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The Ecological Geography of Cloud Forest in Panama

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Few places in the tropics have been less affected by man than the remote cloud forests. Because of their disjunct distribution and relative isolation, cloud forests are particularly interesting from ecological, biogeographic, and taxonomic viewpoints, but they are not often easy of access and, therefore, are poorly known. During 1964 to 1967 I devoted full time to collecting and studying amphibians and reptiles in the Republic of Panama; consequently I established camps in as many remote regions as possible, including selected areas of cloud forest. Because this habitat is virtually ignored in Panamanian literature, the present account should be a useful preliminary source of information. Hopefully, other biologists will be encouraged to visit these places to make more detailed studies, and for that reason I have included notes from my itineraries. I confess that I viewed the landscape through the eyes of a zoologist, with no forethought of writing the present paper; thus, the physiognomic descriptions are not all that I would like them to be, and anything of floristic importance is virtually lacking. Some original data on frogs (*Eleutherodactylus*) are presented in the discussion to illustrate a few of the problems that can be studied in cloud forests, even during brief visits.

I have not given coordinates for the localities discussed, for to do so would imply greater geographical sophistication than in fact exists. Seldom have I been able to pinpoint my camps on the inadequate maps

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available to me during my field work. Nevertheless, sufficient information is given at least to point the prospective traveler in the right direction and, for present purposes, the localities are adequately mapped in figure 1. Elevations were taken from a Lufft pocket altimeter (20-meter graduations), which was read immediately upon arriving at a campsite, and reset, if necessary, before leaving. I believe that most of my readings were accurate within ± 100 meters. Certainly, they have proved more reliable than many calculated elevations on available maps. For example, some maps show the Altos de Quia on the Colombian border (near longitude 77° 30′ W.) to be 1361 meters above sea level; but, after opening a trail, the summit was found to be only 830 meters, and it lacked the anticipated cloud forest.

ACKNOWLEDGMENTS

Field work in Panama was made possible by a grant from the National Institutes of Health (GM 12020) to the University of Kansas. Mr. Tomás Quintero assisted capably in almost all of my work and in so doing acquired an unusual familiarity with his country. Drs. William E. Duellman and Linda Trueb were my companions in the high, wet forests of Cerro Pando, and it was a memorable trip. For making arrangements and for other favors in eastern Panama, I am grateful to Mr. Pablo Othón and to Mr. and Mrs. Enrique Othón, El Real, Darién. At the other end of the country, the help of Messrs. Ratibor and Wladimir Hartmann, Santa Clara, Chiriquí, was likewise indispensable. My travels commenced at Panama City, where incessant "red tape" would have meant fewer trips had it not been for the help of my wife, Joan, and the staff of the Gorgas Memorial Laboratory, particularly Dr. Martin D. Young, Mr. Pedro Galindo, Dr. Carl M. Johnson, and Mr. José Antonio Tarté. Finally, without the expert woodsmanship and strong backs of a host of *morenos, indios,* and *latinos,* I would never have reached my destinations.

The following physiographical, climatic, and vegetational descriptions are based mainly on my own observations, and on inferences drawn from various maps, especially those in the "Atlas de Panamá" (Comisión del Atlas de Panamá, 1965) and the 12-sheet 1:250,000 "Mapa General de la República de Panamá" (Dirección de Cartographía, 1967). But I also profited greatly from information supplied by various colleagues, especially Dr. William E. Duellman, Dr. Graham B. Fairchild, Mr. Pedro Galindo, Dr. Charles O. Handley, Jr., and Mr. Charles M. Keenan, to all of whom I offer sincere thanks. Several persons have read the manuscript, and for critical comments I thank Drs. Charles M. Bogert, William E. Duellman, A. W. Küchler, and Richard G. Zweifel.

PHYSIOGRAPHY OF PANAMA

The Isthmus of Panama (fig. 1) is a narrow sigmoidal arch that lies entirely within the tropics and has an east-west axis (although it is often thought that it runs north and south). The continental divide on the western part of the isthmus is formed by the Cordillera de Talamanca and the Serranía del Tabasará, which end to end comprise a narrow, rugged highland that is nearly unbroken up to the 1200-meter contour; there are several extinct volcanoes in the region. Elevations above 2200 meters are frequent in the Talamanca Range, with the Volcán de Chiriquí (Volcán Barú) lying south of the divide and being the highest mountain (3250 meters) in the Republic. Elevations average well below 2000 meters in the more eastern Tabasará chain, with the apparently unexplored Cerro Santiago being the highest point at about 2800 meters. Cerro Santiago is a volcano according to Terry (1956, p. 11) and as indicated by its size and the appearance of its summit (as seen from a boat off the north coast). A low volcanic uplift of about 1000 meters is situated east-southeast of the main Tabasará ridge and includes the biologically important localities of El Valle and Cerro Campana. To the northeast is a hilly, lowland region through which the Panama Canal was cut. The Azuero Peninsula forms a major irregularity on the southern (Pacific) side of the western part of the isthmus and at its extremity contains an isolated highland with a few peaks of nearly 1500 meters elevation.

East of the Canal Zone region is a broad, low uplift, the drainage of which furnishes most of the water for Gatun Lake and the canal; few peaks rise above 800 meters, and the highest is Cerro Jefe at about 980 meters. From here eastward the continental divide extends close along the Atlantic coast, with little, if any, west to east differentiation between the Cordillera de San Blas and the Serranía del Darién. Elevations along this part of the divide average less than 500 meters until near the Colombian border, where the divide swings southward and Cerro Tacarcuna rises to about 1875 meters. Several small but significant highlands rise from the peneplained and nearly base-leveled Pacific lowlands of eastern Panama. The biologically unexplored Serranía de Cañazas, which lies near the coast at the eastern edge of Panamá Province, is a system of razorback ridges that seem to exceed 800 meters in places; the crests of these ridges are occasionally visible from the air. Three anticlinal fault blocks (Terry, 1956, p. 68) project northward from near the Colombian border in extreme southeastern Panama. The highest, the Serranía de Pirre, is an unbroken ridge with a maximum elevation of 1550 meters. A lower ridge lies between the Pirre ridge and the Serranía del Sapo,

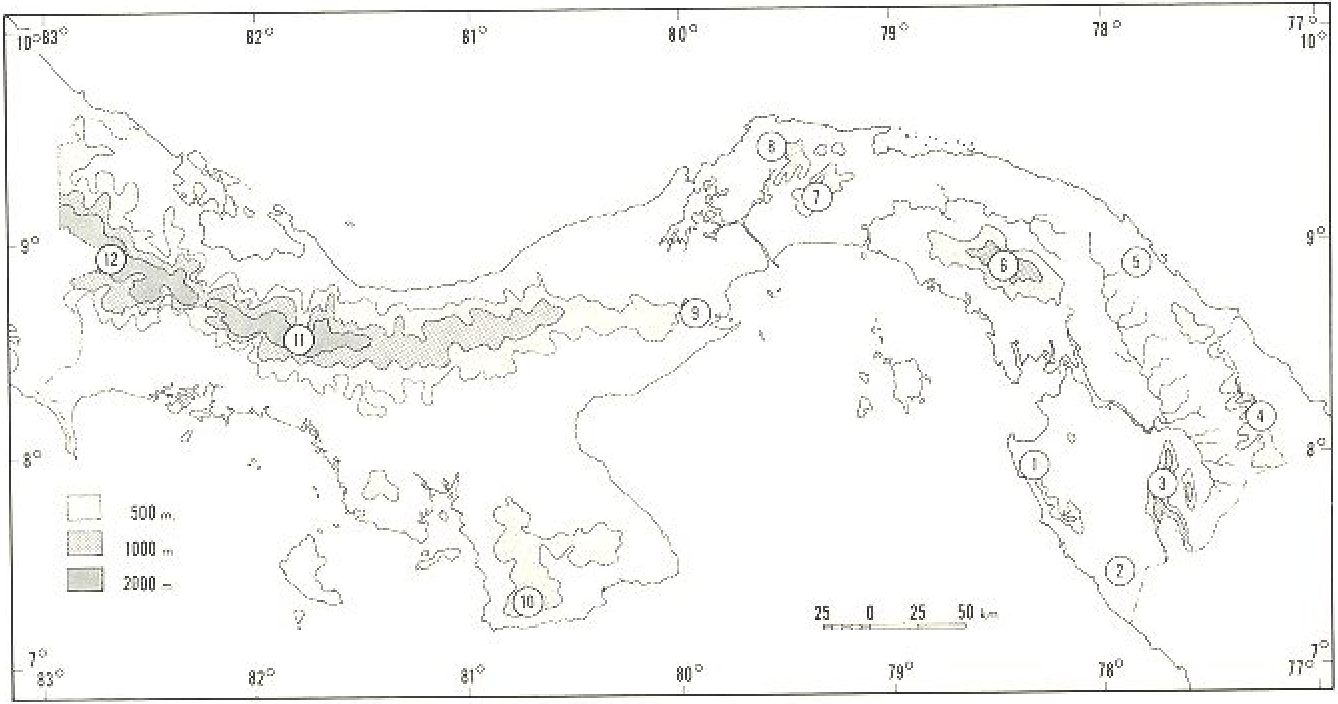

FIG. 1. Map of Panama, showing localities discussed in text. 1. Cerro Sapo; 2. Jaqué-Imamadó Divide; 3. Serranía de Pirre; 4. Cerros Tacarcuna and Malí; 5. Camp Summit, 358 meters elevation in the Serranía del Darién; 6. Serranía de Cañazas; 7. Cerro Jefe; 8. Cerro Bruja; 9. Cerro Campana; 10. Cerro Hoya, Azuero Peninsula; 11. Cerro Santiago; 12. Cerro Pando.

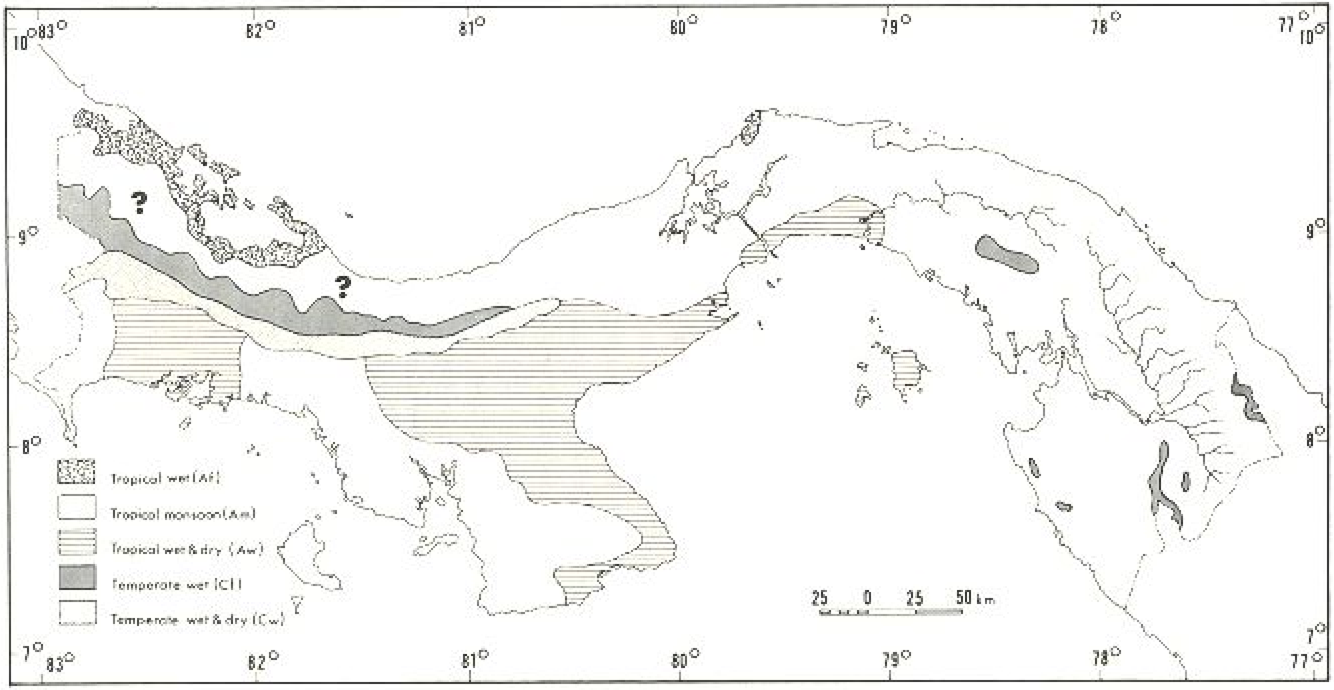

FIG. 2. Map of Panama, showing Köppen macroclimates, slightly modified from Rubio (1965). The climatic notations (see above) also broadly correspond with natural areas of "climatic climax" vegetation, as follows: *Af*, lowland tropical rain forest; *Aw*, and *Cw*, evergreen and semi-evergreen seasonal forests (monsoon forests); *Am*, lowland savanna (perhaps dry forest originally); *Cf*, montane and lower montane rain forests.

