

## FUNCTIONAL STRUCTURE OF BAT COMMUNITIES IN TROPICAL RAINFORESTS AND ANDEAN CLOUD FORESTS

### ESTRUCTURA FUNCIONAL DE LAS COMUNIDADES DE MURCIELAGOS EN SELVAS HUMEDAS TROPICALES Y SELVAS NUBLADAS ANDINAS

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#### SUMMARY

The use of functional groups, such as trophic categories, is more useful for ecological interpretation of differences in community structure than the simple comparison of lists of names. Using these trophic categories demonstrates that bat assemblages from Andean cloud forests show greater taxonomic and functional simplicity than those from lowland rainforests. This altitudinal decrease has been interpreted as a consequence of the reduction of available resources. However, this is not manifested proportionally in all functional groups or trophic guilds or even in all taxa within the same guild. The insectivore guild seems to be directly responsible for the decrease, showing a high correlation with total bat species richness, while on the contrary, the rest of the functional categories decrease in other ways. Diet has a large influence on the metabolic rate of these mammals and therefore on their thermoregulatory capacities. Bats whose diet is based on protein (insects) in general have lower metabolic rates than those whose diet is comprised primarily of carbohydrates (fruit and nectar). In contrast to lowland forests where insectivores dominate bat communities, frugivores constitute the most important trophic category in cloud forests. I here postulate that the explanation for this difference in internal richness of these functional groups is found in the differential response capacities of each species to the thermoregulatory demands of the environment, which are directly related to their dietary regime. All these facts lead us to believe that the decrease of species richness with altitude is due to the inefficient thermoregulation of species of tropical origin, which make up most of the insectivore guild. Apparently, all insectivores of Neotropical origin have a «ceiling» in their vertical distribution which prevents them reaching the higher altitudinal belts, whereas the only bats reaching these high forests belong to the Vespertilionidae family of Nearctic origin as well as a few representatives of the Molossidae.

**Key words:** Bat communities, Andes, Neotropics, functional categories, Venezuela, cloud forests, rainforests.

#### RESUMEN

El empleo de grupos funcionales, tales como categorías tróficas, es más útil en la interpretación ecológica de las diferencias estructurales entre comunidades que la simple comparación de listas de nombres. Usando estas categorías tróficas se demuestra que las comunidades de murciélagos de selvas nubladas andinas exhiben mayor simplicidad taxonómica y funcional que las correspondientes a selvas húmedas de tierras bajas. Esta declinación altitudinal se ha interpretado como la consecuencia de una reducción en los recursos disponibles; sin embargo, no se manifiesta proporcionalmente en todos los grupos funcionales o gremios tróficos y tampoco en todos los taxa de un mismo gremio. Los insectívoros parecen ser los responsables directos de la declinación referida, al mostrar una alta correlación con la declinación total de los murciélagos, mientras que, por el contrario, el resto de las categorías funcionales declinan siguiendo otras tendencias. La dieta tiene una gran influencia en la tasa metabólica de estos mamíferos y por ende en sus capacidades termorreguladoras. Los quirópteros con dietas basadas en proteínas (insectos) tendrán metabolismos más bajos que aquellos cuya dieta está compuesta por carbohidratos (frutas y nectar). Contrariamente a las selvas de baja altitud, donde dominan los insectívoros, en las selvas nubladas destacan los frugívoros como la categoría trófica más importante. Se postula que la explicación de tal diferencia en la «riqueza interna» de estos grupos funcionales, se encuentra en las distintas capacidades de respuesta de cada especie ante las exigencias termo-reguladoras del ambiente, las cuales se relacionan directamente con su régimen alimentario. Estos hechos nos conducen a pensar que la declinación de especies con la altitud es debida a la ineficiente termoregulación de las especies de origen tropical que conforman la mayoría de los insectívoros. Aparentemente, todos los insectívoros de origen neotropical tienen un «techo» en su distribución altitudinal que les impide acceder a las selvas nubladas andinas y los únicos que alcanzan estas selvas, pertenecen a la familia Vespertilionidae, de origen neártico, y algunos representantes de la Molossidae.

**Palabras clave:** Comunidades de murciélagos, Andes, Neotrópico, categorías funcionales, selvas nubladas andinas, selvas húmedas tropicales, Venezuela.

## INTRODUCTION

Bat communities represent approximately 50% of the mammal fauna associated with Neotropical forest ecosystems (Voss & Emmons 1996). Although there is now some reliable information concerning the exact composition of a few Neotropical communities, the number of localities with reasonably complete species lists is still extremely limited. The majority such sites are low elevation forest environments where preliminary inventories indicate between 35 and 65 species (Handley 1976, Ibáñez 1981, Mok *et al.* 1982, Webster and Jones 1984, Jones *et al.* 1988, Ochoa *et al.* 1988, 1992, 1993, Brosset and Charles-Dominique 1990, Ascorra *et al.* 1991, 1993, Medellín 1993, Pacheco *et al.* 1993, Voss and Emmons 1996). Inherent limitations in methodology mean that community lists are incomplete and biased. Therefore, only the fraction of species occupying the lower strata (easily sampled with mistnets) is well represented. Most species of the family Molossidae are missing, and only a few Emballonuridae and Vespertilionidae species are listed, which carry out their activity above the forest canopy (Handley 1967, Fleming 1972, Voss & Emmons 1996).

