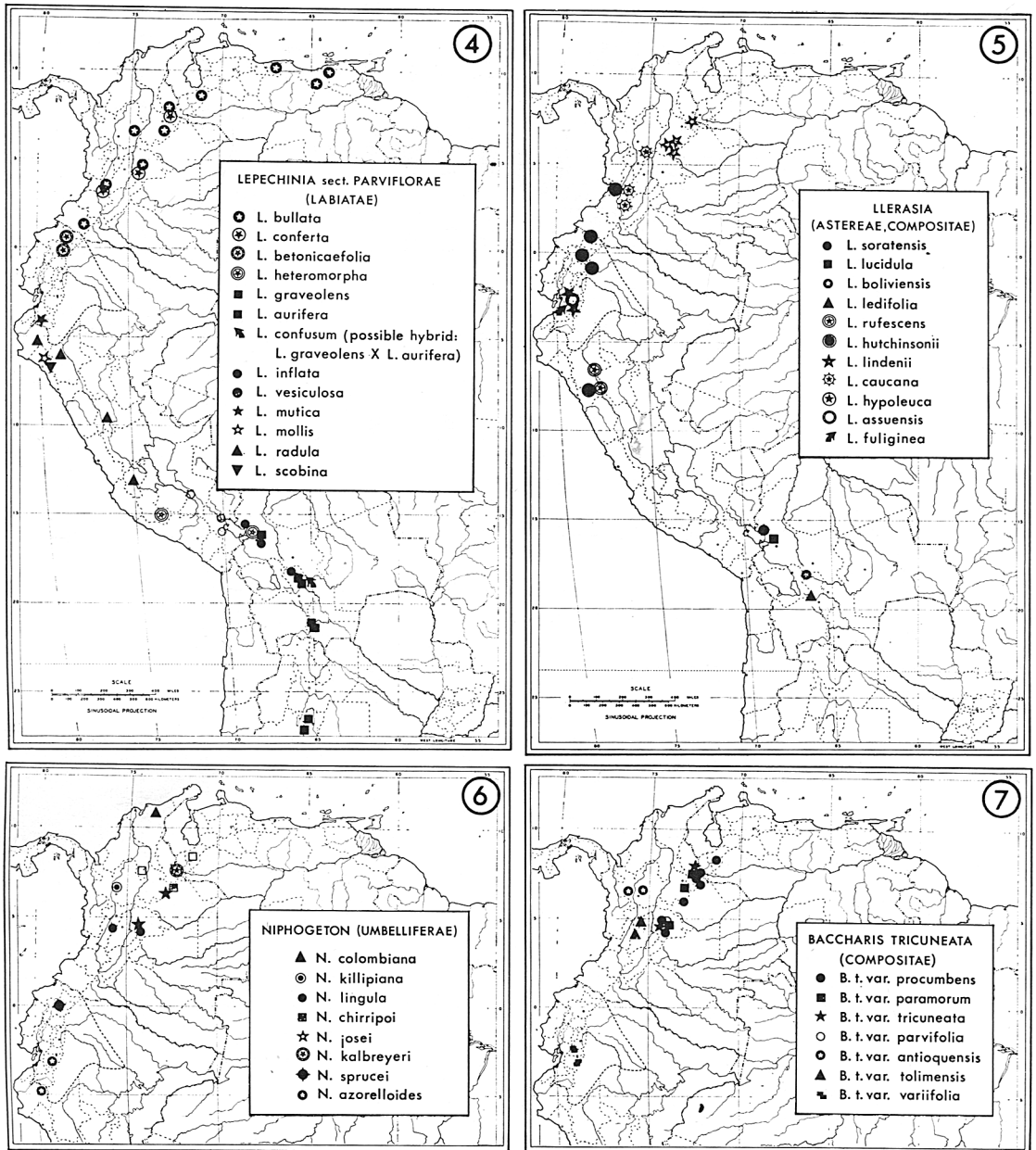
The situation with the endemic taxa is less clear. Unlike the studies of both Vuilleumier (1970) and Johnson and Raven (1970, 1973)



TABLE 2. Correlation matrix of modern<sup>a</sup> and glacial-age<sup>b</sup> paramo islands and/or their logarithms.<sup>c</sup>

|       | S      | E      | A      | ELE   | DL     | DE    | DS    | AVD    | L-S   | L-E   | L-A    | L-ELE  | L-DL   | L-DE  | L-DS   | L-AVD  |
|-------|--------|--------|--------|-------|--------|-------|-------|--------|-------|-------|--------|--------|--------|-------|--------|--------|
| S     |        | .274   | .722** | .580* | -.095  | -.137 | -.289 | -.083  |       | .461  | .823** | .640*  | -.134  | .004  | -.385  | -.153  |
| E     |        |        | .027   | .521  | .127   | .586* | .462  | .682** | .319  |       | .254   | .631   | .106   | .488  | .305   | .350   |
| A     | .959** |        |        | .583* | .229   | .111  | -.040 | -.132  | .600* | .200  |        | .630*  | .281   | .167  | -.120  | .012   |
| ELE   | .754   |        | .651   |       | .027   | .123  | .081  | .425   | .598* | .471  | .693** |        | .154   | .060  | -.007  | .348   |
| DL    | -.720  | -.812* | -.477  |       |        | .371  | .610  | .090   | -.149 | .164  | .028   | .032   |        | .371  | .534   | .289   |
| DE    |        |        |        |       |        |       | .518  | .342   | -.125 | .610* | .081   | .003   | .309   |       | .394   | .274   |
| DS    |        |        |        |       |        |       |       | .560   | -.245 | .376  | -.118  | .062   | .695** | .452  |        | .620*  |
| AVD   |        |        |        |       |        |       |       |        | -.138 | .397  | -.100  | .303   | .288   | .327  | .544*  |        |
| L-S   |        |        | .853*  | .851  | -.701  |       |       |        |       | .516  | .755** | .685   | -.202  | -.083 | -.366  | -.249  |
| L-E   |        |        |        |       |        |       |       |        |       |       | .441   | .431   | .056   | .562* | .190   | .133   |
| L-A   | .806** |        |        | .775* | -.815* |       |       |        | .763* |       |        | .743** | .023   | .048  | -.253  | -.148  |
| L-ELE | .747   |        | .651   |       | -.526  |       |       |        | .848* |       | .813*  |        | -.154  | -.056 | -.026  | .253   |
| L-DL  | -.739  | -.830* | -.504  |       |        |       |       |        | -.720 |       | -.819* | -.547  |        | .311  | .666** | .534   |
| L-DE  |        |        |        |       |        |       |       |        |       |       |        |        |        |       | .364   | .349   |
| L-DS  |        |        |        |       |        |       |       |        |       |       |        |        |        |       |        | .709** |
| L-AVD |        |        |        |       |        |       |       |        |       |       |        |        |        |       |        |        |