The various kinds of cloud forest occur as special situations in areas of *Cf* and *Cw* climates, some small areas of which are not shown on the map (see fig. 1, site numbers 2, 7, 8, 9, and 10).

which is situated along the Pacific coast. Unlike Pirre, the Sapo region is highly dissected and has only a few elevations in excess of 1000 meters. Contrary to Barbour and Brooks (1923, p. 213) and most maps, I believe that Cerro Sapo may be the highest peak in this *serranía*. The uplift that lies north of Puerto Piña seemed lower to me when I looked southeast from the 1080-meter summit of Cerro Sapo at the northern end of the range, although the new 1:250,000 map (Dirección de Cartographía, 1967) has it at 1551 meters elevation.

The highlands that form the backbone of the western part of the isthmus are in an early stage of erosion and are essentially a southeastward extension of the Costa Rican uplift. The eastern highlands are more advanced in the erosional cycle and appear to be related with the Andean orogeny.

CLIMATIC AND VEGETATIONAL REGIONS[1] OF PANAMA

CLIMATE: The foregoing account of the Panamanian highlands, and the map (fig. 1), indicate the only regions in which cloud forest may be expected in Panama, although it is by no means continuous within these areas. The effect of the highlands on moisture-laden air accounts in large measure for the several distinct climatic (fig. 2) and vegetational regions of the isthmus. During most of the year, Panama is enveloped in tropical maritime air masses that produce abundant rainfall. From about late December to April, the subtropical anticyclones are farthest south, pressure is high, the inversion is low, and rain shadow and leeward effects are maximized (Trewartha, 1966, p. 65). In this season the strong and relatively dry northeast trade winds blow steadily, bringing a dry season to most of the lowlands and foothills. Owing to the high mountains in western Panama, and because of a peculiarly local situation in the Portobelo area of central Panama, there is sufficient year-round orographic rainfall to produce a tropical wet climate (*Af*) on sections of the Atlantic drainage. In striking contrast, several disjunct rain shadow regions south of the continental divide have pronounced dry seasons and, hence, tropical wet and dry climates (*Aw*). The remaining and largest part of the

[1] An important work by Bennett (1968) was received after manuscript for the present paper had been nearly completed. Bennett's climatic map agrees generally with the one published herein, but fails to indicate that some montane areas are perpetually wet (i.e., with *Cf* climates). Bennett provided especially valuable map interpretations of the past and present phytophysiognomy, as related primarily to cultural exploitation. Cloud forest areas are included under "mature forest" having had "only minor or very intermittent cultural disturbance throughout entire period of human occupance on the isthmus." (Bennett, 1968, map no. 4.)

isthmian low regions have a monsoon type of climate (*Am*), in which annual precipitation has a definite seasonal distribution as in *Aw* climate but a total amount that resembles *Af* situations; this intermediate climatic type typically has a shorter dry season than does *Aw*. The highlands have cooler, temperate rainy climates with a pronounced winter dry season (*Cw*) or not (*Cf*).

Despite these varying conditions on so small a land mass, ascending air currents throughout the year carry sufficient moisture to produce cloud formation on the higher peaks and ridges on many parts of the isthmus. Northerly winds prevail throughout the year along the Atlantic coast and, consequently, rainfall and cloud formation are heaviest on the north-facing slopes of the continental divide (fig. 3). Onshore currents produce heavy cloud formation on the Pacific slopes of the Serranía del Sapo, and also on the south sides of the Azuero Peninsula and the Serranía de Cañazas; but even these ranges on the Pacific side are influenced by northerly winds from across the narrow isthmus (see discussion under Cerro Hoya, Azuero Peninsula, for example).

Vegetational Regions: There is widespread recognition that the major climatic types of Köppen (1931) are broadly equivalent to major vegetational regions. Thus, in Panama, the *Af* and *Aw* symbols (fig. 2) may be understood to represent not only climates but also regions of tropical rain forest and tropical savanna, respectively. On well-drained ground, *Am* climate supports a "climatic climax" forest type that is often called rain forest (e.g. Kenoyer, 1929; Trewartha, 1954, p. 381), as well as such other names as evergreen seasonal forest and monsoon forest (Beard, 1944, pp. 137, 138; Richards, 1952, p. 150). Whatever term is used, it is in some places difficult to distinguish between forests growing under *Af* and *Am* climates, except during the dry season of the latter, when many forest trees may shed their leaves. *Am* conditions are widespread in Panama, but the extensive lowland forests on the Pacific drainage in the eastern half of the country grow on nearly base-level terrain and in partial consequence are dominated by a single species of tree (the cuipo, *Cavanillesia platanifolia*). The cuipo forests (and interspersed river-swamp forests) lack the general physiognomy of evergreen seasonal forest or "monsoon rain forest." The temperate rainy climates in Panama support montane forests having wet (*Cf*) or seasonally wet (*Cw*) climates. Most of the forest growing under *Cw* conditions has been cleared for years, but forest with *Cf* climate is largely intact.

Definition of Cloud Forest: Panamanian cloud forests may be considered as having temperate rainy climates (usually *Cf*, but also *Cw* in some borderline situations), but the Köppen climatic system is broadly

FIG. 3. Serranía del Tabasará, western Panama, looking eastward toward Cerro Santiago (in clouds, left of center). Notice the heavy cloud formation that conceals the Atlantic lowlands to the north (left) of the continental divide, whereas the distant Pacific lowlands on the south (right) are visible through reduced cloud cover. The Atlantic slopes receive more continual precipitation throughout the year. This photograph was taken from the highest point in Panama—the north rim of Volcán de Chiriquí, about 3250 meters elevation (3475 meters on some maps), in the western end of the Cordillera de Talamanca (December 10, 1966).

generalized and not very useful when applied to vegetational classification of small areas (Bennett, 1963, pp. 2, 3). For this purpose, floristic standards or finer physiognomic criteria are normally used. Few floristic data are given here and, in any case, such data probably would be of slight value in defining Panamanian cloud forest as a whole, although several associations could certainly be recognized. It is also difficult, however, to provide a physiognomic definition that will apply to every area of Panamanian forest that is normally swathed in cloud. Beard (1944, 1955), in already classic essays about tropical American vegetation, equated cloud forest with "montane rain forest," which is physiognomically defined. But Beard's definition of montane rain forest (1944, p. 145; 1955, pp. 93, 94) is applicable in Panama mainly to rather extensive forest that lies below the cloud bank in western Atlantic Panama (fig. 16) and for which "cloud forest" is not a reasonable synonym. The definition does seem more or less applicable to some montane cloud forests that extend through a few hundred meters in elevation, but the physiognomy of cloud forest that is confined to the tops of narrow ridges is likely to be quite different because of thinner soil and greater exposure to wind.

It is sufficient for most purposes to define cloud forest in the broadest possible terms, without reliance on major climatic regions, floristics, or precise physiognomic criteria. I cannot improve the wording of Carr (1950, p. 580), who considered cloud forest as, "any upland woods that owes its character to lower temperatures and cloud condensation, or perhaps more directly to the resulting low evaporation rates . . . rather than to direct precipitation." The "character" of cloud forest may be thought of as the over-all physiognomic aspect of the vegetation, which is usually conspicuously lusher and denser than in adjacent areas of little or no cloud formation, but this is not to say that different cloud forests necessarily look alike (compare figs. 9 and 11 for example). The following site descriptions, photographs, and discussion will clarify this concept. It should be stressed that the above definition also includes "montane thicket" and "elfin woodland" as characterized by Beard (1955, pp. 93, 94, 97, 98). I do not propose abandonment of these very useful terms but, for the purpose of this paper, I consider montane thicket and elfin woodland as specialized kinds of cloud forest. Thus, habitats are discussed herein that are floristically and physiognomically diverse but which have in common cool temperatures and extremely high humidity imposed by enveloping clouds.

Comment on the Holdridge Life Zone Model: Holdridge (1964, p. 74) correctly stated that quite diverse physiognomies and sets of species occur within the fog or mist belt, and he suggested that these be "specifically assigned to moist atmospheric *associations* of life zones of the altitudinal belts." (Italics mine.) Holdridge (1964, pp. 33–35) defined an association as "an area occupied by a community" or as "a range of environmental conditions . . ." and stated that the same association may be composed of widely differing sets of species in different regions. The word "association," however, has been formally defined by various international botanical congresses, and most ecologists (Whittaker, 1962, p. 70) base the association on floristic criteria. Partly because of such difficulties with the terminology, but mainly because of reasons listed below, I have not adopted Holdridge's ingenious "life zone" classification of terrestrial ecosystems (Holdridge, 1947, 1964; Tosi, 1964), which is receiving widespread use especially among biologists working in Costa Rica. In any case, it should be mentioned that tropical cloud forest, as defined by Carr (see above), occurs in several of the Holdridge life zones, in the "subtropical"-"lower montane" belt, and probably also in the "montane" belt. Holdridge's diagram of the world life zones, together with one of latitudinal regions and altitudinal belts, will be found in several places, including Dasmann (1964), Holdridge (1964), and Tosi (1964).

Both the Köppen and Holdridge models are based primarily on climatic data but, in practice, such data are not often available and must be interpreted from vegetational features, at least those features that seem to be determined mainly by climate. Although the reasoning is circular, the results may be practical. It seems to me fairly easy to use a combination of vegetational physiognomy and elevation to determine the broad Köppen regions, or the plant formations as defined by Beard, but similar use of the Holdridge system requires special indoctrination or blind reliance on published statements or maps (for life zone maps of Panama see Holdridge and Budowski, 1956, 1959). The world plant formations are divided into finer units in the Holdridge model than in other systems, and there are few published guidelines for effective field determination of the formations as they are conceived by Holdridge. Tosi (1964, p. 180) assured us that the Holdridge formations can be recognized by "trained ecologists (and others) . . . by observations and measurement of the physiognomic, life-form, and structural characteristics of the native and cultivated vegetation, which is distinctive for each formation." Notwithstanding, Holdridge and his associates seem to consider indicator species as having as great (or greater) importance than physiognomy, and this approach immediately lessens any broad usefulness that might be inherent in the Holdridge model. Indicator species obviously are of no use in defining "world" formations, and few field biologists have the necessary training or experience to recognize indicator species in new areas, most especially in the wet tropics. But according to Holdridge and Budowski (1956, p. 97), "the indicator trees . . . are of special importance in classifying an area and . . . permit interpretation not only of climatic and edaphic factors but also of present and potential agricultural use." I repeat, world plant formations are not classified floristically.

Although it is desirable to study and characterize the different communities that make up a formation, I object to such a useful term as rain forest being arbitrarily defined nearly out of existence (but see Holdridge, 1965, for a different viewpoint). There seems to be no published justification that such a formation as tropical rain forest (*sensu lato*) can be subdivided on a graph and that these same subdivisions can then be easily and usefully recognized by physiognomic features that are applicable on a world-wide basis.

It is not only the correlation of smaller units with lack of published guidelines that causes problems in using the Holdridge classification. The effect of seasonal, climatic change is given little intrinsic importance, with the result that Panamanian rain forest growing under *Af* climate is lumped together with evergreen seasonal (monsoon) forest of *Am* climate, and the whole is called "tropical moist forest" (Holdridge and Budowski, 1956) or "*bosque húmedo tropical*" (Holdridge and Budowski, 1959). Faunistically, at least, there is ample reason to consider these environments separately. Areas of cuipo forest (*Am* climate) in eastern Panama are considered by Holdridge and Budowski (1956, 1959) as transitions to still different life zones on each side of the *bosque húmedo tropical* (i.e., toward "*bosque seco tropical*" or "*bosque muy húmedo tropical*"); again, these authors (1956, pp. 98, 99) gave no other criterion than a purported indidator species (cuipo). I believe that edaphic features somehow associated with base-leveling must be the principal reason for the existence of this curious forest, in which cuipo is the most conspicuous tree. Little elevation is needed in this region for the development of a forest of recognizable "climatic climax" type, such as the seasonal forests that occur around part of the Bayano-Chucunaque-Tuira river drainages, which is to say in the hills (and mountains) around the nearly base-level region comprising the "transition" zones of Holdridge and Budowski. The demarcation between these habitats is also shown in another map of the Darién region (Viksne and others, 1969, fig. 7), although the seasonal forests and cuipo forest are inappropriately labeled "evergreen rain forest" and "mixed semideciduous and evergreen forest (jungle)," respectively. It seems likely that the cuipo forest owes its character to the present topography rather than to a climate that would have to be amazingly correlated with this particular landscape.