Recent inventories carried out in the Venezuelan Guiana (south of the Orinoco river) register up to 78 species coexisting, as shown by Ochoa (1995, 1997) in the Imataca Forest Reserve. Brosset *et al.* (1996) found 75 species in a rainforest of French Guiana. However, Voss and Emmons (1996) estimate that in the Amazon delta, exhaustive inventories made using different collection and detection methods could show values of between 90 and 110 sympatric species.

This great species richness, combined with the diverse diets of Neotropical Chiroptera, make this taxon an ideal study model for use in searching for general rules which explain diversity in the tropics. Neotropical bats, like birds, have a wide range of feeding habits which permit use of the functional group or "guild" concept, defined as "a group of species which exploit the same resource in a similar way" (Terborgh and Robinson 1986).

When trying to characterize a given community, very little ecological information may be inferred from a list of names, since the functional role of each species is the factor determining its presence in the list. When the functional role of each species is taken into account, the focus of analysis becomes more ecological since the

composition of a given community is a reflection of the equilibrium between the intra- and interspecific relationships with the rest of the living and physical environment. Thus, the species list will be a result of environmental resource availability and the way resources are shared between the components, i.e. the number of realized niches (*sensu* Hutchinson 1959) in the environment. Using these ideas, several authors have contributed significantly to the theoretical framework in the study of Neotropical bat communities, defining the basic functional groups and providing empirical data (Tamsitt 1967, McNab 1971, Fleming *et al.* 1972, Wilson 1973, Findley 1976, LaVal and Fitch 1977, Bonaccorso 1979, and Fleming 1986).

In an attempt to find general rules that determine the organization of Neotropical bat communities, Fleming (1986) carried out an analysis of the taxonomic and functional composition of the bat fauna registered in various lowland Venezuelan localities, using Handley's (1976) data. In this study, he only considered the Phyllostomidae family, due to the fact this family encompassed nearly the whole spectrum of functional categories (trophic habits) found in bats and possesses almost half the species recorded in the Neotropics.

Nevertheless, the exclusion of the rest of Neotropical bat families in an analysis aiming to clarify the factors determining community organization, creates a large initial bias, which alters possible conclusions. For example, one attribute shared by almost all the species of Phyllostominae is that they are no longer considered strict insectivores (Gardner 1977). It may be said that the reason for their great evolutionary success is mainly due to great ecological differentiation, into guilds distinct from those of the insectivores, and this allowing the large adaptive spread characteristic of this family (Smith 1976). Therefore, the insectivore category is not truly represented in this taxon, although many members of the subfamily Phyllostominae do eat primarily insects. Secondly, the exclusion of the other families reduces Neotropical bat species richness by almost 50% (Wilson and Reeder 1993); with the exception of one species from Noctilionidae, all the species excluded by Fleming are strict insectivores.

One phenomenon widely referred to in the literature is the decline in the species number from different fauna groups associated with an altitudinal gradient (Terborgh 1971, 1977, Karr 1971, Heaney *et al.* 1989, Graham 1990, Patterson *et al.* 1996,

Narváez and Soriano 1996, Shepherd and Kelt 1999. Terborgh (1977) showed that the reduction in richness of bird species along an altitudinal gradient in the Peruvian Andes is affected differentially according to the feeding habits of the species in question. The richness of insectivorous birds is reduced 5.2 fold between the extremes of the gradient, whereas the reduction in frugivores is only 2.3 fold. No change is present in the nectarivores. These data show that it is not only the trophic habit which is important in the study of community structure, but also the effect of environmental changes associated with altitude which are manifested in different ways according to the functional group being considered.

As with bird species, the decrease in number of bat species does not affect all functional categories equally (Graham 1983, 1990, Fleming 1986, Soriano *et al.* 1999). Adequate analysis of these facts and the establishment of causale relationships has been made difficult by the scarcity of complete community inventories, particularly obvious in the altitudinal belt generally between 2000 and 3000 m elevation, where humid plant formations, called cloud forests, are situated. For these high mountain forests the only available information comes from the Peruvian Andes (Tuttle 1970, Koopman 1978, 1982, Graham, 1983, Patterson *et al.* 1996).

In his study on the changes of bat diversity and species richness along the altitudinal gradient of the eastern slopes of Peruvian Andes, Graham (1983) found a significant reduction in species richness associated with a decrease in abundance (measured as individuals captured per effort unit). He concluded that the possible causal factors of this phenomenon might be the concomitant decrease in temperature, environmental complexity and resource abundance, which can act independently or in concert. This shows that whichever the causal factor might be, the members of the different functional categories respond to them independently. Therefore it is necessary to carry out a detailed study of these potential factors for each case, which will allow the postulation and testing of corresponding alternative hypotheses.