<sup>a</sup> Values for modern paramos are in the upper right of the matrix.  
<sup>b</sup> Values for glacial-age paramos are in the lower left of the matrix. Not all of the independent variables used for the analysis of the modern paramos were used in the historical analysis (see Table 4).  
<sup>c</sup> L indicates the logarithm of a variable.  
 \* Indicates significant at the .05 level.  
 \*\* Indicates significant at the .01 level. For modern islands, 14 paired observations, 2 df,  $r \geq .532$  for .05 level,  $\geq .661$  at .01 level. For glacial islands,  $r \geq .754$  at .05 and  $\geq .874$  at .01.



FIGURES 4–7. The distributions of high altitude genera in the northern Andes. Only *Niphogeton* (Figure 6) is restricted to the high paramos. Note that the distributions of species of other genera, which fringe into, or are related to, species of the upper Andean forests, are broader than those of many species of *Niphogeton*. **Figure 4.** Distribution of species of *Lepechinia* in northern South America. *Lepechinia* is closely knit genus native to the New World and Hawaii. Most of its species, including the 40 found in South America, are found in montane habitats. According to Epling, the species listed here may actually belong in 5 species groups: (1) *L. scobina* and *L. radula*, (2) *L. inflata* and *L. vesiculosa* (3) *L. bullata*, *L. betonicaefolia*, *L. heteromorpha* and *L. paniculata*, (4) *L. graveolens*, *L. aurifera* and *L. confusa*, (5) *L. mollis* and *L. mutica*. Note the possible hybrid in the eastern part of the Altiplano. Data from Epling (1948). **Figure 5.** *Llerasia* is a genus of the uppermost montane forests. The 11 species, native to the high northern and central Andes, are trees, shrubs or vines. From Cuatrecasas (1970). **Figure 6.** *Niphogeton*, a characteristic element of the high northern Andes, has many species with restricted distributions. The remaining species are shown in Figure 6. *N. ternata* also occurs in Costa Rica. **Figure 7.** The varieties of *Baccharis tricuneata* show distributions similar to those of species of other genera. The influence of the river valleys separating the Colombian

TABLE 3.<sup>a</sup> Regressions of total plant species diversity and endemic taxa of the paramo habitat islands in modern and glacial times.

| Time    | Dependent variable | Model   | Independent variable in order entered                    | Multiple correlation coefficient R <sup>2</sup> |
|---------|--------------------|---------|--|---|
| MODERN  | TOTAL SPECIES      | semilog | <i>log A, log DS, log AVD, log DL, log DE, log ELE</i>   | .7337   |
|         |                    | log-log | <i>log A, log DL, log ELE, log AVD, log DE, log DS</i>   | .7111   |
|         |                    | linear  | A, DL, ELE, DS, DE, AVD                                  | .6584   |
|         | ENDEMIC TAXA       | linear  | DAV, DE*, ELE, A, DL, DS                                 | .7177   |
|         |                    | log-log | <i>log DE*, log A*, log DL, log DS, log ELE, log AVD</i> | .6790   |
|         |                    | semilog | <i>log DE, log ELE*, log DL, log DS, log AVD, log A</i>  | .5701   |
| GLACIAL | TOTAL SPECIES      | linear  | A, ELE <sup>b</sup> , DL                                 | .9565   |
|         |                    | log-log | <i>log ELE*, log DL, log A</i>                           | .8410   |
|         |                    | semilog | <i>log A*, log ELE, log DL</i>                           | .7169   |

<sup>a</sup> See Simpson 1974 for a discussion of these results and a comparison with the Galapagos Islands. Values in italics contribute significantly to R<sup>2</sup> at the .01 level. \*values contribute significantly at the .05 level. <sup>b</sup> This variable does not contribute significantly as indicated in Simpson 1974.

a linear model provided better predictions than semi-log or log-log models. However, the linear model and the curvilinear models were close in their amounts of predictability. Also, whereas Johnson and Raven found a correlation (although not significant) between the number of endemics and area, the plants of the paramo show no such correlation. Rather, they agree better with Vuilleumier's conclusions that the number of endemic species can be best predicted by some measure of isolation, the most useful of which was the average distance from the two closest "islands."