I do not intend that any of the preceding remarks be construed as belittlement of a truly major attempt at ecosystem classification. The Holdridge model is an important and thought-provoking contribution, whether or not a given worker finds it acceptable for his purposes. The continued refinement of the system is watched with interest, particularly the development of quantitative physiognomic criteria (Holdridge, 1965).

CLOUD FOREST IN PANAMA

Localities are listed from east to west, except for the first few. The number preceding the name of each locality corresponds to the numerical equivalent on the map (fig. 1). For the sake of completeness, I mention a few places that I did not visit.

1. Cerro Sapo

Figures 4–9

This locality is at the northern end of the Serranía del Sapo in Darién Province and is reached by walking south from the coastal village of Garachiné. The best route is up the narrow valley of the Río San Antonio to an elevation of approximately 190 meters, at the foot of a ridge known locally as "La Jarcia," the crest of which is then followed southeastward to 660 meters, where it joins "Chuculero," a northeastern spur of the mountain; this main spur then can be followed directly to the summit of Cerro Sapo. Local guides are necessary. Water is available on the northeastern slope of La Jarcia, about 20 to 30 meters elevation below a flat place on its crest at 560 meters; this place can be reached in five or six hours from Garachiné (with loaded packers) and is a good camping site, although tabanid flies may be numerous. From here, the summit of Cerro Sapo is a two- to three-hour walk. In order to better work in the cloud forest, and for quicker access to the summit, I established a dry camp at 880 meters elevation, and was supplied with water by packers stationed at the lower camp. I worked in the area for two weeks in May, 1967, and during this time the top of Cerro Sapo was covered by clouds except for short periods. These usually occurred an hour or two before dusk, when a panorama of the near and distant mountains, lowlands, and ocean presented itself.

Vegetational zonation on the above route is more striking than I have seen elsewhere in eastern Panama and is worth describing for the entire ascent, particularly because Cerro Sapo is the only area in which I observed two physiognomically distinct kinds of cloud forest. An additional

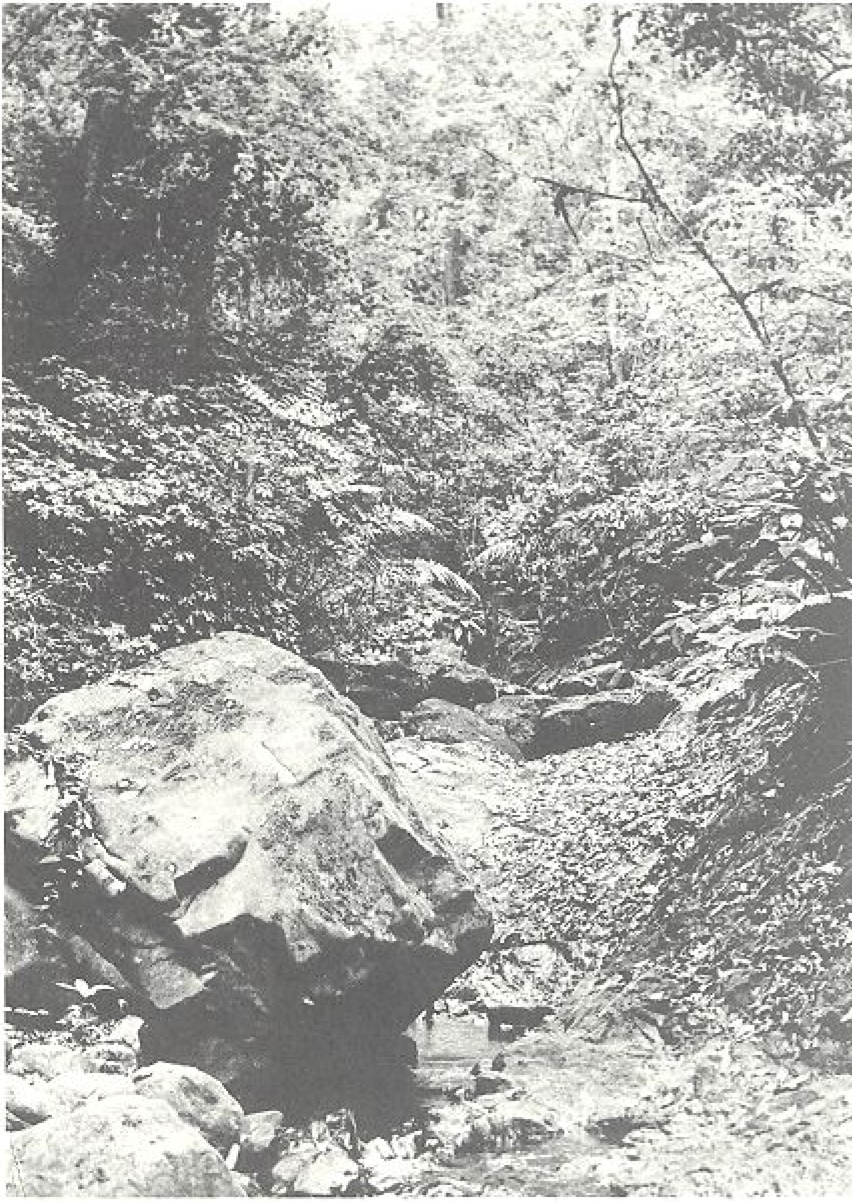

FIG. 4. Lowland hill forest (evergreen seasonal forest) along upper Río San Antonio, 190 meters elevation, north-northeast of Cerro Sapo (May 28, 1967).

peculiarity is the absence of a bamboo zone below the cloud forest, unless such a zone is present on the steeper, virtually inaccessible slopes. The vegetational zonation to be described is due more to relatively abrupt changes in population densities and microclimatic conditions than to absolute differences in the distribution of species and life forms. Therefore, I have not arbitrarily divided a smooth continuum.

Flat Lowland Forest: The cutover forest about Garachiné is a relatively xeric facies of the extensive cuipo association that dominates lowland Darién, except in tidal and swamp forest situations. As mentioned, this forest does not have the physiognomy of the "climatic climax" forest

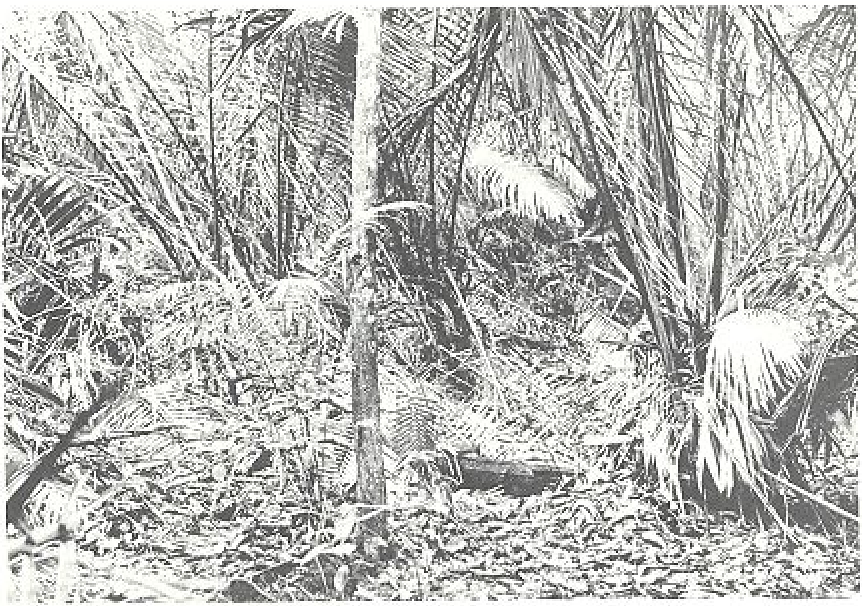

Fig. 5. Ivory nut palm (*Phytelephas* sp.) dominating understory in lowland hill forest (evergreen seasonal forest), 430 meters elevation, on the ridge "La Jarcia," Cerro Sapo (May 26, 1967).

of *Am* climate. The cuipo emerges conspicuously above a broken canopy and is sparsely distributed a few hundred meters up into the next zone.

Lowland Hill Forest (Evergreen Seasonal or Monsoon Rain Forest): This forest has a denser canopy than the cuipo forest of lower ground. It grows in foothill situations from elevations of about 50 to 650 meters. The forest is especially luxuriant along the upper Río San Antonio (fig. 4), where some trees attain heights of 35 meters or more. The ivory nut palm, or *tagua* (locally pronounced "tawa"), is a conspicuous understory dominant. This palm (*Phytelephas* sp.) was economically im-

FIG. 6. Lowland hill forest (evergreen seasonal forest), 560 meters elevation, on the ridge "La Jarcia," Cerro Sapo (May 26, 1967).

FIG. 7. Cloud forest transition zone, 700 meters elevation, on the ridge "Chuculero," Cerro Sapo. Compare with figure 6, which was photographed only 45 minutes prior to this scene and at 140 meters lower elevation (May 26, 1967).

FIG. 8. Lower cloud forest, 800 meters elevation, northeast slope of Cerro Sapo (May 24, 1967).

portant before the advent of plastics. In the lower regions *tagua* grows on an open, shaded forest floor, and becomes much denser on La Jarcia, between elevations of 220 and 450 meters, where it grows to the exclusion

FIG. 9. Upper cloud forest (elfin woodland), 1040 meters elevation, near summit of Cerro Sapo (May 22, 1967).

of almost anything else in the understory (fig. 5). At higher elevations, about 450 to 650 meters, there is a great increase in the amount of brush, herbs, and ferns, and a corresponding decrease in the density of *tagua* (fig. 6). Buttressed trees are easily found on the lower slopes but are relatively rare above 450 meters elevation, where tree trunks are smaller and denser and tall stilt palms are conspicuous. If there is no rain for several days, the modest leaf layer atop the reddish brown soil dries fairly rapidly.

CLOUD FOREST TRANSITION, 650–750 METERS: The ridge forest between these approximate elevations is perceptibly moister and, from my limited observation, has more rain and fog than lower elevations (fig. 7, compare with fig. 6). The canopy is denser, making the forest somewhat darker even during periods free of fog. Bromeliads become conspicuous and, at the same time, ivory nut palms and tabanid flies lessen, although the flies were amazingly abundant in the lower zone, in which they were a definite strain on good temper and peace of mind. This zone perhaps could as easily be considered a distinctive facies of cloud forest as well as a transition.

LOWER CLOUD FOREST, 750–1000 METERS: This is a dense, wet forest of trees of moderate size, in which bromeliads are profuse (fig. 8). Fog is more frequent than at lower elevations, tree ferns and especially epiphytes are more abundant, the moss on tree trunks is thicker, and the soil probably is perpetually wet. Palms are much scarcer in the understory than in lower zones; a palm called "*puerto rico*" is the most common.

Upper Cloud Forest (Elfin Woodland), 1000–1080 meters: This is the best-defined altitudinal zone on the mountain and the ecotone between it and the lower zone is very narrow. The canopy is exceptionally low for a Panamanian forest, less then 10 meters, and the vegetation is very dense, being mainly comprised of a few species of hard-leaved trees that have intertwined trunks and roots (fig. 9). The moss on tree trunks is thick, soaking wet, and cold to the touch; bromeliads, palms, and tree ferns are rare, and there is a great decrease in the number of low herbaceous plants. In this area one usually stands on a mat of roots and decaying vegetation, from several inches to several feet above ground level. A small summit area of Cerro Sapo has been cleared by a geodetic field crew, and so it could be seen that the slightly lower neighboring peaks are also capped with the same low, wet sclerophyllous vegetation.

2. Jaqué-Imamadó Divide

Figures 10, 11

This is a ridge situated in extreme southeastern Panama, in the Cordillera de Juradó, which is a low uplift that below the 400-meter contour is continuous with the Serranía del Sapo to the northwest and the Serranía de Pirre to the northeast. In times of high water, the Río Jaqué can be traveled by *piraqua* and outboard motor in less than a day, from the coast to the mouth of the Río Imamadó. The entire valley to this point is highly cutover, but the forest above is less disturbed as the river becomes impossible to navigate with a motor. Contrary to what is implied by the climatic map in the "Atlas de Panamá" (Comisión, etc., 1965, pl. 11), local inhabitants informed me that the upper Jaqué Valley has a distinct dry season. Possibly, however, the dry season is shorter or the yearly rainfall at least higher than in the rest of lowland Darién. I camped on the Jaqué about 1½ kilometers above its junction with the Río Imamadó. From here a trail was opened to a sinuous ridge that forms the Jaqué-Imamadó divide. This winding ridge was followed first northeast and then southeast, from 380 to 800 meters, where a camp was established for one week in the last half of April, 1967. Beyond the place where I camped the ridge runs again northeastward to a high point of 960 meters, past which there is a rapid drop to the north. Water was found on a southwestern slope, 70 meters lower than camp.