In the case of the cloud forests of the Venezuelan Andes, information has been limited to work of Davis (1966), Linares (1973), La Val (1973), Handley (1976), Soriano and Molinari (1984), and Soriano (1990), coming from preliminary inventories carried out in different localities not giving a complete list of species. Consequently, it

is difficult to establish pertinent comparisons with respect to lower elevation sites. The information I will present and discuss below, in the sections corresponding to montane communities, comes from a study on mammal communities in the Venezuelan Andes. This study was part of a general research program including the exhaustive revision of bibliography and collections throughout the country, and new collection of specimens from different localities and ecological units (Soriano *et al.* 1999), providing the most complete list of bats in Andean cloud forests of Venezuela. This approach has the benefit of taking advantage of many inventories to assess the potential richness in a single ecological zone. However, it may overestimate true alpha richness, as not all species found in a particular forest type are necessarily found at any one site.

In this paper, the existing information on functional analysis of Neotropical bat communities will be examined and small changes in the in the approaches used up until now will be proposed, in order to find general rules for interpreting the configuration of these communities. Firstly, basic characteristics of known functional categories in low elevation rainforests will be described. I have assumed that such communities are subjected to what we may call ideal conditions from the point of view of the most important environmental variables such temperature and humidity. In consequence, in these environments bats operate with minimal restrictive intensity, allowing maximal expression of the potential of other functions in the community. The benefits of using these categories when comparing communities subjected to similar environmental pressures will be shown, as will their sensitivity to the discrimination between bat assemblages associated with different ecological units in low elevation localities. Finally, this analysis will be applied to bat communities of the high Venezuelan and Peruvian Andean cloud forests, and I will discuss the possible causal relationships of the structural differences found contrasted to those of the lowland rainforests.

## FUNCTIONAL STRUCTURE

For the functional characterization of Neotropical bat communities, trophic habit and animal body size can be considered the most relevant parameters of the niche due to their significance in the ecological differentiation of the community (McNab 1971, Wilson 1973, Smith and

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**Table 1.** Distinctive features of the representatives of the Nomadic and Sedentary strategies in frugivore bats.

FEEDING STRATEGY	MAIN ECOLOGICAL FEATURES				TAXA
	HOME RANGE	DIURNAL SHELTER	MORFOECOLOGICAL FEATURES	PREFERENT STRATUM	
NOMADIC	Ambulatory (large)	Ambulatory (foliage)	Facial stripes (present)	High (canopy)	Stenodermatinae except <i>Sturnira</i>
SEDENTARY	Permanent (small)	Permanent (hollow trees, caves)	Facial stripes (absent)	Low (understory)	Carollinae, Phyllostominae, <i>Sturnira</i>

Genoways 1974). These parameters may also be used to interpret species richness, which characterizes low and medium altitude forest areas of the Neotropical region.

**The trophic role**

The principal feeding regime of each species allows us to establish independent categories such as insectivores, frugivores, nectarivores, carnivores, piscivores and hematophages (McNab 1971, Wilson 1973, Fleming *et al.* 1972, Howell and Burch 1974, Fleming and Heithaus 1981, Bonaccorso 1979, Humphrey *et al.* 1983, Soriano 1983, 1985). Also, variations in the way food is captured, differences in size, certain anatomical features, and the use of flying space among species found in the same category constitute additional dimensions of the niche, which allow higher resolution of ecological segregation (Handley 1967, Smith and Genoways 1974, Carranza *et al.* 1982, Humphrey *et al.* 1983, Soriano *et al.* 1983, 1985). Thus, in the best represented guilds (the fruit eaters and insect eaters), at least two general feeding strategies can be clearly differentiated:

Among the variety of insect eaters are the **aerial insectivores** which capture their prey while flying in contrast to the **foliage gleaners** which detect and capture prey found on the ground or on leaves. Aerial insectivores may preferentially fly in one particular stratum within the forest or even above the canopy. For example, Molossidae carry out their activity above the canopy and have a flying behavior similar to that of swallows (Fenton 1972, 1990, Norberg and Rayner 1987). These species show a

marked narrowing of their wings which makes them more efficient when capturing prey in open spaces (Norberg and Rainer 1987, Fenton 1990). On the other hand, it is common to find that foliage gleaners have lengthened earlobes permitting more efficient capture of the sounds made by their prey while perched lying in wait in the vegetation (Norberg and Rayner 1987, Fenton 1990). This strategy optimizes the energy budget by investing less energy in flight.

Among the frugivores, we can distinguish two categories adapted to consumption of fruit from plants with different phenology and spatial arrangement: **nomadic frugivores** are those species whose strategy consists of feeding on trees with massive, short-duration fruit production per individual tree, and individuals usually being spatially distant from each other. These characteristics mean that consumer populations (bats) must move to different regions of the forest as the resources are used up in one area and production begins in another (Soriano 1983). This strategy means that shelters must be often renewed. Morrison (1979) showed that *Artibeus jamaicensis* may travel up 10 km in one night between its roosting site and feeding area. In contrast, the strategy of **sedentary frugivores** consists of more-or-less fixed search itineraries each night and preferential consumption of fruit from plants with continual production throughout the year, but with few ripe fruits available per night.