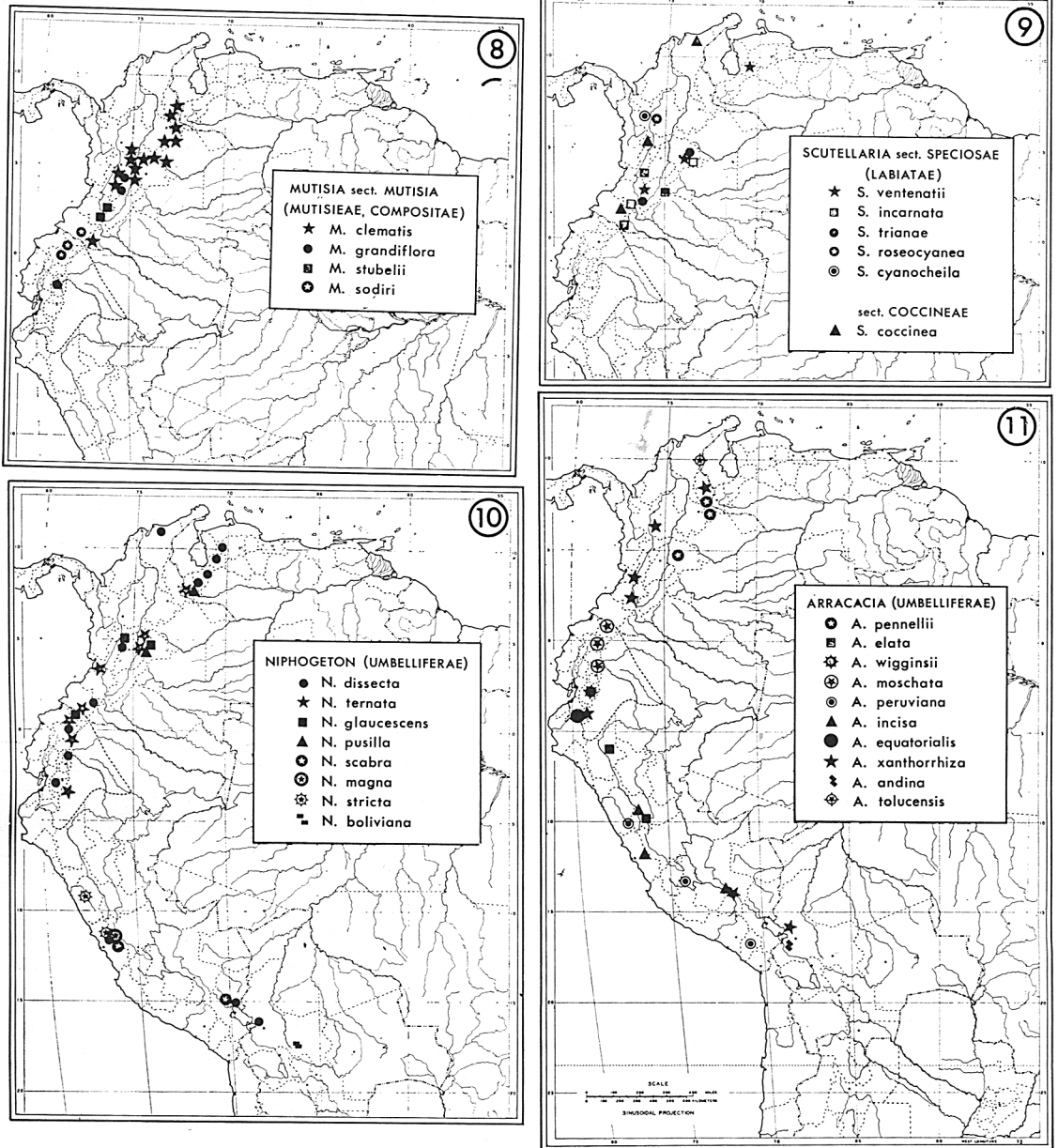
The results using multiple regression led first to the conclusion that dispersal to, and subsequent differentiation of, this segment of the flora of the paramos has proceeded like that of oceanic islands. Yet we know that during glacial periods the vegetation zones were lowered and migration patterns should have been altered. Consequently, in order to test whether the modern situation might still reflect glacial conditions, I ran the same analy-

sis as that described above for the modern paramo patches ("islands" 1 to 14 in Table 1 and Figure 3) except that I used the glacial-age form of the paramos, assuming that there was a constant lowering of vegetation zones (Figure 3, Table 4; Simpson 1974). The area of these glacial "islands," their distances from source areas, and their elevations were used as independent variables against the number of modern species included within that area (Table 4). The lower left diagonal of the matrix in Table 2 gives the correlations of all of these variables and their logarithms. The table shows significant correlations between area and the number of species ( $r = .959$ ) and the log of the number of species and the log of the area ( $r = .763$ ). In addition, there were high (although not significant) negative correlations between the number of species and the distance to the nearest source of propagules ( $r = -.739$ ) and their logarithms ( $r = -.720$ ).

The results of the multiple regression analysis show that area and distance in a linear

←

cordilleras is evident. The remaining varieties (excluding the Patagonian variety) are shown in Figure 14. Data from Cuatrecasas (1967, 1968).



FIGURES 8–11. Species distributions of high altitude genera of the northern and central Andes. **Figure 8.** *Mutisia* is a genus of predominantly shrubby vines. The 59 species in the genus occur primarily in the upper regions of the Andes, but some are found at low elevations in eastern South America. The distribution of *M. clematis* indicates colonization from the south up part of the Central Cordillera and for a long distance along the Eastern Cordillera. Data from Cabrera (1965). **Figure 9.** Unlike *Lepechinia* (Figure 4), species of *Scutellaria* are poor colonizers. The genus as a whole is cosmopolitan and contains about 300 species but few species have reached islands. About 113 species occur in the New World. The distributions of the species in Figure 9 indicate that species migrated along the cordilleras in glacial periods and have left isolates now given specific status in some areas. The influence of the Patia River valley in separating *S. roseocyanea* and *S. cyanocheila* is obvious. Data from herbarium specimens and Epling (1942). **Figure 10.** Distributions of the only two widespread species of *Niphogeton* in the Northern Andes (compare with Figure 6) and the species of the central Andes. Note that there is differentiation of species along the western Cordillera of the northern Peruvian Andes and that two species show disjunct distributions between the western slopes at about the latitude of Lima and the eastern slopes near Cuzco (see Figure 20 for localities). **Figure 11.** *Arracacia* is a genus native to

model accounts for 95% ( $R^2 = .949$ ) of the variation in the number of species on the glacial "islands" (Table 3). The semi-log model, while accounting for less of the variation, still provides almost as good a prediction as any of the models using the modern paramo parameters ( $R^2 = .841$ ).