At its lower elevations, about 150–500 meters, the ridge is rather dry; the conspicuous understory dominant is the *trupa*, a palm from which cooking oil is obtained. Dry conditions atop lower parts of the ridge are due to drainage and wind exposure, and adjacent ravines are moister. Isolated thickets of a small bamboo (fig. 10) occur from 570 to 730 meters above sea level. Wet cloud forest (fig. 11) prevails above the zone of bamboo, and the days passed much quieter here, because of the absence of a species of large cicada, whose drone was loud and constant in the lowlands. During the week at the 800-meter camp, there was rain and fog nearly every afternoon; mornings and nights were often free of fog, and although there occasionally was rain in the morning there was none at night. The few noticeable winds came out of the northeast. In contrast, there was much sun and very little rain at the camp on the Río Jaqué. Spot temperature checks in open shade gave a range of 22° to 35° C. at the lowland camp, whereas the observed range was 17.5° to 21° C. in the cool cloud forest.

The high-ridge vegetation deserves the name cloud forest even though daily fog formation is less than on the Sapo and Pirre heights and the forest is not so dense. The canopy is moderately high, perhaps averaging 20 meters in pockets where there is gentle slope and sufficient soil. Most of the larger trees are buttressed. Palms are abundant in the understory; the ivory nut (*Phytelephas* sp.) is the most common, but there is only a scattering of such tall stilt palms as *gira*. Tree ferns are common. Brush varies from moderately open to moderately dense and a machete is helpful if one is to travel any distance. Low herbaceous plants are abundant. On level places the orangish brown soil is covered completely by about an inch of fallen leaves, whereas on slopes there are frequent patches of bare earth. Bromeliads are abundant only on the highest places (about 850–960 meters) and even there do not occur on the ground as is common in the best-developed cloud forests. Moss on tree trunks is thin.

3. Serranía de Pirre

Figure 12

This *serranía* is a mountain ridge that extends northward for about 35 kilometers from the Colombian border. The highest peak is Cerro Pirre, which is situated on the middle of the ridge at 1550 meters according to my reading, which shows good correspondence with the 1515 meters on the official 1:250,000 map. The few natives familiar with the region apply the name Cerro Cana to this peak, and reserve the name Pirre for a height on the northern end of the ridge. As explained elsewhere (Myers, 1966b, p. 667), I prefer to regard "Cerro Cana" as synonymous with the

FIG. 10. Bamboo thicket, 730 meters elevation, on the Jaqué-Imamadó divide (April 24, 1967). In Panama, such thickets of small bamboos often occur not far below the lower edge of cloud forest.

FIG. 11. Cloud forest, 800 meters elevation, on the Jaqué-Imamadó divide (April, 1967).

Cerro Pirre of technical publications (e.g., Goldman, 1920; Terry, 1956) and most maps. I camped for several days at 1440 meters on Cerro Pirre in late May, 1965; there was a water source 40 meters below on the western slope of the ridge. "The camp . . . was reached by cutting a trail from the old gold mines of Santa Cruz de Cana (500 meters), on the southeastern base of the mountain. Cana itself, a jungle-covered townsite dating from the end of the 16th century, was approached by reopening 50 km. of trail from Boca de Cupe, a town to the northeastward, on the Río Tuira; this trail sometimes crossed deteriorated and frequently buried track of the Cana tramroad, which was described by Goldman (1920)." (Myers, 1966b, p. 665). In January, 1966, two weeks were spent on the northern end of the Pirre ridge; a trail was opened up the north end from the town of El Real, and a base camp was established near a tiny stream at 500 meters. A second camp was set up for a few nights at 960 meters on the summit of the northernmost of two adjacent peaks, which, on a clear day, are visible from El Real. After additional trail was cut, a two and a half hour walk took us south over the 1110-meter peak of Cerro Cituro ("1445 meters" on the official map) to a campsite at 1100 meters, with water being obtainable 100 meters below camp, on the eastern side of the ridge. The following description begins with the north end of the Pirre ridge and ends with conditions on Cerro Pirre at the middle of the ridge.

The forest on the lower slopes of the Serranía de Pirre becomes dry in the period of January to March. Ivory nut palm is a conspicuous understory dominant on slopes below 600 meters. The vegetation becomes denser above 650 meters, at which point the ascending ridgetop is more exposed to wind and a small yellow-flowered bromeliad suddenly becomes abundant. A species of small bamboo was first noticed at 880 meters and cloud forest prevails on the crest of the ridge above 900 meters. Probably because of wind and the narrowness of the ridge, the average tree height near the 960-meter camp is low, less than 18 meters; the vegetation is quite dense, as there is scarcely a half-foot length of ground lacking a plant stalk. Moss is common on trees, the branches and trunks of which are choked with bromeliads and other epiphytes; tree ferns are occasional and palms are scarce.

Farther south at 1100 meters (fig. 12), the ridge is wider and the average canopy height was estimated to be between 21 and 25 meters. The forest is more open, although prolonged travel is difficult without a machete because of fallen trees. There are not enough palms available for shelter thatching. Tree ferns, moss on tree trunks, and bromeliads growing low on tree trunks are abundant, and there is a well-developed

FIG. 12. Cloud forest, 1100 meters elevation, on northern end of the Serranía de Pirre (January 24, 1966).

ground stratum of herbs and ferns.

The luxuriant vegetation on top of the Pirre ridge indicates that cloudy conditions prevail throughout the year. In eight days at the 1100-meter camp, there was only one day with direct sun for about an hour at a time and that was the only day in which we glimpsed blue sky; in contrast, a helper stationed at the base camp (500 meters) reported almost continuous drying sun during those eight days (early dry season). Cloud formation is confined nearly to the crest of the Pirre ridge, on its northern end. Thus, there is extensive horizontal development of cloud forest on the ridgetop, but virtually none below the crest. Occasionally, where the sides of the ridge are less steep than normal, one can descend through a striking vegetational change in several minutes and in less than 100 meters of elevation. The forest opens up, there are many more saplings, no bromeliad-choked trees, and a decided thinning-out of tree ferns and moss on tree trunks. This abrupt change in the environment was especially evident in the case of frog populations at the 1100-meter camp. Frogs were conspicuous on the forested ridge at night, and the combined calls of *Eleutherodactylus diastema* and *E. vocator* made it a rather noisy place. But only about 5 meters of elevation below the crest of the ridge, the forest was almost silent, with only an occasional *E. vocator* heard and few frogs of any kind seen. This was during the dry season; at other times of the year I would expect dispersal and increased activity on the slopes, but in the cloud forest it seems probable that populations of some frogs are able to benefit by continuous reproduction.

On Cerro Pirre, the physiognomy of the cloud forest vegetation is similar to that described for the north Pirre ridge at 1100 meters, with the notable change that bromeliads are quite abundant on the ground as well as on the trees. However, Cerro Pirre is higher (1550 meters) than the rest of the ridge and there is a consequential change in the elevation of the vegetational zones. Thus, on the spur ridge leading up the southeastern face of Cerro Pirre, bamboo was found at 1220 meters rather than at 880 meters as happens on the north end of the *serranía*. Gradually, moister conditions are met above 1220 meters and good cloud forest develops between 1300 and 1400 meters, in contrast to about 900 meters to the north. Granted that unknown peculiarities associated with the direction of local air currents[1] may contribute slightly to the differences, this nevertheless seems a good example of the "*Massenerhebung* effect," which is the adjustment of vegetational zonation to the height of mountains or, in this case, to the height of various parts of a single montane ridge.

4. Cerros Tacarcuna and Malí

Cerro Tacarcuna is a short mountain ridge that protrudes west from the Panama–Colombia border, where the border follows the continental divide in a southeasterly direction. I agree with Anthony (1923, p. 316) that Barbour and Brooks (1923, p. 213) were incomprehensible in their insistence that "Tatarcuna" is the correct spelling. Cerro Tacarcuna is the highest point in eastern Panama. The map elevation of 1875 meters is close to an estimate of ± 6000 feet (1829 meters) made by Charles O. Handley (*in litt.*) from a helicopter; Anthony (1916) obtained a reading of 5650 feet (1723 meters) with a barometer carried by hand. Cerro Malí is a much shorter and lower mountain ridge that also projects from the border, in the area southeast of Cerro Tacarcuna and the headwaters of the Río Pucro. The region is difficult to travel because of broken ridges. Anthony (1916, pp. 360–363, figs. 1, 5), who is probably the only biolo-

[1] Solar radiation can be ignored because, as pointed out by Eyre (1963, p. 268), "The complication of differences in insolation between north-facing and south-facing slopes, which is of such significance in higher latitudes, only attains any degree of importance [in the tropics] as one approaches the fringes of tropical regions."

gist to have attained the summit of Cerro Tacarcuna, provided the following account:

"The character of the forest growth remains the same eastward from the mouth of the Tuyra [Río Tuira] until an elevation of about 4500 feet [1372 meters], on the slopes of Mt. Tacarcuna, is reached. The density of the growth decreases with the rise in elevation but at the mountain a different type of forest is found. The growth is neither so heavy nor the trees so large as in the lowlands and it is evident that a new floral zone has been entered. Here a variety of tree ferns grow, but when an elevation of 5000 to 5500 feet [1524–1677 meters] is reached the appearance of the forest is much like that of northern forests of hard woods and birches. The heavy growth of the lowlands penetrates in favorable gulches up into the higher zone to about 5000 feet.

"Mt. Tacarcuna itself is a steep conical peak that rises about 800 feet from the main range. Its slopes are strewn with great blocks of stone, of a basaltic nature as nearly as could be ascertained for lichens and other vegetation clothed the rocks so densely that their determination was difficult, and its summit is overgrown with a dense, exceedingly hard-wooded shrub that made progress almost impossible. Mists continually sweep over it and it is seldom that a complete view of the surrounding country may be obtained from the peak."

Anthony's remarks (see above, and 1923, p. 321) about a gnarled, hard-wooded, dense shrubbery, almost certainly mean the presence of an elfin woodland type of cloud forest, such as caps the much lower Cerro Sapo. This is also indicated by Handley (*in litt.*), who observed from a helicopter that vegetation near the summit of Tacarcuna "is scrubby and virtually palmless." Handley noted that good cloud forest with a high incidence of palms occurs between 4800 and 5500 feet (1463–1677 meters), the principal areas of which are, according to his field sketch, on the Tacarcuna ridge east of the summit and on the international border just northeast of the Malí ridge. Cerro Malí is high (about 1410 meters) and wet, but is affected by the dry season and much of its forest is possibly no more than transition to cloud forest. I spent only one night on the ridge, in July, 1963, and the following description is from the journal of William E. Duellman, who worked there for several days: "The forest contains many small trees, including palms, reaching heights of ± 12 meters. Larger trees up to ± 30 meters are scattered through the forest. There is an understory of bushes and ferns. Most of the trees have a thin covering of moss on the trunks. There is a thick mulch layer on the ground and many rotting logs. Many bromeliads and a few orchids present; few tree ferns."

Fig. 13. Camp Summit, 358 meters elevation, Serrania del Darién, on the continental divide between San Blas Territory and Darién Province. Even during the dry season this low divide receives frequent mist and is usually hazy, as seen in this view photographed from a helicopter (February 2, 1967).

5. Camp Summit, Serranía del Darién

Figure 13

In January and February, 1967, I worked on the Atlantic coastal plain of San Blas and hiked from there up to the low continental divide, to spend six days at Camp Summit (358 meters), an Interoceanic Sea-Level Canal survey camp. Elevations in this immediate part of the *serranía* seldom exceed 400 meters and there is no cloud forest. Nevertheless, the effect of even such low hills on northerly breezes from the Atlantic is instructive. The coastal plain was exposed to the sun and even forest soil was drying rapidly in late January, but in traveling up from the lowlands the trails changed from dry to muddy above 200 meters. The divide area received some light rain and most of each day was hazy, in contrast to the bright lowlands. As convectional air currents reached the crest there was sparse but nearly constant condensation of fog (fig. 13). When crossing the divide in a helicopter, I noticed a sharp increase in light intensity as the haze dissipated over the slopes on the Pacific side. I suspect that elevations no greater than 700–800 meters are needed to cause the formation of cloud forest on the continental divide between

San Blas territory and the provinces of Darién and Panamá, but in this long stretch there are few elevations of even such modest height.