Each strategy confers other additional attributes to a species (Table 1). In general, nomades have large and variable home ranges since their roosts, usually found in the foliage, change according

to their movements. The individuals of the sedentary species have relatively smaller activity areas which are more permanent and their roosts, such as hollow trees and caves, will also be more stable over time. The nomadic strategy is found only in the subfamily Stenoderminae with the exception of the genus *Sturnira*, while the sedentary strategy is found in the Carollinae and Phyllostominae subfamilies and the genus *Sturnira*. It is very significant that only the Stenoderminae with dorsal and/or facial white stripes are nomads. I hypothesize that these stripes constitute an adaptive characteristic, which allows them to “break” the search image of a diurnal predator (remembering that they find refuge hanging between leaves). It is obvious that this “disguise” would not have much adaptive value for animals with darker and less exposed refuges, as those of the sedentary species. The possession of dorsal and/or facial stripes is a morphoecological attribute which permits us to distinguish between the two strategies in frugivores.

According to feeding preferences, some bat species may appear in more than one functional category. For instance, one species whose overall diet includes 20% insects, 30% nectar and 50% fruits, is difficult to place in only one functional category. Thus, if we decide to place it as a frugivore (by the most important kind of food in their diet) we do not take into account at least a half of their alimentary spectrum. To solve this difficulty, Wilson (1973) proposed the trophic value ( $TV$ ) as a decimal fraction representing the importance of each species in a certain trophic category. In this way, this species can be “decomposed” in three fragments: one (with a value of 0.2) for the insectivore’s category, another of 0.3 for the nectarivores, and another of 0.5 for the frugivores. Likewise, for a species that is strictly insectivore, its  $TV$  will be 1.0 in this category and zero in all the others.

Smith and Genoways (1974) consider the importance value ( $IV$ ) of a certain trophic category to be the percentage obtained from the quotient between the total of trophic values in that category and the number of species in the community, as follows:

$$IV = \frac{(\sum_{i=1}^s TV_i)}{S} \cdot 100$$

Where  $TV_i$  represents the trophic value for species  $i$  in that category and  $S$  is the number of species in the community.

This transformation may be misleading since the values obtained for each trophic category are influenced by those from other categories. Therefore, it is only useful in making the trophic characterization and establishing the relationships of importance of these levels therein; it is not appropriate for making comparisons between different localities or between communities of a given category.

For such comparative purposes, it is better to use the sum of the trophic values ( $TV$ ), given the relative independence among the different functional categories. This sum is performed for each trophic category and it represents the total value of the contributions of all the species. I propose to call this total value trophic equivalent ( $TE$ ), expressed in species units, as follows:

$$TE = \sum_{i=1}^s TV_i$$

Therefore, the trophic value, being a fraction of the whole, may be interpreted as the fraction or portion of the species associated with the category in question. Thus the sum of the partial contributions of all species to a given category (for example, nectarivores), will represent the hypothetical number of species with  $TV = 1$  for that category. Within the concept of trophic equivalents underlies the idea that in each community there is a finite number of species with  $TV = 1$  linked to a specific functional role. Consequently, the trophic equivalents are a measure of those numbers, indicating the saturation limit of a certain trophic category in a particular community.

Classification by trophic category, trophic value, and trophic equivalent enables us to make a functional separation of the species that make up a community and to obtain a more ecological characterization of the community. In turn, comparisons between communities belonging to different biomes and even to distinct biogeographical regions are now possible, as are comparisons between zoological groups such as birds and bats.

### Animal size

The energy expended by a bat in foraging activities is directly proportional to its size (Kleiber 1972, McNab 1971b, 1982a, 1983, 1984). In the case of bats that must transport their food flying from the site where they found it to the place where they eat it, large bats include larger prey items or fruits in their diet than those consumed by smaller

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**Table 2.** Trophic Equivalents by functional category in Neotropical bat assemblages from: (a) lowland rain forests, selected from North, Central y South America localities, and (b) Andean cloud forests from Venezuela and Perú.

