Citar como:

Monasterio, M., Vuilleumier, F. 1986. Introduction: High tropical mountain biota of the world. En: Vuilleumier, F., Monasterio, M. (Eds). High Altitude Tropical Biogeography. Oxford University Press, pp. 3-7.

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Introduction: High Tropical Mountain Biota of the World

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The term "high tropical mountain biota of the world" means the flora and fauna, either integrated together into local communities or into ecosystems, or separated into some of its taxonomic components (birds, vascular plants), found at high altitudes above the upper altitudinal limit of continuous forest vegetation of both the Old and New World. If trees are defined on the basis of architectural models (see Hallé, Oldeman, and Tomlinson, 1978), then trees conforming to Corner's model of growth occur in the highest Andes. In the tropical mountains, furthermore, one must distinguish between timberline formed by continuous forest vegetation, and "timberline" that results from patches of trees (defined now on the basis of branching patterns) above continuous forest. In this book, we distinguish between forest and nonforest vegetation on the basis of the traditional concepts of tree and forest.

High montane ecosystems occurring between the Tropic of Cancer and the Tropic of Capricorn (Fig. 1–1) are known by the name given to the most distinctive local plant formations. Thus the names of páramo (northern Andes), puna (central Andes), afroalpine (East African mountains), or tropical-alpine (Malesia) appear regularly in this book. Unfortunately, no single name encompasses all the types of high tropical mountain vegetation above the continuous timberline. The afroalpine and the tropical-alpine correspond rather closely to the Andean páramo in vegetation physiognomy, but the puna of the

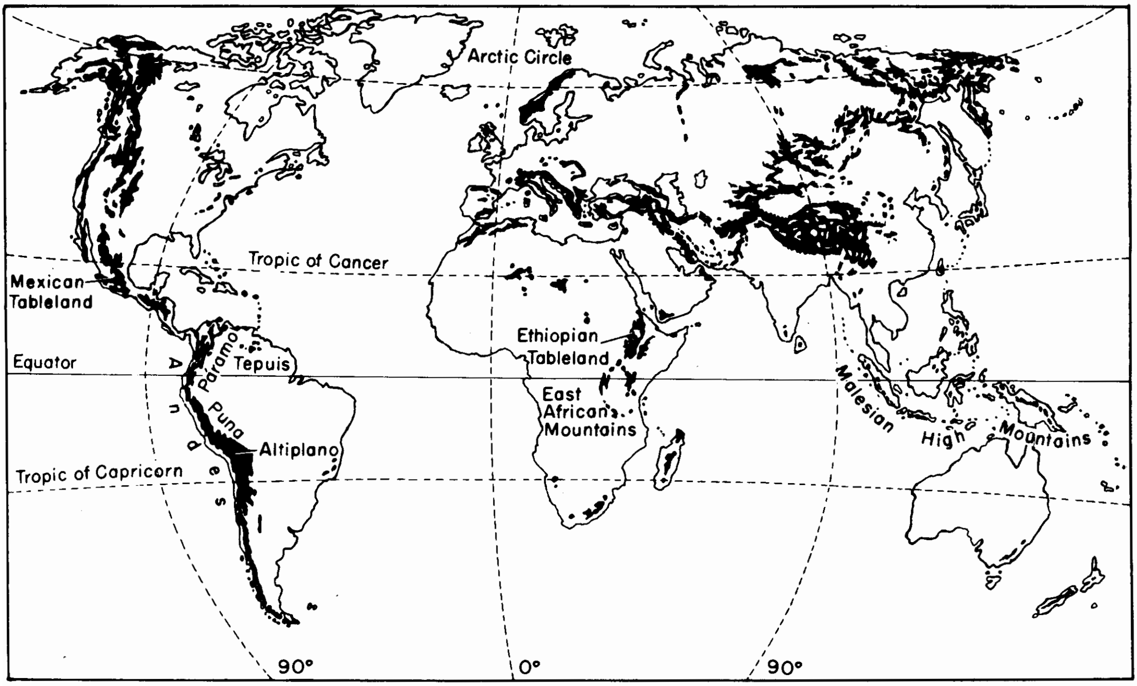

FIG. 1–1. Distribution of mountain vegetation worldwide, showing the extent of montane vegetation in the intertropical zone. Modified and simplified from world vegetation map, *Times* (London) *Atlas*, vol. I (1958), Plate 4, scale 1:65,000,000.

central Andes has no real equivalent in the Old World tropics; indeed, in some ways, the puna appears more similar to the steppes of the Tibetan Plateau. In spite of such differences in the aspect of vegetation and underlying climate (see Chap. 2) of various high tropical mountain areas of the world, it might be useful, for the sake of nomenclatural simplicity if for no other reason, to call all high tropical mountain biota above the timberline simply *páramo*. The addition of a geographic adjective, if necessary, would then be all that is needed to characterize the particular area that is being discussed, for example, Andean páramo, African páramo, Papuan páramo, and so forth.