6. Serranía de Cañazas

This small but rugged highland area is biologically unexplored and is listed here because it almost certainly bears limited areas of good ridge-top cloud forest. Elevations of over 800 meters are attained on razorback ridges northeast of the coastal village of Chimán, and flights along the coast usually show these ridges to be cloud covered.

7. Cerro Jefe
8. Cerro Bruja

The extensive ridge and hill country east of the Canal Zone has an annual rainfall in excess of 100 inches, with some fringe areas averaging more than 130 inches, according to an isohyetal map compiled by the Meteorological and Hydrographic Branch of the Panama Canal Company. Elevations are mostly under 600 meters, which is too low for cloud forest. Cerro Jefe, about 37 kilometers northeast of Panama City on the Pacific side, and Cerro Bruja, about 13 kilometers southeast of Portobelo on the Atlantic side are exceptions.

Cerro Jefe is in Panamá Province and is reached by dry weather road, the turnoff to the summit being about 8.8 kilometers (5.5 miles) past the community of Cerro Azul. I camped on Cerro Jefe for a few nights in mid-January, 1965, but my notes on the vegetation are regrettably incomplete. The summit is at 980 meters elevation. An odd fact is that the wind-swept forest is comprised largely of palms. Moss is heavy on tree trunks and bromeliads are abundant both on the ground and in the trees. The entire forest is low and dense and the ground is spongy. In this unusual forest almost constant wind blew from the north and there was much fog during my stay. The forest seemed nearly devoid of amphibians and reptiles. The lower surrounding ridges support evergreen seasonal forest. The summit of Cerro Jefe may represent a disturbed situation; certainly the various successional changes possible in cloud forest are little understood and deserve additional study (see Griscom, 1932, p. 56, for a discussion of succession following volcanic destruction of Guatemalan cloud forest).

Cerro Bruja is in Colón Province and is shown at 3200 feet (976 meters) on some maps. I was unable to find a passage above the 500-meter contour in the ridge system southwest of the mountain, although persistence should allow access from that direction. However, I suspect that anyone wanting to visit Bruja might find guides and perhaps easier access from the vicinity of Portobelo.

9. Cerro Campana

This is a prominent landmark situated about 60 kilometers southwest of Panama City, in Panamá Province; it and the neighboring Cerro Trinidad are visible from the Inter-American Highway. An all-weather side road to the community of Chica first leads onto open grassy heights at about 790 meters on the south slope of Cerro Campana. A trail to the 1000-meter summit starts in nearby forest at 820 meters, at the edge of a side road. A small area of cloud forest occurs above approximately 870 meters, where ground bromeliads first become common. The forest is of moderate height and has few large trees. There are many small trees, a scattering of tree ferns and small palms, and a few stilt palms. There is a dense cover of bushes, herbs, and ferns and a uniform layer of fallen leaves. Once abundant tree and ground bromeliads and other epiphytes have been reduced by collectors. The vegetation on the summit is disturbed because of former clearing on the top, perhaps for a wartime or geodetic installation.

Although in view of the Pacific Ocean, the 1000-meter summit of Cerro Campana is high enough to catch northerly winds that sweep across the low, central part of the isthmus without prior interference. Similar small areas of mountaintop cloud forest are to be expected on the adjacent Cerro Trinidad, and also near the continental divide north of El Valle de Antón, a low Pleistocene volcanic crater about 20 kilometers southwest of Cerro Campana. There are roads, and a detailed topographic map is available for the El Valle area, which is fairly well populated.

10. Cerro Hoya, Azuero Peninsula

Figure 14

The Azuero highlands are isolated by the *Curatella* savannas of the Santiago Plain, a flat erosional surface that stretches eastward across the base of the Azuero Peninsula (*Aw* climate, fig. 2). The southwestern half of the peninsula is influenced by tropical monsoon (*Am*) tendencies except in the valleys of the Río Tonosí and Río Guánico, where there seems to be an extension of the *Aw* zone that runs around the southeastern end of the peninsula (fig. 2). This is indicated by xerophytic types of plants, especially cacti and bullhorn *Acacia* which are abundant enough to gather for fences; small patches of forest in the Tonosí-Guánico Valley were 50 per cent deciduous in March, 1967. The few mountains high enough for the vegetation to approach cloud forest are restricted to the southern half of the peninsula, near the border between Veraguas and Los Santos provinces. Aldrich and Bole (1937) provided a good account of a section of the Azuero Peninsula to the east of Montijo Bay, but unfortunately they did not give much information about a narrow strip of "cloud forest" that was encountered between 3000 and 3200 feet (915–976 meters), between the headwaters of the Río Mariato and the Río Negro. "Above 1000 feet, one is in the humid tropical forest up to 3000 feet, at which elevation indications of the Subtropical Zone (or cloud forest conditions), such as heavy festooning of moss on the branches of trees, begin to put in their appearance. After ascending through a narrow strip of this cloud forest [to 3200 feet, p. 8], one emerges upon open grassy savannahs which clothe the peaks and a large part of the crest of the divide in the region explored by us. The forest extends in narrow tongues along the water-courses up into these highland savannahs, the trees becoming more and more stunted and gradually disappearing altogether." (Aldrich and Bole, 1937, p. 11.) Epiphytic growth is not indicated in their photographs, nor is the interior of the forest pictured. Whatever the nature of this purported cloud forest, Aldrich and Bole (*loc. cit.*) were very probably correct in stating that the upland savannas are the result of repeated firing; man has been living for centuries in the relatively dry lands to the northeast.

The highest mountain, Cerro Hoya, lies near the southern extremity of the Azuero Peninsula and can be approached with difficulty from the upper valley of the Río Guánico. It takes a minimum of two long days, from the community of Jobero, to pack in to a mountain ridge lying east of Cerro Hoya. Although the airline distance is only about 15 kilometers, much of it is at right angles to the ridges and soil on the steep slopes is often dangerously loose and powdery in the dry season, and travel is doubtlessly even more difficult in the rainy season. I spent 13 days in these mountains at the end of the dry season in March and April, 1967. My trip was facilitated by a sketch map and information supplied by Charles O. Handley, Jr., who worked in the area in 1962. About halfway to our destination, we struck the barely discernible remains of a trail that Handley had opened with much difficulty from the town of Las Palmitas (locally known as "Guánico Arriba") and followed the trail to a campsite at 940 meters elevation on the ridge that lies just east of the summit of Cerro Hoya, across the headwater valley of the Río Pedregal. From this base camp it was possible to explore an area of cloud forest to the northwest, on a ridge that rises to a peak of 1270 meters; this peak is the middle of "Los Tres Cerros," of which the third and highest is Cerro Hoya itself, which appeared to have a maximum elevation of about 1500 meters. A trail probably could be opened directly to the summit of Cerro Hoya from the coast at the southern tip of the peninsula, by following the ridge between the Quebrada Punta Blanca and the Río Pedregal. This section of coastline is now accessible on a dry season logging road from Cambutal.[1]

The mountains in the extremity of the Azuero Peninsula are capped with limestone; the underlying igneous material was seen only in river gorges of a few hundred meters above sea level. Loose, red soil supports an evergreen seasonal forest in which there is little brush; movement is easy except for occasional tangles of lianas or bamboo thickets, especially on ridgetops. It is noteworthy that there is no well-defined elevation at which bamboo grows in greatest abundance; a small kind of bamboo ("*carrizio*") was found locally common from a few hundred to 1000 meters above sea level. Judged from the frequency of acorns in the dry leaf litter, oak trees are common and perhaps dominants, at least between 800 and 1000 meters elevation, where I spent most time. Despite frequent strong winds, falling trees are not commonplace and I seldom heard the sound of one, which, however, is an almost daily occurrence in the forests of eastern Panama. Palms and bromeliads are rather uncommon below 1000 meters, and the palms remain sparse even above this elevation. Tree ferns are frequently seen above 800 meters, especially in pockets of damp soil between the ridges, and they become moderately abundant above 1200 meters.

Possible tendencies toward cloud forest (i.e. sudden abundance of bromeliads) were noted on particularly exposed ridges at elevations as low as 820 meters, but were rare and localized. Stronger tendencies toward cloud forest occur generally above 1000 meters, on the exposed ridges. Forest on the ridge that led northwest from our base camp to a summit of about 1270 meters was closed and brushy in some places, but along most of its crest the undergrowth was sparse and travel was easy. The canopy is of moderate height and thin enough to allow frequent

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[1] The forest in the proximity of the ocean near the Veraguas-Los Santos border is different from the hill and montane forest between Jobero and Cerro Hoya. It is more mesic and has a very high canopy, probably in excess of 30 meters, from which numerous large lianas trail to the ground. On rocky or better drained slopes facing the ocean, the mesic forest gives way to small relictual stands of cuipo trees (*Cavanillesia platanifolia*), which frequently are gigantic in this area and which previously were unrecorded from west of the Bejuco area in southwestern Panamá Province. The species is easily recognized by its swollen and peculiarly ringed trunk, small crown, and large winged seeds. I hope that this digression will encourage biological exploration before this magnificent forest is destroyed completely by settlers who, as always, are following the newly opened road.

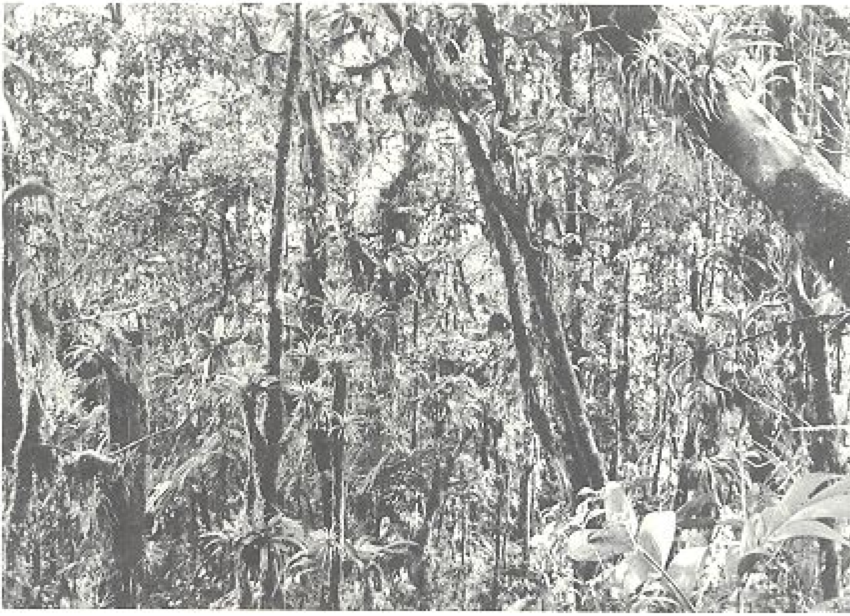

FIG. 14. A borderline cloud forest that loses much of its moisture late in the dry season; but notice the abundance of bromeliads. Ridge east of Cerro Hoya, 1250 meters elevation, Azuero Peninsula (April 3, 1966).

spots of sunlight to pattern the forest floor. There are more tree ferns and a slight thickening of moss on the tree trunks, but this ridge differs from ridges of lower elevation mainly in having localized areas of extreme bromeliad development (fig. 14). These epiphytes occur in profusion on trees and on the ground. Unlike most cloud forest areas in which bromeliads are abundant, brush and low herbaceous plants are sparse, and in most places on this ridge one can move about without using a machete.

Actually the above describes a borderline case of cloud forest; better conditions presumably occur atop the main peak of Cerro Hoya, which is a few hundred meters higher than the one described. An elfin woodland type of cloud forest possibly caps the summit of Cerro Hoya. I know of only one person who has claimed knowledge of Cerro Hoya. He was a guide employed by Aldrich and Bole. These authors (1937, p. 12) gave the following secondhand account: "the upper slopes of Cerro Hoya are densely clothed with low trees, the branches of which are so matted and interwoven that it is often possible to walk on the tops of them." Almost constant fog undoubtedly clings to the high ridges in the rainy season, but fog does not seem sufficiently intense throughout the dry season to maintain the dense, luxuriant vegetation that is characteristic of cloud forest, except possibly on Cerro Hoya itself. Charles O. Handley, Jr. (*in litt.*) wrote that cloud cover always concealed the ridge northwest of camp from mid-January to March, during the time of his trip in 1962. But in late March and early April, 1967, near the end of the dry season, daily cloud formation was the exception rather than the rule, and frequent northerly winds brought almost xeric conditions to the forest. It is instructive to note that winds originating over the Atlantic have such a significant effect even this far south on the isthmus. Although there may well be variable onshore winds from the Pacific in the rainy season, the northeast trades are the important factor in the dry months. Handley reported particularly strong and persistent winds from the northeast, to 75 or 80 miles per hour, that prevented him from utilizing supply helicopters on his trip, but these winds evidently carried more moisture than at the time of my trip. Aldrich and Bole (1937, p. 15) also mentioned the strong dry-season winds of the Azuero, including an instance in which a loaded packhorse was blown off the trail!