Localities by forest type	CAR	PIS	HEM	INS		FRU		NEC	No. spp.
				FOL	AER	NOM	SED		
<b>(a) lowland rain forests</b>									
Montes Azules. Chiapas. Mex. <sup>a</sup>	2.7	0.8	3	11.5	25.5	11.4	6.4	2.7	64
La Selva. Costa Rica. <sup>b</sup>	3.7	0.8	1	13.6	21.5	10.5	8.6	5.3	65
Barro Colorado. Panamá <sup>b</sup>	3.7	0.8	1	11.1	23.5	14.1	6.9	2.9	64
Sn Juan de Manapiare. Vzla. <sup>c</sup>	3.8	0.3	2	12.7	21.3	14.4	7.6	4.9	67
Imataca. Bolívar. Venezuela <sup>d</sup>	3.8	0.8	1	12.9	26.5	16.6	9.2	7.2	78
Manú. Perú. <sup>e</sup>	3.8	0.8	2	11.3	15.5	22.5	10.8	4.3	71
Loreto. Perú <sup>f</sup>	2	0.3	1	11.1	16.3	14.9	10.7	4.7	61
French Guiana <sup>g</sup>	4	0	1	16.2	23.0	15.2	10.1	5.5	75
AVERAGES	(3.4)	(0.6)	(1.5)	(12.6)	(21.6)	(15.0)	(8.8)	(4.7)	(68.1)
<b>(b) Andean cloud forests</b>									
Cordillera de Mérida. Vzla. <sup>h</sup>	0.0	0.0	1.0	5.8	8.0	7.5	7.5	2.2	32
Vilcabamba. Perú <sup>i</sup>	0.2	0.0	1.0	5.1	6.0	4.7	5.6	1.4	24
AVERAGES	(0.1)	(0.0)	(1.0)	(5.5)	(7.0)	(6.1)	(6.6)	(1.8)	(28.1)

Abreviatures: CAR = Carnívoros. PIS = Piscívoros. HEM = Hematófagos. INS = Insectívoros. Fol = Foliage gleaners. AER = Aerial insectívoros. FRU = Frugívoros. Nom = Nomádicos. SED = Sedentários. NEC = Nectarívoros. The original lists come from: <sup>a</sup> Medellín (1994). <sup>b</sup> Voss and Emonds (1996). <sup>c</sup> Handley (1976). <sup>d</sup> Ochoa (1995). <sup>e</sup> Pacheco *et al.* 1993. <sup>f</sup> Ascorra *et al.* (1993). <sup>g</sup> Brosset *et al.* (1996). <sup>h</sup> Soriano *et al.* 1999. <sup>i</sup> Graham (1983).

bats (Howell and Burch 1974). The conclusion of this reasoning is that within the same functional group, natural selection will favor the segregation of sizes as an adaptive response which allows better use to be made of the food resources in a certain environment (Howe and Smallwood 1982).

Works by Klopfer and Mac Arthur (1961) on birds, and Tamsitt (1967) on bats suggest that the same relationships exists in these groups as those found by Hutchinson (1959) for aquatic invertebrates. Thus, where size differences among species using the same type of resources show a relation between them of 1.26 in linear measures and that this relationship is  $2.0 = (1.26)^3$  when considering weight. Thus such differences seem to be sufficient to avoid competitive exclusion and allow species' coexistence. This could be the case for the genus *Artibeus*, where up to four species may be found coexisting in the relationship just mentioned (Tamsitt 1967). Nevertheless, I share the reasoning of McNab (1971) where two bat species may coexist using partially the same resources and partially different resources; in this way their size or weight relationship may be substantially lower. In other words, in order for Hutchinson's relationship

to be followed, a large overlap in the diet of the species involved must exist. For these reasons, I consider that size or weight relations alone are not sufficient for establishing ecological separation between species. However, it is possible to combine them with trophic categories and trophic values for construction of niche matrices as proposed by Smith and Genoways (1974).

**FUNCTIONAL ORGANIZATION OF BAT COMMUNITIES**

**Lowland rainforests**

In the Neotropics, lowland rainforests constitute the environment accommodating bat assemblages with the greatest number of sympatric species (Voss and Emmons 1996). These environments extend widely, occupying a large part of North, Central and South America, all sharing very similar environmental conditions. Nevertheless, the distances, which separate the distinct localities, combined with barriers caused by the presence of other less humid or dry environments, as well as topographic "accidents" such as mountain ranges, have caused an insular effect favoring allopatric

**Table 3.** Functional and taxonomic similarity matrixes between Neotropical bat communities from selected lowland rainforests, from North, Central and South America localities, and Andean cloud forests from Venezuela y Perú.

## FUNCTIONAL SIMILARITY

LOCALITIES	Imataca Venezuela	Manapiare Venezuela	French Guiana	La Selva Costa Rica	Barro Colorado, Panamá	Loreto Perú	Manú Perú	Chiapas México	Cordillera de Mérida Venezuela	Sierra de Vilcabamba Perú
Imataca. Venezuela.	1	0.92	0.92	0.90	0.90	0.86	0.84	0.87	0.58	0.47
Manapiare. Ven.	0.69	1	0.93	0.94	0.94	0.89	0.85	0.91	0.64	0.52
Frenc Guiana	0.73	0.63	1	0.92	0.90	0.88	0.84	0.84	0.60	0.49
La Selva. Costa Rica	0.60	0.54	0.51	1	0.91	0.86	0.82	0.88	0.66	0.54
Barro Colorado. Pan.	0.59	0.61	0.53	0.76	1	0.87	0.83	0.93	0.65	0.54
Loreto. Perú	0.63	0.62	0.53	0.48	0.54	1	0.91	0.82	0.69	0.56
Manú. Perú	0.66	0.60	0.56	0.53	0.58	0.68	1	0.78	0.62	0.50
Chiapas. México	0.44	0.58	0.43	0.62	0.51	0.43	0.45	1	0.64	0.54
Cord. Mérida. Ven.	0.16	0.22	0.15	0.14	0.15	0.13	0.15	0.17	1	0.85
Vilcabamba. Perú	0.14	0.17	0.12	0.09	0.09	0.21	0.23	0.14	0.53	1

## TAXONOMIC SIMILARITY

differentiation of species. At the same time, climatic changes, which occurred during the Pleistocene, caused the recurrent expansion and retreat of these environments (Haffer 1979), an additional factor which favored the increase of biological diversity. As an interpretation of the final result of this group of processes, two hypotheses arise:

**Hypothesis 1:** Geographically distant localities should show important differences in species composition, proportional to distance of separation and degree of isolation.