We will use this simplified nomenclature in this introductory chapter, although the authors of chapters in this book have used the more traditional nomenclature.

Basically, páramos are high mountain grasslands, in general dominated physiognomically by the presence of bunch grass (Gramineae), but also containing other plants, especially shrubs or rosette trees of the family Compositae. Some páramos are almost pure dense grassland, but at the other extreme, especially at very high altitudes, other páramos are almost totally devoid of grasses and dominated instead by the peculiar giant rosettes of members of the family Compositae. Elsewhere mixtures predominate. In at least one case, Mt. Kinabalu in Borneo, there is no grassland, and in fact very little soil and vegetation, above the timberline.

Other plant groups are also important in the composition of páramo vegetation, especially (locally) some Bromeliaceae (particularly the genus *Puya*), some Campanulaceae (*Lobelia*), some Cruciferae (*Draba*), some Rosaceae (*Polylepis*), and some Cyatheaceae (*Cyathea*). The "ground" can be either a dense, mirelike, spongy mass of plant life (mosses and others) covering the soil entirely with a thick layer, or else the soil is essentially dry and barren, with sparse cushion and rosette plants, growing in the more sheltered areas. At very high altitudes, frequent or regular nightly frosts produce conspicuous frost polygons and striated ground, characteristics one usually associates with the arctic, not the tropics.

Páramos can thus appear either as lush environments, with many plants that look strange to a biologist from the temperate zone, or as very open, desert-like landscapes, with occasional oases of somewhat denser vegetation in thermally privileged, usually rocky, areas.

Montane rain forests or cloud forests are the vegetation formations encountered below páramos on wet mountains or along the wet slopes of some mountains. The ecotone between páramo and upper montane rain forest is usually a tangled thicket of epiphyte-laden shrubs or gnarled trees growing in impenetrable copses surrounded by tall grassland. Elsewhere the timberline is very sharp, making the transition from forest to páramo quite abrupt. Along dry slopes, transitions can be more subtle, since forest is usually absent at montane elevations and replaced instead by an open vegetation of shrubs and locally of cacti, more or less rapidly giving ground to the páramo plants.

Animal life in páramos is usually much poorer than in tropical environments at lower altitudes, whether wet or dry. There are fewer species of fewer taxonomic groups, but characteristically some groups (families, genera) dominate the communities. This is one of the features of insularity. It clearly looks as if the rigors of a high-altitude environment severely limited the ability of tropical groups to establish themselves permanently there. In fact, páramos are perhaps the tropical environment with the largest representation of temperate groups (this is also true for plants).

Thus the páramos are both "bridge and barrier": the first for temperate taxa, the second for tropical ones, although such an overly dichotomous view has obvious exceptions. By and large, páramo animals lack the extravagance of color and form assumed by their relatives in the lowland tropics: they are either smaller, or duller, or both. Often also, páramo animals appear scarce. Many of them lead hidden lives, in nooks and crannies of the vegetation or of the inanimate substrate.

The greatest extension of páramo *sensu lato* is in the Andes, where the dry and open formation called puna has a vast and continuous distribution in a region known as the altiplano (central and southern Peru, Bolivia, northern Chile, and northern Argentina); the páramo *sensu stricto* occurs in smaller and disjunct patches in Venezuela, Colombia, Ecuador, and northern Peru. In Africa, the approximate equivalent of the Andean altiplano is found on the Ethiopian tableland, whereas the African páramo, like the Andean páramo *sensu stricto*, is disjunct on the isolated summits of East African mountains. In Asia and the Pacific area (Malesian and Melanesian high mountains) all páramos are patchy and discontinuous, occurring either on single small or relatively small islands (like Borneo) or in patches on large, continentlike islands (New Guinea).