11. Cerro Santiago

Figure 3

Cerro Santiago is a volcano situated on the continental divide between Chiriquí and Bocas del Toro provinces. I have not yet visited this place nor do I know of anyone who has. An expedition from the American Museum of Natural History traveled into the general area some years ago, but the exact location of their "Cerro Flores" is not known. One of the members of that party, Rex R. Benson of San José, Costa Rica, told me that after leaving San Felix, Chiriquí, and arriving in high country they never quite knew where they were. However, they managed to reach cloud forest that evidently is of the montane thicket or elfin woodland type. Griscom (1924, p. 516) provided the following account:

"We reached the continental divide at 6000 feet [1829 meters], and could look off forty miles or so to the northwest, where lay the Caribbean lowlands. To the west about ten miles away rose a cone-shaped peak about 1000 feet [305 meters] higher than the crest on which we were standing, with a big break in altitude between. Perhaps it was the real Cerro Santiago. The forest had changed with the altitude to a gnarled and stunted one, and every tree was loaded with parasitic plants of many kinds. Above 5000 feet [1524 meters] the very ground had been left behind, and we struggled upward in a gigantic bed of moss of unknown depth, with manholes between the roots of the trees, through which we could have dropped as much as fifteen feet. Everything dripped with moisture, everything was slimy and moldy, and everything gave way at one's touch. The slopes were markedly precipitous, with the result that water was unreachable in some gully 1000 feet below. There was not a square yard of even gently sloping hillside and there was no dry wood.[1] A camp in the cloud forest was impossible."

A Guaymi Indian trail crosses the continental divide west of Cerro Santiago and some 1000 meters lower. Anyone wishing to use this trail to the divide, would be well advised to start from the open Pacific slopes, where horses probably could be rented for at least part of the distance. The passage up the Río Cricamola on the Atlantic side is quite difficult according to Sr. Tomás Quintero, who scouted the trail for me as far south as Piedra Roja and was delayed frequently by floods and uncooperative Indian packers.

12. Cerro Pando

Figures 15–17

The summit of Cerro Pando is at the junction of the common boundary of Chiriquí and Bocas del Toro provinces with the Costa Rican border. William E. Duellman, Linda Trueb, and I spent the month of May, 1966, working a vertical transect of the northern slopes of Cerro Pando. We traveled by horse from 1200 to 1790 meters elevation up the valley of the Río Candella in Chiriquí Province. Then a footpath took us through nearly undisturbed forest to the 2290-meter summit of Cerro Pando, where there is an international border monument. We followed the international boundary northwestward for two and a half hours, and our way then dropped from 2100 meters on the divide to a campsite at 1920 meters on the north slope in Bocas del Toro Province. Additional camps were later established at 1450, 910, and 830 meters. This is a region of montane and lower montane rain forest that is disturbed occasionally by the trails and diggings of small parties of men who cross the divide from Chiriquí, seeking pre-Columbian Indian graves for golden *huacos* and other artifacts.

That section of divide traversed between elevations of 2100 and 2290 meters supports a low, dense cloud forest (or "montane thicket," fig. 15), which is characterized by a relatively low canopy and closely spaced trees that often have horizontal and intertwined roots and trunks near ground level, making travel exceedingly difficult away from an established trail.

[1] This can be a serious problem in cloud forest (especially above 1500 meters) and in montane rain forest, where even laboriously obtained heartwood burns wretchedly, if at all. A portable pressure stove, preferably kerosene, is recommended.

FIG. 15. High cloud forest (montane thicket) on Cerro Pando, 2290 meters elevation, border between Costa Rica and Panama (May 27, 1966).

The trees have an abundance of wet moss that is cold to the touch. The herbaceous vegetation is fairly well developed and small palms and tree ferns are common in the understory. Bromeliads are rare. Unlike the cloud forests previously described, this one differs noticeably in that it is not wetter than an adjacent (Atlantic slope), lower zone which is mostly cloud free. The montane rain forest (fig. 16) extends from the vicinity of the ridgetop cloud forest down to about 1800 meters. It has larger and more palms and tree ferns, is more open, and has a higher canopy (about 20 meters) than the cloud forest. Bromeliads are common only high on the trees; moss is abundant as it is on the ridge. There was light rain every afternoon and the ground was saturated. The occasional morning sun was insufficient even to begin to dry our camp clearing at 1920 meters elevation. Although the cloud forest and the rain forest seemed equally wet, there was a great deal less fog formation within the latter area. The clouds skimmed overhead most of each day, to pile up on the crest of the ridge and bathe its forest in nearly constant mist. Therefore I differ with Trueb (1968, p. 285), who called the ridgetop cloud forest (fig. 15) "elfin forest" and the forest at 1920 meters (fig. 16) "cloud forest." Certainly the ridge forest is physiognomically close to elfin wood-

FIG. 16. Montane rain forest, 1930 meters elevation, north slope of Cerro Pando on Atlantic drainage (May 7, 1966). Note the great abundance of palms in this perpetually saturated forest.

FIG. 17. Lower montane rain forest, 1450 meters elevation, north slope of Cerro Pando on Atlantic drainage (May 17, 1966). This area receives heavy rainfall but is not so continuously wet as higher elevations (compare fig. 16).

land (but even closer to "montane thicket" *sensu* Beard, 1955, pp. 93, 94), but as already indicated the forest down on the slopes seldom received any fog, except for occasional, brief periods of mist at night. Montane rain forest (Beard, 1944, 1955) seems to be a better term than cloud forest in the latter case.

Below 1800 meters on the Atlantic slope, the moss on trunks thins out and so does not cause the illusionary enlargement of trunks and branches (fig. 17), and palms become relatively scarce (compare figs. 16 and 17). Although Trueb (1968, p. 285) mentioned "an understory of palms" in the forest at 1450 meters elevation, it is difficult to find sufficient palms for the thatching of any but the smallest of shelters.[1] Heavy rains occurred at our lower camps, in contrast to the usual mist or light rains of the upper region. I did not see any bamboo growing on the Atlantic side, or at least did not mention it in my notes; on the Pacific side I first noticed bamboo at 2000 meters elevation, well below the cloud forest.

GENERAL AND ECOLOGICAL CONSIDERATIONS

The preceding descriptions reveal a considerable amount of structural diversity between communities here classified as cloud forest. Although I had neither qualifications nor time for floristic analysis, it should also be evident that there are considerable differences between the floras of certain communities. Likewise, there are differences between the faunas, but even when the same two species occur together in more than one cloud forest, it cannot be safely assumed that interactions between them will stay the same (see page 45). Admittedly, this broad concept of cloud forest is less useful to a phytosociologist than to a zoologist interested in collecting frogs, or a botanist looking for bromeliads. Nevertheless, from the viewpoints of biogeography and ecology, a concept of cloud forest as a major habitat or type of community is useful in at least the preliminary organization of data and the definition of problems, as is well exemplified by Martin's (1955) study in a Mexican cloud forest. And indeed, some life forms of plants, types of animals, and individual species occur in their highest densities even in rather dissimilar cloud forests of a region, probably responding to certain of a few features common to this habitat generally. Outlined below are what seem to me the generalities of cloud forest and some of the ecological implications that are involved.

The following factors, approximately arranged in simplified causal

[1] It is wise to carry plastic sheets (10 X 15 feet or larger) on any backcountry trip where a jungle hammock alone will not suffice. The plastic is light, expendable, and a piece also can be used to catch rainfall to supplement water in mountaintop camps.

sequence, can be considered a priori characteristics of cloud forests in general: 1) Moderate elevation; 2) Cool or "mild" temperatures; 3) Frequent, usually daily fog; 4) Humid conditions; 5) Low evaporation; 6) Luxuriant vegetation.

With reference to factor number six, the vegetation, of course, must be of a forest type; we are not concerned here with still higher vegetation zones that might otherwise meet these criteria. Also excluded are the occasional extratropical lowland fog forests which meet all criteria except the first. Most of the literature of Middle American cloud forest has been summarized or cited by Martin (1955) and Shelford (1963, pp. 465–468). An excellent South American study is that of Beebe and Crane (1947).

Elevation and Temperature: In Panama, cloud forest tendencies (frequent fog and denser vegetation) are seen on occasional ridges as low as 650 meters elevation, although trends toward the requisite atmospheric features are obvious even at 358 meters in the low part of the Serranía del Darién (fig. 13). What I regard as good cloud forest was found at elevations starting from 750 meters in eastern Panama and from 2100 meters in western Panama, but the vertical extent was never more than about 300 meters and usually much less. I have not previously seen cloud forest in Middle America documented for elevations below 900 meters, but such forest occurs lower in eastern Panama, where low ridges not backed by higher elevations protrude into currents of moist air. Cloud forest in northern Venezuela may start at elevations as low as in eastern Panama. According to Beebe and Crane (1947, pp. 48, 56), cloud forest near Rancho Grande occurs from around 700 or 800 meters upward on the Caribbean slopes and from about 1000 meters on the opposite slopes. These authors (*loc. cit.*) also record a much greater vertical extent for Venezuelan cloud forest than has been found in Panama. The borders of cloud forest in Middle America seem most frequently to lie somewhere between 1000 and 2500 meters in elevation. In Panama, cloud forest occurs as high as 2290 meters on Cerro Pando but might conceivably extend higher on the northern face of Cerro Santiago or Volcán Chiriquí (see page 44).

Because of elevation and cloud cover, temperatures are depressed and are cool relative to the tropical lowlands, or "mild" if compared with higher regions. Frost does not usually occur except in tropical fringe areas, as in Tamaulipas, Mexico, latitude 23° N., where, according to Martin (1955), light frosts are expected annually and there are even occasional severe freezes (−6° C., minimum); he suggested a mean annual temperature of about 19° C. and a mean seasonal variation of about 5° C. In Panama, I have not recorded a temperature in cloud forest below about 14° C., and I doubt that there are drops below 10° C. even in the highest Panamanian cloud forest. On the basis of partial records, Beebe and Crane (1947, p. 54) report monthly means of 18.5° to 20.9° C. (total range 14°–24° C.) at Rancho Grande (1097 meters), Venezuela.

The cooler temperature probably is an important limiting factor that stops the upward migration of numerous tropical lowland plants and animals. But for many other organisms the temperature (and other factors) is within ranges of tolerance. Thus, I found the predominantly lowland toad, *Bufo marinus*, appropriately on the very summit of Cerro Sapo in cloud forest at 1080 meters elevation, and Duellman (1966; and pers. commun.) encountered it near cloud forest at 2050 meters in Costa Rica. Jaguar, peccary, and tapir are among the larger kinds of organisms whose vertical distributions include cloud forest. In places where there are higher vegetational zones, cloud forest will also receive a faunal influence from colder regions, but this is seldom the case in Panama (see page 44). To a much greater degree than in higher montane assemblages, any distinctiveness of a cloud forest fauna will be blurred by species that enter from other zones, especially from below. The same general principle applies in plants, but to a lesser degree; it seems that cloud forests generally may have more distinctive floras than faunas, judged from statements made by Carr (1950) and Martin (1955), for example. Of course, more is involved than temperature.

Winds: Moist air may be carried into cloud forest on gentle currents, but stronger winds often remove moisture, as discussed in the next section. The seasonal northeast trades lose much of their limited moisture before reaching the Azuero highlands, and appear to influence the Azuero cloud forest more profoundly than they do some areas farther north. The strength of these winds is mentioned in the site description (Cerro Hoya, Azuero Peninsula). Frequent strong winds probably are one determinant of the elfin woodland type of cloud forest, by causing excessive transpiration as well as by a pruning effect (Beard, 1955, p. 98; Carr, 1950, p. 582). Strong winds also are noticeable when a rotten, epiphyte-burdened tree is blown down, particularly if it falls into your camp, as happened to me in the Serranía de Pirre. Dense vegetation may mark the site of a clearing made by a fallen tree after the tree itself has rotted away.