**Hypothesis 2:** Being subjected to similar environmental pressures, those communities should show great similarity in their functional structure.

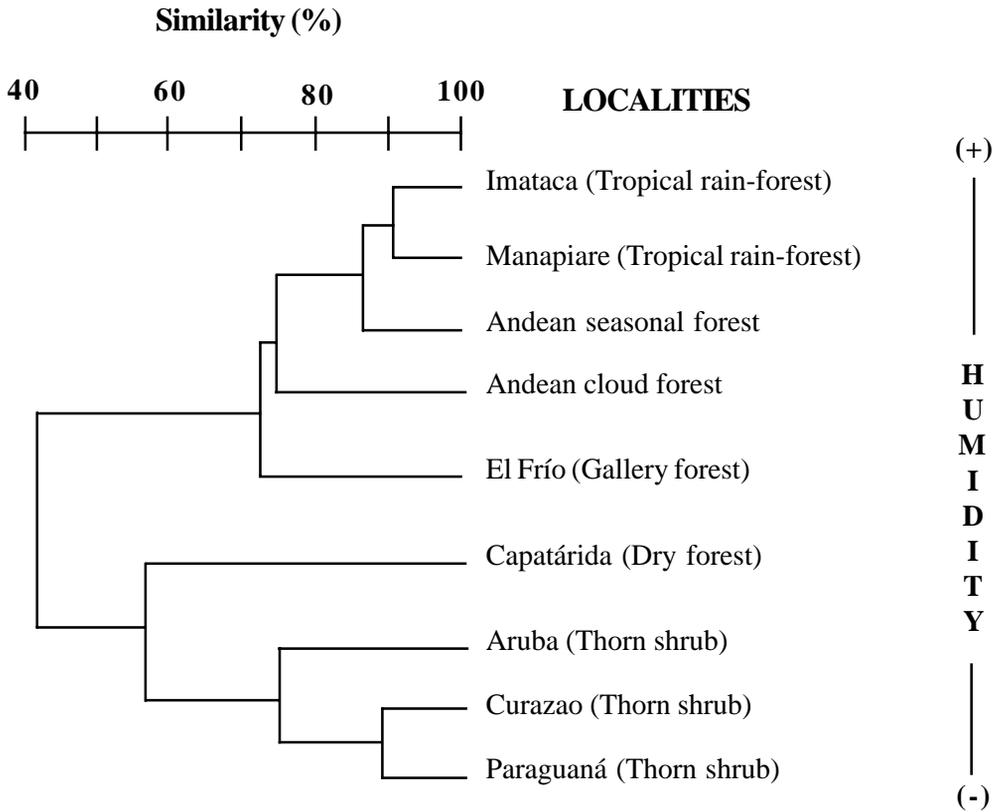
In order to test these hypotheses the following procedure was carried out: 1) The most complete species lists available were selected, offered by different authors for eight lowland rainforest locations in North, Central and South America, unifying the taxonomic nomenclature according to that used by Wilson and Reeder (1993). 2) The functional structure of each community was performed as follows: i) assigning a *TV* to each species according to values used by Wilson (1973) and the information of diet synthesized by Gardner (1977) (see Appendix 1; in Table 2a these data are summarized); ii) *TE* values were calculated for the different categories in each community. 3) Two similarity analyses were carried out, one functional and other taxonomic, using the Sørensen quantitative

similarity coefficient ( $C_N$ ) for the first and the Sørensen qualitative similarity coefficient ( $C_S$ ) for the second (Magurran 1988).

The values of the resulting matrix of taxonomic similarities (Table 3) show that: i) between the localities being considered there is little similarity in taxonomic composition; ii) the lowest similarity values are found between the most geographically separated localities, which are Chiapas (México) and Loreto (Perú) and French Guiana; iii) the highest similarity values are observed between the closest localities, such as: La Selva (Costa Rica) and Barro Colorado (Panamá), followed by Imataca (Venezuela and French Guiana); iv) the rest of localities show intermediate values, all supporting the prediction made by Hypothesis 1. On the contrary, the results of the functional similarity analysis (Table 3) show high values between all locations ( $C_N$  between 0.78 and 0.94). This suggests that the functional organization of these communities responds to similar environmental pressures, where the species which make up each category carry out equivalent ecological roles, independent of the relationships presented in the taxonomic lists.