Although "alpinelike" in some of their characteristics, the páramo of high tropical mountains differs in important respects from alpine biota in North America, Europe, Asia, or New Zealand at high latitudes. Several of these differences derive from the fact that the oscillations of the main climatic variables (temperature, precipitation) at high altitudes in intertropical regions are quite distinct in their periodicity from those prevailing at temperate latitudes (see Chap. 2). A number of ecological and evolutionary consequences have resulted in adaptations unique to the taxa living in the páramo environment. Several of these adaptations will be discussed later in this book. High-altitude tropical areas are available year-round as habitats for both plants and animals. In the most favorable cases, year-round reproduction is possible and in some instances does occur. This constant or virtually constant availability, contrasted to the highly seasonal unavailability of alpine biota at temperate latitudes because of the unproductive and snow-bound winter period, is likely to have been one of the factors that has permitted the páramo biota to be much richer in habitat types, and in species, than their temperate, alpine, counterparts. For these reasons we prefer to call tropical high mountain biota páramo rather than alpinelike. In our view, therefore, alpine is a term that should be restricted to the seasonal areas of high mountain biota at high latitudes, and páramo should include only the year-round available habitats of high tropical mountains.

The páramo biota discussed in this book are for the most part geologically very young. Phases of uplift in the main mountain systems in the intertropical regions of the world have "created" these ecosystems out of different vegetation types, whether savannalike or forestlike, at lower elevations. The appearance of the cold tropics in the late Cenozoic permitted immigration to and subsequent occupation of new vegetation types. Various plant and animal taxa were able to expand into this new area from other regions, either at lower elevations or at lower latitudes. Some of these taxa adapted to their new environment and even underwent extensive adaptive radiation there, as described in several chapters here. Differences in the ability of various taxa to disperse and colonize the proto-páramo must have been due in part to the intrinsic capacity for dispersal and adaptation to new environments, and partly to the geographic positions of the cold tropics on each continent. Thus in the Americas, the high mountains are located along the western margin of the tropical area. The Andes could thus have served both as a corridor between northern temperate and southern temperate (Patagonian or Fuegian) elements, and as a new area for colonists from lower altitudes along the tropical slopes. In Africa, the islandlike nature of the páramo on East African mountains can be contrasted with the plateaulike distribution of high tropical biota on the Ethiopian tableland. In the Indo-Pacific, the insular nature of both the páramo environment and of the lower altitudinal belts below, especially montane forest, and the linear arrangement of these vegetation types between continental Asia and insular New Guinea produced yet another background for colonization and establishment.

The study of páramo biota began a long time ago, at first of course with various phases of exploration and collection of botanical and zoological material. Jeannel (1950) described these early explorations in the high mountains of East Africa in a superb monograph, to cite only one reference. This type of work is still carried out today, but less intensively than in the past. Yet it must go on, for we still need to make thorough inventories of a number of plant and animal groups. We do know a great deal about the taxonomic composition and geographic distribution of many taxa of vascular plants in most high-altitude tropical areas, and a similar statement can be made for several animal groups, for instance, birds, some mammals, and to a lesser extent some Lepidoptera. But our knowledge of the basis facts of taxonomy, relationships, distribution, and ecological preferences of many other plant and animal groups is woefully incomplete. Among taxa in greatest need of such basic study we can cite lichens, fungi, earthworms, Collembola, Arachnida, many Insecta, especially perhaps Diptera and Hymenoptera. Not only are these groups important in themselves, but they are also a fundamental part of the communities as links in the food webs and trophic chains. Thus until we know what taxa we are dealing with we will not be able to answer ecological or evolutionary questions. Basic taxonomic work is urgently needed before more problem-oriented research can begin.

At the present state in our understanding of páramo biota, we can offer hypotheses and scenarios about the dispersion and origins of selected taxa of plants and animals, or of some plant or animal "communities" (the term is here used in the sense of taxocene, for instance, the "community" of birds of the Andean páramos). We have enough information to start verifying several ecological or evolutionary hypotheses about specific aspects of adaptations to high altitudes in the tropics, for example, plant breeding strategies and adaptive syndromes, or resource limitations in high-altitude hummingbirds. But we cannot yet make very profound commentaries about these habitats as ecosystems. For instance, we know very little about energy transfer and flow, evolution of biomass, trophic relationships, or the role of predation in regulating community structure. We can describe some of the parts of the páramo biota of the world, but we are not yet ready to integrate them into a functional whole.