Moisture: I have experienced a few torrential rains in cloud forest, but precipitation occurs usually as condensation of moisture on solid surfaces, and as mist and light rain. There seems to be a general consensus that this zone may receive no more rainfall than some adjacent lower areas, and it is not uncommon from a cloud forest camp to hear the roar of a rainstorm lower on the mountain or in some valley. Carr (1950) gave evidence suggesting that cloud forest can develop on heights that receive no more actual rainfall than surrounding semi-arid lowlands. The fog-shrouded vegetation is usually dripping wet, because little of the slight, but almost constant, precipitation is returned to the atmosphere directly, most of it being lost by runoff. Several authors (especially Carr, 1950, fig. 5; see also Beebe and Crane, 1947, p. 52) suggest that the luxuriance of cloud forest vegetation is more directly attributable to low rates of evaporation rather than to the amount of precipitation. I concur, but it would be a mistake to assume from this that cloud forest organisms need have no particular behavioral or physiological traits to conserve water. On some ridges and mountaintops, stiff winds are apt to spring up and dry vegetational surfaces more thoroughly than an equal period of direct sun on a calm day, because a constant wind can permeate the forest and remove moisture more readily than sunlight. Carr (1950, p. 582) mentioned different ways that water is conserved by wind-exposed cloud forest vegetation in Honduras. Occasional dry winds, even of short duration, profoundly influence the activities of animals living in cloud forest. For example, there was ample rain on May 27, 1965, on the summit of Cerro Pirre, but shortly before dusk a wind started up and dried the leaf surfaces in a surprisingly short time. After dark I could push through the dense foliage without getting wet and fewer than a dozen frogs were seen, even though collecting was excellent on other nights when plants were drenched from the foggy mist. Winds often make collecting difficult on Cerro Campana. At such times most amphibians and other animals that are subject to rapid desiccation remain in the ground litter, bromeliads, or other moist hiding places. Eggs of Panamanian frogs of the genus *Eleutherodactylus* seem characteristically to be hidden in the ground litter, even though the adults may be largely arboreal, and it seems that the eggs normally are left unguarded. *Eleutherodactylus cruentus* deserts its eggs after laying them inside of either terrestrial or arboreal bromeliads, and some other species probably also lay in bromeliads or crevices in trees, as well as in ground litter. However, *E. caryophyllaceus,* a species characteristic of cloud forest and other mesic upland environments, places its eggs on exposed leaf surfaces aboveground and proceeds to brood the clutch until hatching (fig. 18). A brooding female from Cerro Pirre remained closely huddled to her 25 eggs even when the leaf was collected and put into a plastic bag, but when a little water was later trickled onto the leaf, or when much moisture was allowed to condense in the bag, she would elevate her body and expose the eggs. This individual remained on the eggs even when carried in my pack for parts

FIG. 18. A female *Eleutherodactylus caryophyllaceus* brooding its eggs (Univ. Kansas No. 114002, Cerro Sapo, Darién, May 18, 1967).

of three days, until the eggs hatched on May 30, five days after they were found. Another female, from Cerro Sapo, had to be stiffly poked to remove her from leaf and 19 eggs, which were then divided about equally on leaf sections and placed into different jars, with the adult in one. She brooded her fragmented clutch irregularly from May 18 to May 25, then she left it for good. The screen-capped jars were kept in a shaded place in the cloud forest camp and the eggs were never watered, although a little water was dropped on the female in an attempt to induce her back to the eggs. The untended eggs desiccated and molded on May 25, eight days after initiation of the experiment. The eggs that were brooded for parts of these eight days did not desiccate and mold until June 1, 15 days after initiation and seven days after desertion by the frog. From the preceding observations and because the frogs make no attempt to actually defend the eggs, it seems that egg-brooding behavior (unusual in frogs) is needed by *Eleutherodactylus caryophyllaceus* even in cloud forest, to prevent desiccation of the eggs.

LIGHT: Along with temperature, moisture, and wind, light is an important limiting factor in cloud forest situations. The low intensity of light that results from frequent fog is accentuated by usually dense foliage, and shade tolerant plants and animals are the rule. Basking reptiles, such as lizards that colonize new clearings, are more common in lowland situations; although clearings made by fallen trees are common in some cloud forests (probably because of wind and the often tremendous burdens of epiphytes), reptiles are not usually found in these situations. But because of their greater mobility, insects rapidly find such clearings and some groups (e.g. cerambycid beetles) are represented in great diversity.

COMMON PLANT AND ANIMAL TYPES: Certain genera and species of plants (animals to a much lesser degree) are excellent indicators of cloud forest communities within relatively small geographic areas, but lower taxa are useless when considering cloud forest as an environmental category over a broad region. For example, northern trees such as maple and sweetgum are highly characteristic of a cloud forest biogeocenose in southern Mexico, but such trees do not occur at all in Panama. But certain life forms of plants, and higher taxonomic groups of plants and animals, are useful in discussing the ecology of cloud forest over a broader region. The more extensive the region, the higher will the taxonomic category have to be and the more useful will the life form become. The discussions following are based primarily on observations in Panama, but seem to apply to Middle American cloud forest generally.

A. Epiphytes: Probably the most universal biotic feature of cloud forest is that of lush epiphytic growth. Although hardly confined to cloud forest, epiphytes seem nearly always to be more conspicuous in that environment than elsewhere. Küchler (1967, p. 184) noted that: "Strictly speaking, epiphytes are not life forms. They range from mosses and lichens to ferns and many flowering plants. Obviously, they include a great variety of life forms. . . . While they are therefore not at all uniform in appearance, they do introduce a new physiognomic element into the life forms of their host plants, and it is this changed look of the latter that is here significant." In Middle America, bromeliads, mosses, orchids, and ferns are among the most obvious kinds of epiphytes, although others occur. In the previous site descriptions I stressed only the bromeliads and mosses, since my field notes were made primarily with the idea of describing potential microhabitats of amphibians and reptiles. Bromeliads are of particular ecological significance in the Western Hemisphere, because they often contain a rich fauna and provide little pools of moisture in times of relative dryness. Bromeliads are virtually absent in some cloud forest communities (i.e. elfin woodland and perhaps montane thicket) of low and twisted aspect that seem to owe their character partly to wind action; examples in Panama are seen on Cerro Pando and on the summit of Cerro Sapo; the "*Peña* wind scrub" in Honduras is another case (Carr, 1950, p. 582 and pl. 13). In these kinds of communities mosses may be the predominant feature of epiphytic growth and they too probably contain characteristic microfaunas.

B. Tuft plants: This is a special life form category that consists of plants having an often unbranched trunk that carries at its apex a tuft of leaves (Küchler, 1967, p. 184), such as palms and tree ferns. Palms, including those with stilt roots, are often conspicuous in cloud forest but are likely to be more abundant in lower forests; exceptions in Panama are Cerro Jefe and the vicinity of Cerro Hoya, in which palms are more common in the borderline cloud forests than at lower elevations. Tree ferns, on the other hand, occur from sea level but in many places reach a high density only in cloud forest. An increasing abundance of tree ferns up a moist mountainside may indicate that cloud forest is being approached, but where cloud forest borders on markedly drier communities, the abrupt appearance or sudden increase in density of these plants may be striking. Like bromeliads, tree ferns may be nearly absent from the elfin woodland type of cloud forest.

C. Woody plants: The primary generalization to be made of the tree and shrub life forms is their principally evergreen appearance in cloud forest, even though adjacent forests may be at least irregularly semi-deciduous, or "tropophyllous" (*sensu* Küchler, 1967, p. 373). In any case, deciduousness is either absent or only of a very minor degree in cloud forests, as when confined to a few trees in the upper canopy (e.g. Martin, 1955, p. 351). Other features, such as buttressed trunks, stilt roots, height, density, or elevated and intertwined roots vary according to a complex of factors, such as moisture, soil depth, wind exposure, and kind of species present. Woody vegetation is most distinctive in the elfin woodland type of cloud forest (fig. 9), which is a nearly impenetrable thicket of low, gnarled sclerophyllous trees that have very hard wood.

D. Common animal types: Certain groups of animals are apt to be more abundant in cloud forest than in other drier areas or even low, wet areas. Two groups of amphibians in Middle America—plethodontid salamanders of several genera and leptodactylid frogs of the genus *Eleutherodactylus*—have been particularly successful in cloud forest (Duellman, 1966, p. 707); a principal reason for their success is that the tropical plethodontids and all *Eleutherodactylus* have terrestrial eggs and direct development, hence they are not dependent on bodies of water for breeding and can fully exploit the cloud forest environment. Occasional species of other anuran groups are characteristic of particular cloud forests by virtue of special breeding adaptations, and a few examples might be cited. On Cerro Campana, the tiny *Dendrobates minutus* carries a tadpole (hatched from a terrestrial egg) on its back to some water-filled bromeliad, in which a free larval stage is then completed. The casque-headed *Cerathyla panamensis* is a peculiar kind of "tree frog" (Hylidae) that has direct development of the eggs on its back; this species lives on or near the ground, is one of the few frogs that bites defensively, and seems to find its optimum environment in the Panamanian cloud forest (Myers, 1966a, and subsequent observation). The other classes of terrestrial vertebrates—reptiles, birds, mammals—have better mechanisms for water conservation and have more successfully radiated into a greater variety of environments than have amphibians. These vertebrates usually are less conspicuous in cloud forest than elsewhere, although a few species are characteristic mainly of that habitat. Some kinds of invertebrate animals that often are more common in Panamanian cloud forest than elsewhere include planarian flatworms, onychophorans, and arboreal annelid worms. The invertebrate faunas of cloud forests are interesting and greatly in need of study, but beyond this I hesitate to make further generalizations for fear of being completely wrong. For example, except by accident it would be my impression that Lepidoptera are poorly represented in cloud forest; this would be intellectually satisfying since butterflies and moths largely are delicately winged creatures that should be easily grounded in such a dripping environment. However, a kerosene pressure lantern carried onto the northern Pirre ridge attracted many species of little moths that were more diversified than I have seen anywhere else. Beebe and Crane (1947, p. 58) also comment on the phenomenal numbers of moths that may be attracted to a light in the cloud forest.

Uncharacteristic Life Forms: Certain life forms are less common in cloud forest than elsewhere and deserve mention for that reason. The woody stranglers (e.g. *Ficus* spp.) are absent so far as I have noticed; because they begin growth as epiphytes, they may lose out in the competition right at the start. Lianas are usually present but never seem to form such a conspicuous feature of the landscape as in some communities of lower elevations. Stem succulents are not expected because there is little adaptive reason for a cloud forest plant to store large quantities of water within its tissues. Bamboos (not strictly a life form but a taxonomic group) are sometimes sparsely represented in cloud forest, but at least in Panama they are really abundant only at lower elevations, often in a definite zone somewhat below the level of cloud forest (fig. 10). Schmidt (1936, p. 139) reported dense bamboo thickets at the upper border of cloud forest in Guatemala.

ZONATION: On mountains of low or moderate height, cloud forest will be the uppermost vegetation zone, occurring on the summits and ridges. On higher mountains there are additional communities above cloud forest, as at some places in Mexico and Guatemala, and in the South American Andes and Sierra Nevada de Santa Marta. Most cloud forests of Panama, and those of Honduras (Carr, 1950) and the Rancho Grande area of Venezuela (Beebe and Crane, 1947) are of the former type. Although savannas have been reported (Aldrich and Bole, 1937) at an elevation of ± 1000 meters, on ridges above a narrow zone of reputed cloud forest in the Azuero Peninsula (see page 29), these grassy heights must surely be the result of human influence. But cloud forest almost certainly occurs below other vegetational zones on the unexplored Cerro Santiago, the apparently barren summit which rises to about 2800 meters, making it the second highest mountain in Panama. It is conceivable that a similar situation exists on the northern slopes of Volcán de Chiriquí (Volcán Baru), the highest mountain in the Republic. However, a seasonal rain shadow effect may prevent the development of good cloud forest on Volcán de Chiriquí, which is situated on the Pacific side of the continental divide. I walked up the western side of this mountain in early December, 1967, and passed through several communities on my way to a campsite near the grassy crater; but even in tall forest of rather mesic appearance, the epiphytic moss and the soil were very dry and the vegetation unlike that of cloud forest. The highest elevation forest was low and scrubby, and seemingly exposed to frequent extremes of wet and dry.