Glacial episodes thus seem to have played a major role in determining the present diversity of the high paramo plant taxa used in the preceding analysis. However, glacial climatic changes may have been even more important in the evolution of the floristic elements derived from Neotropical stocks, especially those related to groups growing at the same latitudes but at elevations below 3000 m. Most of the upper montane plant groups which belong in this category can not be included in a statistical analysis because their taxonomies are incomplete.

A qualitative examination of this group of floristic elements, however, indicates how glacial climatic changes affected these species and how their migrations differed from those of the paramo species included in Table 1. First, as would be expected from the greater latitudinal distribution of their habitats, species of genera found in upper montane forests tend to have geographically more extensive distributions than those restricted to the upper paramo zone (compare Figures 4, 6, 8; the latter two figures show species derived from low elevation stocks).

Another characteristic of the species derived from Andean forest elements is that their distributional limits tend to coincide with basic geological discontinuities between structural units (Figure 1). Distributional patterns of several genera of the Andean forests which have species that range into the paramos are shown in Figures 4 to 11. The lack of east-west continuity and the influence of the valleys separating the three cordilleras of Colombia are evident in *Llerasia* (Compositae, Figure 5) and *Scutellaria* (Labiatae, Figure 9). Similar patterns with the Patía and Magdalena Valleys acting as barriers have been

shown to occur in birds (Haffer 1970b). Yet, at some time in the past, high elevation species manage to cross most of these barrier zones. The paleobotanical evidence for lowered vegetation zones in glacial times (van der Hammen 1972) suggests that such times of facilitated migrations were during glaciations.

Many species also show a break in distribution coincident with the low area of the Huancabamba Deflection (5 in Figure 1) in northern Perú (Figures 5, 7, 11, 12). This region has been noted as the area of distributional limits for many organisms (*Celmisia*, Compositae, Solbrig 1960; *Jamesonia*, Tryon 1962; and various animal taxa, B. Vuilleumier 1971). Because this area is now much lower than many inter-andean valleys and because it has always been lower than surrounding regions, it has been a significant barrier to north-south migrations.

### The Upper Montane Slopes of Western Perú

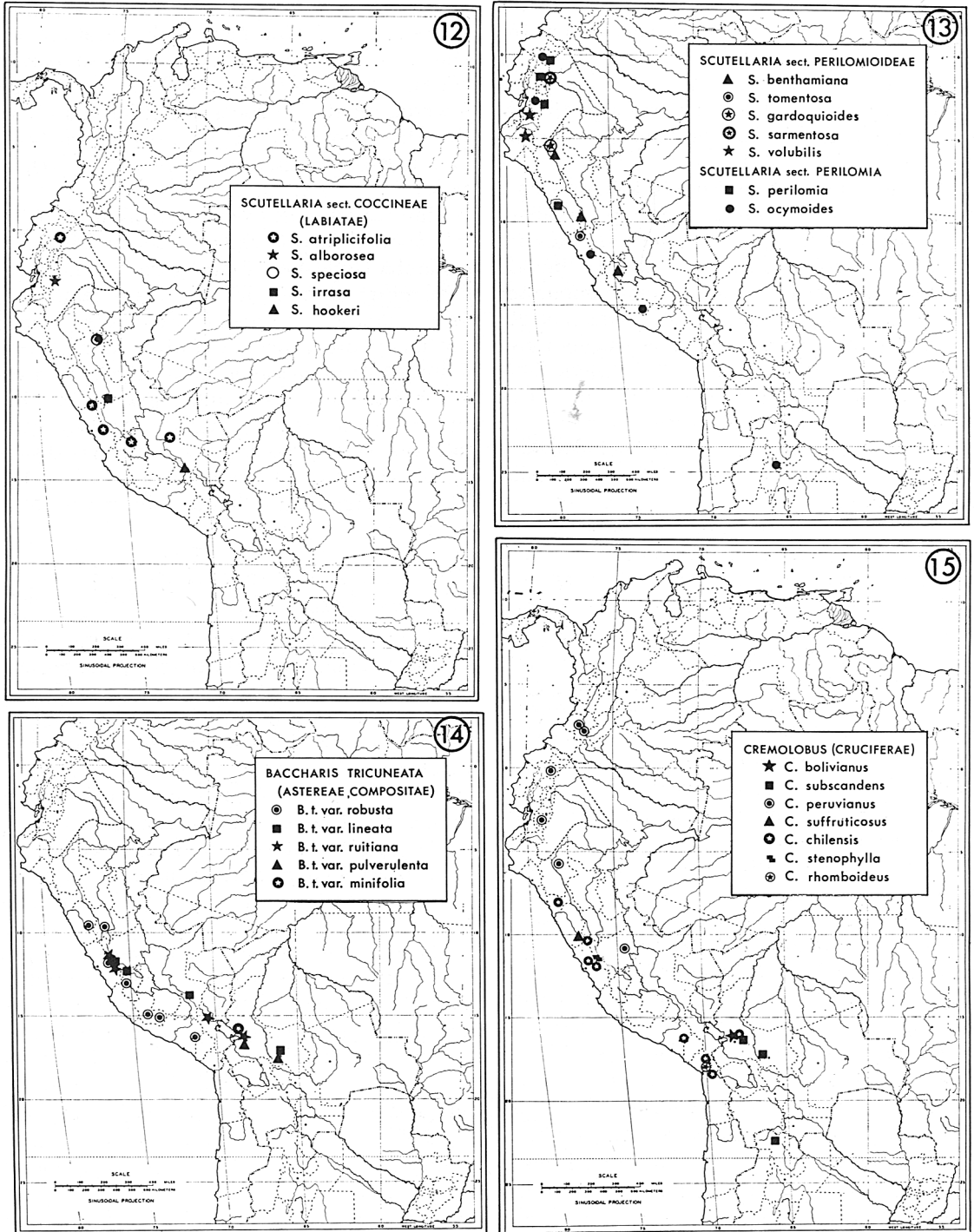
Although separated from the northern Andes by the Huancabamba Deflection, the eastern slopes of the Peruvian Andes are much like those of the north in that they are covered by montane forest. Evidence for the lowering of vegetation zones on the eastern slopes (Hastenrath 1971b) and the absence of evidence for drastic Pleistocene climatic changes (Garner 1959) suggest that plant migrations along this slope proceeded in ways similar to those of the eastern and western slopes of the northern Andes.