**Other tropical environments**

In the previous example, we have seen how different communities subjected to similar environmental pressures (such as the lowland



**Figure 1.** Functional similarity dendrogram among bat communities from localities with different ecological units.

rainforest of tropical America) show similar functional structures. This give rise to the question: How do communities respond to different environmental pressures? Let us examine what happens when we compare localities situated in distinct zones or ecological units that are geographically close.

For this propose, I have used the most complete and reliable lists available for Venezuela and adjacent islands, corresponding to the following ecological units: lowland rainforest (Manapiare, Handley 1976 and Imataca, Ochoa 1995); dry forests (Capatárída, Handley 1976); thorn shrubs of Curazao and Bonaire (Husson 1960) and Venezuela (Paraguaná, Handley 1976); gallery forests of the Venezuelan llanos (Ibáñez 1981); seasonal and cloud forests of the Venezuelan Andes (Soriano *et al.* 1999). Using the information of the *TE* values from these localities (Appendix 1), I calculated a new similarity matrix using the Sørensen quantitative similarity coefficient ( $C_N$ ) and constructed a dendrogram with the values generated by the matrix (Figure 1). This dendrogram confirms the great structural similarity between communities associated to the same

ecological units, in contrast to those communities forming distinct units. For example, in arid zones (thorn shrubs) and dry forests there is grater similarity among localities than in comparison with sites in other zones; this also occurs among localities of humid forests. Thus, we find communities from localities situated in the same ecological unit grouped together, showing their similar functional structure.

**High montane forest communities.**

The first feature distinguishing bat communities from along an altitudinal gradient is the drastic reduction in the number of constituent species (Graham 1983, Fleming 1986, Patterson *et al.* 1996). In the Venezuelan Andes, such a reduction does not occurs in an equitable way among the different functional categories (Soriano *et al.* 1999). Thus, it is appreciated that the insectivore guild seems to be directly responsible for the general decline, showing a high correlation with the total number of bats. On the contrary, the rest of the functional categories show a tendency to decline more moderately. This phenomenon leads us to ask

how the environmental factors affect the insectivores, in other words, what causes the distinct insectivore response?

The cloud forests of the Cordillera de Mérida (Venezuela) and those of the Cordillera de Vilcabamba (Perú) share similar environmental characteristics, such as high cloudiness, precipitation levels and low temperatures, as well as some physiognomic characteristics of vegetation (Ataroff 2000, Graham 1983). Nevertheless, comparison of bat lists of such montane forests shows that they share just half their bat species (Appendix 1), showing a low taxonomic similarity value ( $C_s = 0.53$ , Table 3), probably due to the 2000 km separating these locations. This is consistent with one of the predictions made by Hypothesis 1. In contrast, they exhibit very similar functional structures ( $C_N = 0.85$ , Table 3), suggesting that environmental pressures are similar, as was predicted in Hypothesis 2

On the other hand, the bat assemblages of these forests show a very low taxonomic similarity when compared with those from geographically proximate lowlands where  $C_s$  values only reach a maximum of 0.24 (Table 3). The drastic reduction in taxonomic similarity values may be interpreted as the consequence of the joint action of two causes: i) an important decrease in the number of species occurring in the Andean communities and ii) the substitution of some species for others typical of highlands.

In addition, bat assemblages of both montane forests have low functional similarity when they are compared with those from lowland rainforests, with  $C_N$  values between 0.47 and 0.56 for the cloud forests of Venezuelan Andes and 0.47 and 0.54 for those from Perú (Table 3). Such a comparison allows us to see that although both montane assemblages show very similar values of  $TE$  (Table 2b), their averages are very different from those shown by lowland rainforests bat assemblages (Table 2b). The disappearance of the carnivore and piscivore guilds is highlighted, as is the 75% decrease in insectivores, while the hematophages and frugivores (both nomadic and sedentaries) and nectarivores are reduced to half their previous richness. Nevertheless, it can be noted that the decrease shown by nomadic frugivores largely compensates for experimented by sedentaries.

In order to be able to discuss the possible factors causing the differences in the functional similarity values, I will examine in detail those segments of the functional structure which suffer

greatest modification. For this propose, a two-dimensional niche matrix has been constructed for the cloud forest species of Cordillera de Mérida (Venezuela) using the same criteria as Smith and Genoways (1974) where the bat body size appears as an additional element (Table 4). In this niche matrix, the species are ordered according to the size category to which they belong, and their  $TV$  are expressed in each of the proposed functional categories following Wilson's (1973) criteria, complemented with information from Gardner (1977). The corresponding  $TE$  values for each functional category are obtained from the sum of the partial contributions of each species within each size category.