Cloud forest may be confined strictly to the crest of a ridge, with only a narrow transition below the crest, as on the northern end of the Serranía de Pirre. The Pirre situation was an interesting case in which nighttime frog activity was as good an indicator of the community as was the vegetation itself. But other kinds of cloud forest have more extensive vertical development, in which case there may be a horizontal splitting of the cloud forest into very distinct facies. In Panama this evidently occurs on Cerro Tacarcuna, and probably on Cerro Santiago and Cerro Hoya, but I have personally observed it only on Cerro Sapo on which there are two cloud forest zones (including elfin woodland), or three if a distinctive lower transition zone is counted. Carr (1950) described three major zones in Honduran cloud forest, and also three subzones of the highest major one.

As might be expected, there is some correlation between animal distribution and cloud forest zonation. On Cerro Sapo, some frogs of the genus *Eleutherodactylus* were sufficiently abundant to demonstrate the influence of zonation on a group of moisture-loving animals. The observed vertical distributions of six common species are shown in figure 19. Because a few seemingly unnamed species are involved, each of the six is given a letter designation (A-F). It is seen that of the three species (A-C) occurring in the upper cloud forest (elfin woodland), each occurs also in the lower cloud forest but was not found below that zone. Two species (E-F) that occur in the seasonally dry, lowland hill forest (evergreen seasonal forest) extend their ranges up into the lower cloud forest but not into the upper zone. One species (D) is abundant in the lower cloud forest and was found elsewhere only in the transition zone, in which it is less common. It is not expected that the observed altitudinal distributions are precisely equivalent to the real distributions, but I think that each plotted range does include the area of maximum population density. The lower limit for species B and the upper limit for E are among the most accurate in this latter regard, because the limits are based on abrupt cessation of vocalizations. In the case of species E (*Eleutherodactylus vocator*), the main limiting factor seems to be the greatly reduced density of calling sites (low herbs) on the floor of the upper cloud forest, but it was hard to visualize any reason why species B (*Eleutherodactylus ?diastema*) should suddenly stop calling at its lower limit of 860 meters. The lowermost specimen of C (*Eleutherodactylus* sp.) and the uppermost of D (*Eleutherodactylus caryophyllaceus*) were found within a few feet of each other at 960 meters; each of these species then became common either up or down the mountain, according to kind, suggesting that each species has adapted to a particular fragment of the environment, perhaps because of competition. On Cerro Pirre, where there is essentially one rather than two kinds of cloud forest, both C and D species occur together. These observations are indicative of the variety of ecological differences that occur within and among cloud forests even in the same region.

EVOLUTION AND COLONIZATION: Cloud forest is often thought of as a haven for various kinds of plants and animals that exist nowhere else, but the mere presence of cloud forest is not necessarily synonymous with a rich biota. In Tamaulipas, Martin (1955) found a rich, indigenous flora, but a fauna that is locally derived and that lacks most of the distinctive kinds of animals found in cloud forest in southern Mexico. He suggested that following fragmentation of a widespread cloud forest en-

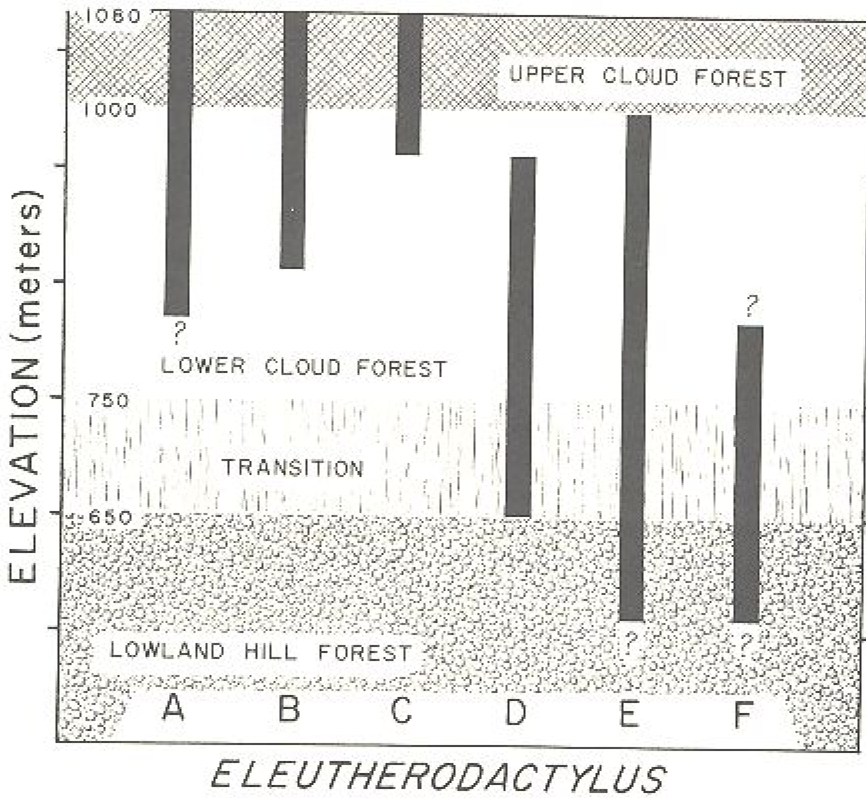

FIG. 19. Vertical distributions of six common frogs of the genus *Eleutherodactylus*, on Cerro Sapo, Darién, eastern Panama. These observed distributions (May, 1967) are believed to include the zones of maximum population density for each species. Two question marks in the lower cloud forest zone indicate unreliability relative to other bars (regarding distribution, not maximum density); question marks in lowland hill forest zone indicate cessation of collecting at that elevation.

Species A. *Eleutherodactylus cruentus;* B. *Eleutherodactylus ?diastema;* C. *Eleutherodactylus* sp., *diastema* complex? (lacks tympanum); D. *Eleutherodactylus caryophyllaceus;* E. *Eleutherodactylus vocator;* F. *Eleutherodactylus* sp. (red-spotted thighs). The various habitats are illustrated in figures 6–9 and a specimen of *E. caryophyllaceus* is shown in figure 18.

vironment, subsequent climatic change depleted the fauna more than the flora, leaving the habitat open to local animals of adjacent zones. The Cerro Hoya region of Panama probably has never been connected with other montane environments, and the amphibian and reptile faunas have perhaps always been very depauperate. With a few exceptions, most of the Pacific lowland species apparently are not able to occupy the mesic forest in the Cerro Hoya region, and very few montane species seem to have reached the region from other highland systems. In 17 days at elevations of 480 to 1260 meters on Cerro Hoya, an experienced assistant and I were able to find only 13 species of amphibians and reptiles. In contrast, we collected examples of 54 species in a total of 20 days in the Serranía de Pirre, at nearly equivalent elevations of 470 to 1550 meters. The dry season affected the Cerro Hoya collecting but it certainly was far from the only factor; a dry season collection in the highlands of Chiriquí (1130–1440 meters) contained 22 species obtained in only six days. The ridges above 1000 meters elevation on Cerro Hoya seemed virtually devoid of amphibians and reptiles. Despite a great abundance of water-containing bromeliads (fig. 14), only the widespread *Eleutherodactylus longirostris* was found in the borderline cloud forest. Rivero ("1964" [1965]) mentioned examining hundreds of bromeliads at a place in the Venezuelan highlands and not finding a single frog. Carr (1950, p. 583) believed there is only a meager fauna in the higher cloud forests of Honduras. If there has been ample opportunity for invasion and permanent colonization, however, even a relatively small cloud forest is likely to have a rich fauna indeed. In the Serranía de Pirre, for example, I know of four or five species of amphibians and reptiles that seemingly have been found nowhere else, plus an additional species that has been found elsewhere only in the Serranía del Sapo. Also, there are many other species found there that have continuous or disjunct distributions elsewhere in the republic, and some of these show local differentiation.

The evolution of isolated endemics is an interesting problem and I suspect that this is more likely to occur in some kinds of cloud forests than in others. The occurrence in the Serranía de Pirre of distinctive populations of the frogs *Eleutherodactylus diastema* and *E. vocator* can be used for some speculation on the formation of cloud forest endemics. As already explained, the wet Pirre cloud forest borders relatively abruptly on drier, lower forest; moisture differences are especially pronounced in the dry season but probably there are significant differences throughout the year. *Eleutherodactylus diastema* and *E. vocator* are wide-ranging species that occur from sea level up into cloud forest; the Pirre populations of both species differ in color from nearby lowland populations. There is no need to go here into the details of coloration, only to assume for the sake of discussion that genetic factors are involved and to ask what keeps the gene pools from being swamped by influence from below. Actually there is a sharp decrease in the population densities of these frogs between the cloud forest and the lowlands (see pp. 23–24). The forest immediately below the cloud forest is a poor environment for the frogs, especially in the dry season, and even during wet seasons there is probably more dispersal from the cloud forest down than in the other direction, since the cloud forest has an obviously denser population than the lowlands (as determined from call frequency). It would seem probable in such cases that the cloud forest populations rose to dense levels in a short time, once a few original invaders succeeded in crossing the less suitable habitat. Any suitable mutations would have been favored because of the low genetic interchange between the cloud forest and the outside, and the mutations would have passed quickly through the restricted habitat. Significant differentiation of such cloud forest populations might also have arisen by non-selective genetic mechanisms, if the original founders of the populations carried particular traits which then became early established. I think that *Eleutherodactylus diastema* and *E. vocator* may breed throughout the year on the Pirre ridge, but they do not do so in the lowlands because of the dry season. Thus there would be more generations per year in cloud forest than in the lowlands, and this too would favor rapid differentiation. A true cloud forest endemic results when the lowland population disappears for some reason or when the two populations gradually become genetically incompatible.

Cloud forest endemics have not necessarily evolved in the places they now occur. Many are doubtlessly relicts of some past time when cool and humid montane environments were of much greater horizontal and vertical extent than they are today. In this category are probably certain undescribed species of Panamanian amphibians and reptiles that occur in isolated cloud forest but not in adjacent lower zones. It was formerly fashionable to attribute considerable age to such relicts, but there is a growing belief that many relictual montane distributions in tropical America are explainable by the alternation of humid and dry periods in Pleistocene and even post-Pleistocene times (Haffer, 1967a, 1967b).

The stress on cloud forest as an ecologically important environment probably is not so warranted in places where it merges with cloud-free but equally wet adjacent zones. In Costa Rica and extreme western Panama, for example, cloud forest probably often borders on montane rain forest (e.g., fig. 16). In such situations, moisture-loving species are apt to occupy more extensive zones and the small area of true cloud forest loses much of its potential, although similar evolutionary possibilities then pertain over the greater area, even if the processes may not be so rapid. If the biotic borders of the cloud forests are indistinct, it is one possible reason why this habitat is little emphasized in the rather sizable biological literature of Costa Rica.

SUMMARY

The physiography, climate, and major vegetational regions of Panama are discussed, with particular reference to factors that influence the distribution and nature of cloud forest. Difficulties were encountered in applying the Holdridge classification of life zones or world plant formations to the natural regions of Panama, and it is concluded that other systems are at least easier to use in the field. The extensive cuipo forests (*Cavanillesia platanifolia* association) of eastern Panama are thought to be largely the result of edaphic factors associated with the nearly base-level terrain, rather than being primarily the result of climatic control as suggested in recent life zone maps.

Cloud forest is thought of as a habitat or community-type in a very broad sense, but the term will not be useful for all purposes and usually needs to be qualified. A cloud forest is any montane forest that owes its character primarily to the atmospheric conditions associated with frequent, enshrouding clouds, even though such forests may be quite diverse by floristic and some physiognomic criteria. The vegetation tends to be conspicuously lusher than in adjacent zones of little or no cloud formation and usually there is a profuse growth of epiphytes. Known cloud forests in Panama are mountaintop and ridge phenomena and do not give way to higher vegetational zones; exceptions probably occur on the unexplored Cerro Santiago, and possibly on the north face of Volcán de Chiriquí, the two highest mountains in Panama. Grassy savannas above a reputed cloud forest in the Azuero Peninsula probably were caused by the activity of man.

Cloud forest first occurs on mountains at the unusually low elevation of 750 meters in eastern Panama and at 2200 meters on higher mountains in western Panama. These forests may be confined almost to the crest of a ridge or extend as much as 300 meters in elevation down the side of a mountain and, in the latter case, there may be distinct subzones, including elfin woodland. Panamanian cloud forests are briefly described and pictured herein, and are discussed in various generalities that probably apply to cloud forest in other places. Some ecological implications of the various topics are illustrated by a few selected plant and animal examples. Cloud forests that border on significantly drier zones (e.g. evergreen seasonal forest on steep slopes) provide at least partial genetic isolation for organisms having high moisture requirements, as is suggested by populations of certain Panamanian frogs. Cloud forests that border on zones equally as wet (i.e., montane rain forest) are perhaps of

less ecological and evolutionary importance.

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