The upper elevations of the western slopes of the Peruvian Andes, however, exhibit a more complex pattern than those of the eastern forested slopes. Recent evidence suggests that the modern distributions of plants found on these slopes can be attributed more to Pleistocene changes in precipitation than to the lowering of vegetation zones per se brought about principally by temperature depression alone.

In contrast to the eastern slopes, the upper western slopes are now arid to semi-arid and

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the New World with 10 of its 77 species inhabiting high, fairly humid, regions of the Andes. The abrupt break in species at the latitude of northern Perú is clearly visible. The sporadic occurrence of two species in isolated humid areas of the Western Cordillera and the former ability of *A. incisa* to cross the Andes near the latitude of Lima is also evident. Data from Constance (1949).



FIGURES 12–15. Species of the central Andes show the sporadic occurrence of upper Andean forest elements on the western slopes of the Andes of north-central Perú and disjunctions in distribution between the western slopes of the Peruvian Andes near Lima and the eastern slopes of the Andes near Cuzco. **Figure 12** and **Figure 13**. Species of three other sections of *Scutellaria* (see Figure 10) data from Epling (1942). **Figure 14**. The remaining varieties of *Baccharis tricuneata* (see Figure 7). Varieties of this species show eastern-western slope disjunctions in Perú like species of many genera (compare Figure 16) and show differentiation

TABLE 4. Number of species of plant taxa<sup>a</sup> and physical parameters of "glacial paramo islands."<sup>b</sup>

|                 | S                 | A                       | ELE                        | DL                              |
|-----------------|-------------------|-------------------------|----------------------------|---------------------------------|
|                 | Number of species | Area (km <sup>2</sup> ) | Elevation (m) <sup>c</sup> | Distance to nearest Paramo (km) |
| <b>PARAMO</b>   |                   |                         |                            |                                 |
| 1, 2, 3, 6      | 63                | 24311                   | 3210                       | 45                              |
| 5, 9, 10, 11    | 72                | 23782                   | 2995                       | 52                              |
| 7 and 8         | 6                 | 2632                    | 1580                       | 67                              |
| 4. Farallones   | 16                | 4427                    | 1550                       | 63                              |
| 12. Mérida      | 21                | 5782                    | 2502                       | 52                              |
| 13. Perijá      | 8                 | 112                     | 1200                       | 75                              |
| 14. Santa Marta | 26                | 1755                    | 3300                       | 75                              |

<sup>a</sup> Plant taxa are those used in Table 1.  
<sup>b</sup> The glacial islands are considered to be those enclosed by the dotted line in Fig. 3.  
<sup>c</sup> Elevation = the highest elevation less the Pleistocene tree-line assumed to be 2500 m as in Fig. 3.

predominantly covered by scrubby vegetation. There is, consequently, a striking difference in the floristic composition of most of the floras of the two slopes. In many cases, species which occur on the Pacific-facing slopes do not occur on the eastern slopes of the Cordillera Oriental north of 12° S and vice versa.

Figures 5 and 12 to 15 illustrate this lack of shared species. When species do occur on both slopes, they almost always also occur north of 8° S and often into Ecuador. This implies there has been little or no dispersal of upper montane elements (non-puna species) over the Andes between latitudes 8° and 12° S. Apparently, the only route by which a species could reach both slopes is around the low area (Huancabamba Deflection) of northern Perú. Although extensive data are lacking for plants, a parallel phenomenon is found in bird species of the upper montane forests. Table 5, a summary of the distribution of the avifauna of the upper montane forests of the eastern and western slopes of the northern Andes, shows that there is a significant correlation

TABLE 5. Distribution of the avifauna of the central high Andes of Perú and Bolivia.<sup>a</sup>

| Distribution of Breeding Bird Species within the Central Andes  |  |  |                              |
|---|--|--|------------------------------|
| Montane Slopes  |  | Altiplano  |                              |
| Restricted to either the Pacific or Amazonian Slopes  | Disjunct, but occurring on both slopes | Altiplano only                                     | Altiplano and montane slopes |
| <i>Number of Species</i>  |  |  |                              |
| 16  | 14                                     | 13   | 27                           |
| Northern Range of Avian Species Occurring on the Upper Montane Slopes of the Central Andes but not on the Altiplano |  |  |                              |
| Occurs at and/or north of the Huancabamba Deflection in northern Perú   |  | Occurs only south of the low area of northern Perú |                              |
|   |  | <i>TOTAL</i>                                       |                              |

*Restricted to one slope of the Andes in Perú* 2 14 16

*Occurring on both slopes of the Andes in Perú* 10 4 14

$\chi^2 = 10.803$ ; highly significant at less than the .01 level

<sup>a</sup> Data supplied by F. Vuilleumier, *in litt.*

between the occurrence of a bird species north of the low area of northern Perú and its presence on both slopes of the northern Peruvian Andes.

A closer examination of the distributional patterns of plant and animal species along the western slopes yields evidence that migrations down the western slopes were, in part, fostered by Pleistocene climatic changes. Although most of these slopes are covered by arid scrub vegetation there are several canyons in areas of Perú between 8° and 16° S that harbor patches of humid upper montane forests similar in aspect and general composition to the

← on the eastern side of Lake Titicaca (compare Figure 16). After Cuatrecasas (1967, 1968). **Figure 15.** The 7 species of *Cremolobus* are mostly found at high elevations although a few have a wide elevational distribution. The species indicate differentiation, probably in isolated rather humid areas, along the western slopes of central Perú. As in other taxa, a species of the western slopes has populations found on the eastern slopes near Cuzco. In Bolivia, there is an area of secondary overlap east of Lake Titicaca. Data from Khanna and Rollins (1965).

ceja forests on the eastern slopes. The Koepckes (1958, 1961) have extensively studied these areas of forest and believe that they represent fragments of a formerly more continuous band of forest along the Pacific slopes. Since data (discussed above) indicate that there was essentially no exchange of upper montane elements across the Andes, the plants and birds common to these forested areas must have migrated from north to south down the western Andes. While these forests are similar in overall composition to the forests of the eastern slopes, the Koepckes (1958, 1961) and Paynter (1972) have found substantial amounts of endemism in the different forest pockets. Figures 13 and 15 show patterns for *Scutellaria* and *Cremolobus* that also have spotty distributions and isolated endemic species.