Most chapters in this book, reflecting what we see as the state of the art in evolutionary and biogeographic research at the level of resolution approached here, deal more with ecology and evolution in broad time and space dimensions than with specific, or punctual and almost dimensionless, analyses of adaptations. The measurement of limiting resources, the definition of niche parameters, the fine-scale study of interspecific interactions (e.g., allelopathy), the quantitative analysis of predation or symbiosis are all areas for future work.

We believe that future research will have to be carried out at one or more of three levels. First, the inventory of taxa (at least key taxa in the functioning of páramo biota) will have to be improved. Only then will it be possible to pose questions at the second level, beginning with how. Finally, at the third level, long-term studies will have to be undertaken at many localities. All three levels are not necessarily independent of each other, of course. Some questions can indeed be asked before the inventory of a given group of plants or animals has begun in earnest, and can in fact direct the survey in fruitful directions. But the long-term research objectives will ultimately depend, in their feasibility, on the availability of local or regional centers of research located within the high tropical montane areas themselves. An example is the plant ecology group at the University of the Andes in Mérida, Venezuela.

To present the reader with a picture of the research carried out on páramo biota of the world we divided the book into five parts, all but the first preceded by a brief editorial introduction. Part I contains a single chapter, in which the peculiar aspects of the climate at high altitude in the tropics are described. This chapter is fundamental for the rest of the book because it gives the climatological background necessary for an understanding of the páramo biota, past and present.

The second part of the book consists of four chapters (two on plants and two on birds), analyzing the adaptive strategies of some of the most obvious or physiognomically dominant components of the biota. *Espeletia* in the Andes and *Dendrosenecio* in East African mountains are certainly among the most conspicuous plants of the páramo landscape. Some of their modes of life are now well known. The two chapters on birds are comparative. Hummingbirds in the New World and sunbirds in the Old are often thought of as ecologically equivalent, if not actually convergent taxa, and their adaptations are studied in a comparative framework. At a broader taxonomic, ecological, and biogeographic level, the avian associations of the high Andes are compared to those of the Ethiopian tableland in an effort to detect communitywide convergences or at least parallelisms in general form and function and in habitat selection. The hypotheses so generated should make much easier the task of testing specific details about parallel or convergent evolutionary pathways between two different páramo avifaunas or their components.

In part III the historical developments of high-altitude biota of the Andes are examined in four chapters treating floras (two chapters) and faunas, especially mammals (two chapters). These chapters present historical data and rely on the results of researches into fossil pollen or fossil bones, interpreted in the light of geologic and climatic evolution. The time span involved is relatively short, since it concerns chiefly the Pliocene and Pleistocene epochs, when the Andes reached their present height and became covered with the vegetation types and the habitats that characterize altitudes above the upper limit of continuous forest.

The fourth part of the book is devoted to studies of adaptive radiation and evolution at the species level, especially speciation, among some of the endemic taxa of the high tropical Andes and the Venezuelan Tepuis: *Polylepis* (the only genus of plants that forms forests or woodlands above the upper limit of continuous forests in the high Andes), the frog genus *Telmatobius* (with a wide range of adaptations to aquatic and semiaquatic habitats), the fish genus *Orestias* found in closed basins of the central Andes, and the very diversified rodents (an extraordinary instance of continental adaptive radiation). The panorama of taxa thus encompasses plants and animals, and among the latter both aquatic and terrestrial groups.

Finally, in part V, the geographic origins of the floras and faunas are examined in detail. A chapter on the African páramo flora is followed by five chapters on various animal groups, both invertebrates (butterflies) and vertebrates (birds). These chapters include Africa, Indo-Australia, and the Andes. In the absence of a fossil record for these taxa, their origins are inferred on the basis of present distributional patterns.

Because high tropical mountain biota are intermediate between the strikingly simple island biota and the extraordinarily complex tropical lowland biota, they constitute a superb natural laboratory for research into fundamental evolutionary and biogeographic processes. They also offer an opportunity to integrate basic research with the expanding needs of human population. The key components of high altitude tropical mountain life, namely insularity within a continental situation, variability along altitudinal gradients, and great diversity in the origins of floristic or faunistic elements, must form the basis of future research programs and must be fully understood before development proceeds further.

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