It is important to note here that there is no marked diminution in numbers of species in these pockets going from north to south along the coast. Consequently, it does not appear that species colonized down the slopes by long distance dispersal or short "hopping." Rather speciation and distribution of elements along the upper slopes follows a pattern which would be predicted by an initially continuous distribution that was subsequently disrupted. But a belt of former continuous vegetation implies that precipitation was greater in the past than at present.

If, however, we look at the evidence from the Pacific islands off the coast of Ecuador, we find that it shows that these islands were no wetter in the Pleistocene than they are at present. Colinvaux's (1972) recent paleobotanical work from the Galapagos Islands implies that present day high elevation lakes dried up at times of low sea level (glacial periods). Hutchinson's (1950) work on the guano islands had previously suggested the same climatic change. We are thus faced with the paradox of increased precipitation at mid- and upper elevations of the west central Andes, synchronous with continued or increased aridity at sea level.

*Pleistocene climatology of the eastern Pacific.*—We now have, from a variety of independent sources, data relating to the climate of the Pleistocene along the west coast of Perú. First, as discussed above, biological patterns strongly suggest the previous existence of a more continuous band of subtropical rain-

forest along the upper slopes of the western Andes of Perú. The existence of such a forest zone would have been possible only if precipitation were greater than that of the present. Evidence from two other sources also indicates that, probably during parts of glacial periods, the Pacific slopes of the Peruvian Andes were wetter than at present. First, the occurrence of iron oxides and fossil drainage patterns reported by Garner (1959) and Tricart et al. (1969) imply former humid conditions. Secondly, Hastenrath's work (1971a, 1971b) on the disproportionate Pleistocene lowering of the snow line on the western slopes clearly demonstrates that they experienced a glacial increase in precipitation.

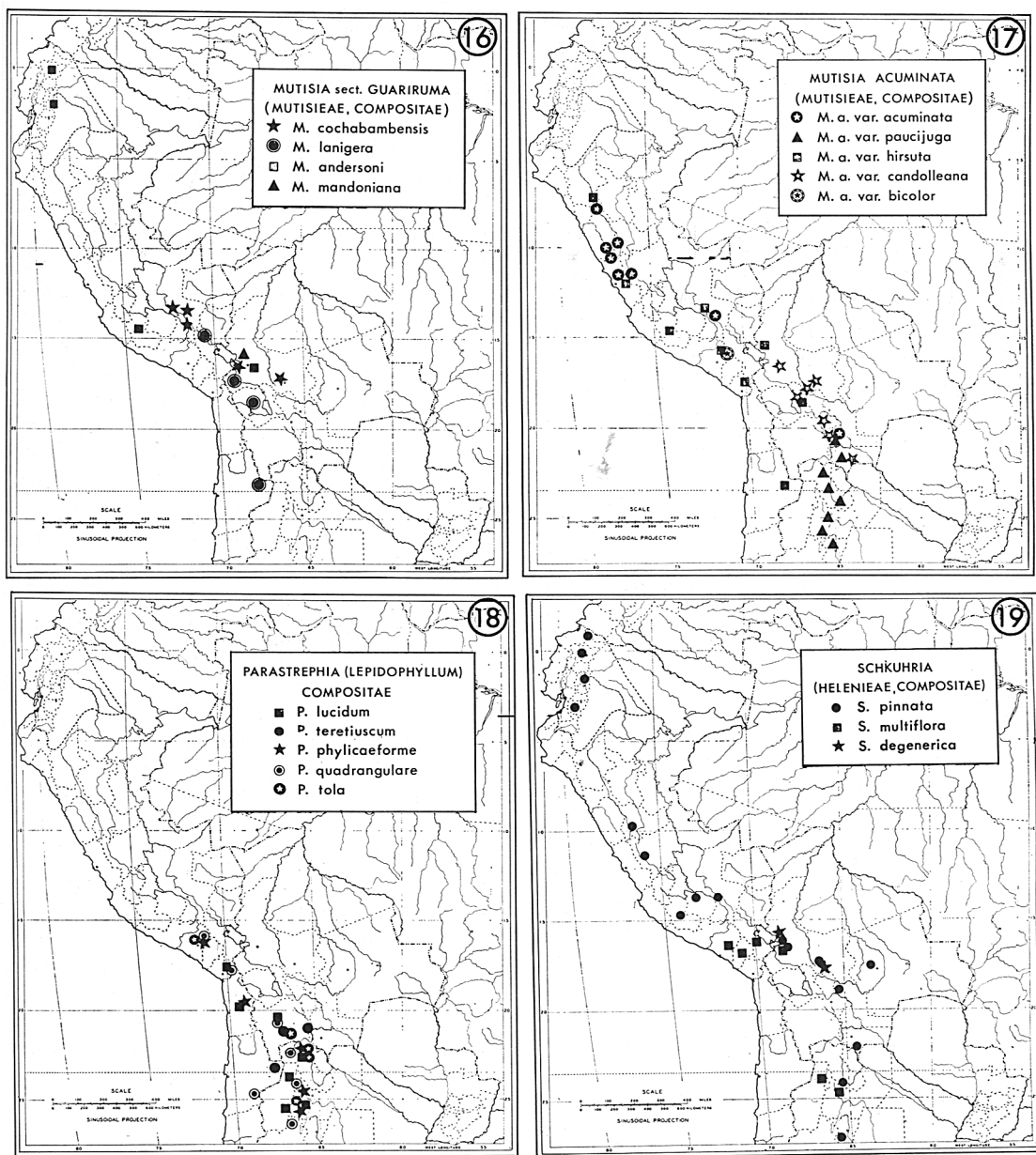
At lower elevations, however, a different situation prevailed in glacial times. The coastal areas seem to have remained arid during glacial periods (Tricart et al. 1969) but apparently during times of deglaciation received large amounts of melt water from the Andes (Tricart 1963).

Other evidence comes from studies of oceanic sediments and the deposition of guano on islands in the eastern Pacific. The work of Arrhenius (1959) shows that there was increased planktonic production in the equatorial zone of the Pacific and hence increased upwelling during glacial periods. Hutchinson's locations of guano deposits (1950) on islands now covered with tropical forest also seemingly point to increased aridity and upwelling in glacial cycles.

Several attempts have been made to explain the climatic factors responsible for the changes in precipitation and upwelling in the eastern Pacific during the glacial periods, but none fully explain the available data.

The following simple mechanism recently proposed (Simpson 1975) is consistent with the fossil and modern data from the eastern Pacific. The precipitation, currently dependent upon the relationship between ocean and land temperatures (Bowman 1916), would presumably have been under the same influence in glacial times. We can therefore find an explanation by examining the glacial temperatures of the Pacific Ocean off the coast of Perú relative to the temperatures of the land. The increased upwelling documented by Hutchinson (1950) and Arrhenius (1959) would, in all probability, have caused surface





FIGURES 16–19. Distribution of species in the central Andes and across the Altiplano. Note the coincidence of an area of differentiation just east or southeast of Lake Titicaca. **Figure 16.** Species of *Mutisia* found on the Altiplano indicate that populations were isolated northeast and southwest of Lake Titicaca and have subsequently expanded their ranges. **Figure 17.** One variety of *Mutisia acuminata* also shows distributional limits near Lake Titicaca. The localities of *M. acuminata* var. *hirsuta* and *M. acuminata* var. *acuminata* indicate disjunct areas along the western slopes where conditions are mesic enough for it to grow. The distribution of *Mutisia acuminata* var. *paucijuga* like that of *Parastrephia* (compare Figure 18) indicates an isolate in the southern part of the Altiplano. Data for Figures 16 and 17 from Cabrera (1965). **Figure 18.** *Parastrephia* is the characteristic “tola” of the western Altiplano. Although the five species now show substantial amounts of overlap in distribution, it is probable that speciation was caused by fragmentation of populations in the western part of the Altiplano in glacial periods. Data from Cabrera (1945). **Figure 19.** The distribution of the South American species of *Schkuhria*. The other two species in the genus occur in the United States and Central America. *S. multiflora* is also found in southwestern U.S. and Mexico. The distribution of the species around the altiplano suggests isolation in the region east of Lake Titicaca and in the western part of the puna. From Heiser (1945).

areas in the equatorial Pacific to experience a decrease in temperature. In addition to increased coastal upwelling, an increase in the strength of the southeast trades occasioned by strong anticyclonic activity would have brought very cold water from far south in the Pacific to equatorial latitudes. The presence of fossils of Foraminifera north of 20° S, which are now found predominantly south of 36° S, indicates how cold the ocean temperature must have been off the coast of Perú in glacial times. Luz's studies (1973) in the eastern tropical Pacific indicate a glacial temperature drop in the ocean of more than 5°C well off shore. We can thus assume a 5 to 6°C sea surface glacial temperature depression along the coast of Perú.

Van der Hammen (1972b) has recently postulated a decrease in land temperature of 4 to 5°C in the tropical American lowlands during glacial periods, but there is little firm evidence to support such a significant depression at low elevations (at high elevations in the tropics, however, temperature depressions may have exceeded 5°C, van der Hammen 1972a, b; Hastenrath 1972). Even if we assume a glacial decrease in the coastal land temperature of 3 to 4°C, it still would not have equaled the decrease in the offshore ocean temperature. The glacial contrast between winter ocean and land temperatures would have been similar to the present summer relationship, and during a glacial summer, the ocean/land contrast would have exceeded that of modern summers. As a result, rain and perhaps snow would have fallen on the Andean slopes more or less continuously during the year and particularly heavily in the glacial summer. The coastal areas, in contrast, would have been dry for most of the year because of the reduction, or absence, of fog.

In interglacial times (such as the present) the opposite conditions would have prevailed, and the coast would have been humid during part of the year and the high Andean slopes arid. In addition, during interglacials, the Pacific anticyclone would have been comparatively weak, allowing penetration of the equatorial rain-bringing westerlies. In an interglacial with conditions warmer than those of the present, these conditions would have been accentuated.

## The Puna of the Altiplano

The Altiplano is a high, broad plateau (Figure 1) that, like the paramos, was uplifted late in the Pliocene (Figure 2) and is covered by non-arborescent vegetation. However, this type of vegetation, known as puna, is strikingly different in floristic composition and aspect from that of the northern mountain peaks. In contrast to the paramos, the puna is a dry, almost unbroken, barren steppe. The sparse vegetation changes from a rather open tussock-grass shrubland in the driest western part to a more meadowlike grass-scrub formation in the wetter eastern section.

Although various authors (cf. Troll 1968) have divided the east and west into two vegetation zones, the dry and the wet puna, there is actually a more or less gradual, although noticeable, transition between them. One would expect this type of a clinal change to occur across the kind of moisture gradient found from west to east across the Altiplano. Certainly there are at present few obvious ecological barriers on the plateau analogous to the deep valleys of Colombia or the Huanca-bamba Deflection in northern Perú. Yet, if we look at distribution patterns across the Altiplano, we find genus after genus with several sympatric species or taxa which show distributional boundaries at specific localities. Examples can be seen in *Lepechinia* (Figure 4, Labiatae), *Niphogeton* (Figure 10, Umbelliferae), *Llerasia* (Figure 5), *Mutisia* (Figures 16 and 17), *Parastephia* (Figure 18), *Baccharis* (Figure 14), and *Schkuhria* (Figure 19), all Compositae. Several bird species complexes such as *Muscisaxicola alpina*, *Agriornis montana* (both Tyranidae, F. Vuilleumier 1971), *Astheres flammulata* (Furnariidae, F. Vuilleumier 1968) and *Diglossa* (Coerebidae, F. Vuilleumier 1969) have partially similar patterns. An examination of these distributions strongly suggests that in the past, populations of many taxa were isolated in at least three major (and probably several minor) areas. One such area seems to have been east and northeast of the region of Lake Titicaca, another in western Bolivia, and a third in a southern sector of the Altiplano.

A study of the glacial-age landscape (Figure 20) shows that the Altiplano was largely covered by a series of lakes during cold periods. The extent of this Pleistocene lake system is

revealed by lacustrine deposits several hundred meters thick across the areas of the puna surface which it covered (Lohmann 1970). The combined effects of the northern Titicaca lake system (Figure 20) and the extensive glaciation of the Cordillera Real east of La Paz probably effectively blocked north-south biotic migrations around the eastern edge of what is now the present lake and, thus, separated plant populations to the north and south (Figures 14 to 17). Another area of isolation seems to have been southwest of the Pleistocene Lake Titicaca (Figures 14, 16 and 18). A third major area of effective isolation might have been south of the enormous glacial Lago Minchín (Figure 20 and Figures 15, 17 and 19). In addition, the mountain ridges of the Cordilleras de los Frailes, Quimsa Cruz and Lipez which serve now as weak barriers would probably have been more effective as barriers to east-west exchange during glacial periods because of the expansion of ice.

It is still too early to attempt to pinpoint any Altiplano "refuge areas," but the evidence does indicate that there was sufficient ecological alteration of the puna surface during the Pleistocene to have caused fragmentation of Altiplano populations and allowed differentiation of taxa. During previous interglacials and at the present time, such populations re-expand their ranges and again come into contact leading to patterns with hybrid zones and secondary overlap.

## Conclusions

The flora of the tropical Andes above 3000 m has colonized and differentiated primarily during the Quaternary. Geological studies show that the Andes were not high enough in most regions prior to the end of the Tertiary to have had appreciable habitats fringing and above treeline. However, the movements of plants into high montane habitats and their subsequent speciation proceeded differently in different parts of the Andes. In northern Colombia and Venezuela, mountain tops now support disjunct areas of paramo (wet meadow) habitat composed both of elements not closely related to species at lower elevations and of taxa related to and derived from Andean forest species. A preliminary analysis of part of the first component of this flora indicates that the species it includes colonized

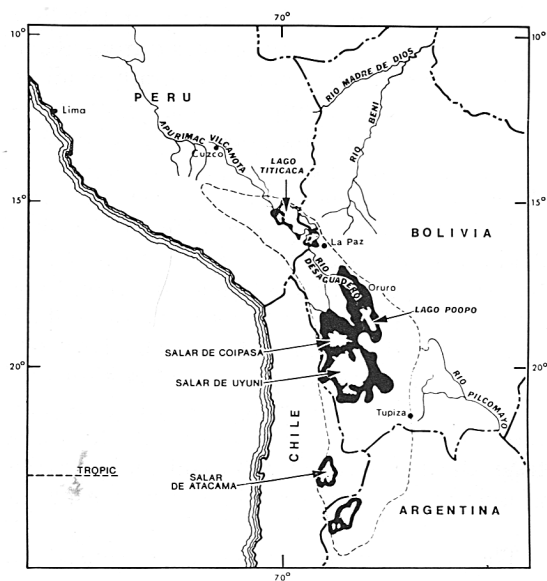


FIGURE 20. The extent of Pleistocene lake systems (darkened area and all the surface included within it) across the Altiplano during glacial times. Note that Lago Titicaca extended to the eastern edge of the Altiplano. Glacial ice from the bordering mountains actually flowed into the lake. The combination of the extended lake and mountain glaciers seemed to have prevented north-south migrations during glacial periods along the eastern side of the lake. The glacial lake Minchín which included Lago Poopó and the Salares de Coipasa and Uyuni probably isolated populations of plants to the north and south of it. Redrawn from Kessler (1963).

in a manner analogous to the way in which plants colonize oceanic islands. Significant correlations have been found between the areas of modern paramos, their distances from source areas, and the numbers of plant taxa now inhabiting them. However, higher correlations exist between glacial parameters of the paramos and the number of species found on modern counterparts. This analysis suggests that the majority of colonization occurred in glacial periods when plant propagules were able to disperse more easily because of the increased size of the paramos and the reduced distances between them. During such times, processes of immigration and extinction may have approached an equilibrium.

Paramo species related to upper Andean forest elements show distribution patterns that indicate migration by direct range expansion. Particularly along both slopes of the ranges in Venezuela, Colombia and Ecuador but also

along the eastern Andes of Perú and Bolivia, the lowering of vegetation zones during glacial periods seem to have been important in allowing the spread of upper montane elements. Evidence of such migrations in glacial times has been documented by paleobotanical evidence in Colombia.

The Pacific-facing slopes of the central Andes also experienced a series of significant, but different, kind of vegetation pulsations. The now arid upper western slopes of Perú were humid during glaciations. This increased humidity allowed expansion of a band of high altitude mesic evergreen forest that is now found only in relictual pockets. At the same time, the low coastal areas and many Pacific islands were more arid than they are at the present time.

These arid-humid cycles were caused by persistent strong winds, accelerated ocean currents, and increased coastal upwelling in glacial periods that in turn maintained a contrast between ocean surface and land temperatures throughout the year. The resultant continuous strong sea breezes produced appreciable rainfall all year at high elevations similar to that which now falls only in the summer.

On the Altiplano, puna plant species patterns indicate a Pleistocene history of weak fragmentation which is reflected in modern localized species, hybrid zones, and large areas of secondary overlap. During glacial periods a huge system of lakes and rivers formed across the Altiplano, and the location of the water barriers and large glacial fields it formed correspond in location to modern species boundaries and areas of secondary overlap.

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