The configuration obtained in the niche matrix (Table 4) reveals that the Andean cloud forest bat assemblages from Venezuela show two relevant characteristics, distinguishing them from those of lowland rainforests:

i) *Trophic simplification*: The importance values ( $IV$ ) for each functional category show that the community is structured mainly on the base of frugivore and insectivore diets with a small contribution from nectarivores. The rest of the categories are either not represented or their contribution is very small, such as hematophages, whose presence in the cloud forests is associated with disturbed areas used for cattle farming.

ii) *Trophic segregation of body sizes*: The species with lowest body mass are largely insectivores, while the inverse relationship is true for the frugivores. The nomadic frugivore species are all large (in size) and the species in the sedentary frugivore guild that are small in size, in reality come from nectarivore guild but which occasionally eat fruits. The high species concentration in the medium size category (11-20 g) is noteworthy.

## POSSIBLE DETERMINANTS OF THE STRUCTURAL CHANGES.

The carnivore guild is conformed by very few species, which inhabit exclusively low or medium altitude rainforests, where the populational richness and/or density of the potential prey species (amphibians, lizards, birds, rodents and other bats) should be much higher than that found in any cloud forest environment. At least in birds, Terborgh (1971) has demonstrated this pattern. Therefore, insufficient resource abundance could be the factor determining the absence of representatives of this guild in high montane forests.

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**Table 4. Two dimension niche matrix for the bat species community from the Cordillera de Mérida Andean cloud forests.** Each cell shows the Trophic Values of species in the bat community, abbreviated as follow: *A. cen.* *Ametrida centurio*, *A. cau.* *Anoura caudifera*, *A. geo.* *Anoura geoffroyi*, *A. lat.* *Anoura latidens*, *A. lui.* *Anoura luismanteli*, *A. amp.* *Artibeus amplus*, *A. lit.* *Artibeus lituratus*, *Car. bre.* *Carollia brevicauda*, *D. gla.* *Dermanura glauca*, *D. rot.* *Desmodus rotundus*, *E. har.* *Enchisthenes hartii*, *E. bra.* *Eptesicus brasiliensis*, *E. fus.* *Eptesicus fuscus*, *E. mon.* *Eptesicus montosus*, *H. mon.* *Histiotus montanus*, *H. hum.* *Histiotus humboldti*, *L. cin.* *Lasiurus cinereus*, *L. bor.* *Lasiurus borealis*, *L. ega.* *Lasiurus ega*, *M. mic.* *Micronycteris microtis*, *M. oxy.* *Myotis oxyotus*, *P. umb.* *Platyrrhinus umbratus*, *P. vit.* *Platyrrhinus vittatus*, *S. tox.* *Sphaeronycteris toxophyllum*, *S. ara.* *Sturnira aratathomasi*, *S. bid.* *Sturnira bidens*, *S. bog.* *Sturnira bogotensis*, *S. ery.* *Sturnira erythromos*, *S. lil.* *Sturnira lilium*, *S. lud.* *Sturnira ludovici*, and *T. bra.* *Tadarida brasiliensis*. The values in parenthesis represent the sum of partial contributions of each species to the functional category cell.

FUNCTIONAL CATEGORIES	I.V. (%)	T.E. (spp.)	SIZE CATEGORIES (body mass in g)						
			0-5	6-10	11-20	21-40	41-80	>81	
Carnivores									
Piscivores									
Hematophagous	3.1	<b>1.0</b>				<i>D. rot.</i> 1.0 <b>(1.0)</b>			
Foliage gleaner Insectivores	18.1	<b>5.8</b>	<i>M. mic.</i> 0.8 <b>(0.8)</b>	<i>A. cau.</i> 0.5 <i>A. lat.</i> 0.5 <i>A. lui.</i> 0.5 <i>H. hum.</i> 1.0 <i>H. mon.</i> 1.0 <b>(3.5)</b>	<i>A. cul.</i> 0.5 <i>A. geo.</i> 0.5 <i>C. bre.</i> 0.2 <i>E. har.</i> 0.1 <i>D. gla.</i> 0.1 <b>(1.4)</b>		<i>A. lit.</i> 0.1 <b>(0.1)</b>		
Aerial Insectivores	25.0	<b>8.0</b>	<i>M. oxy.</i> 1.0 <b>(1.0)</b>	<i>L. bor.</i> 1.0 <i>E. bra.</i> 1.0 <i>E. mon.</i> 1.0 <b>(3.0)</b>	<i>L. ega.</i> 1.0 <i>L. cin.</i> 1.0 <i>E. fus.</i> 1.0 <i>T. bra.</i> 1.0 <b>(4.0)</b>				
Nomadic Frugivores	23.4	<b>7.5</b>			<i>E. har.</i> 0.9 <i>D. gla.</i> 0.8 <i>S. tox.</i> 1.0 <i>A. cen.</i> 1.0 <b>(3.7)</b>	<i>P. umb.</i> 1.0 <b>(1.0)</b>	<i>A. amp.</i> 1.0 <i>A. lit.</i> 0.8 <i>P. vit.</i> 1.0 <b>(2.8)</b>		
Sedentary Frugivores	23.4	<b>7.5</b>	<i>M. mic.</i> 0.2 <b>(0.2)</b>	<i>A. cau.</i> 0.1 <i>A. lat.</i> 0.1 <i>A. lui.</i> 0.1 <b>(0.3)</b>	<i>A. cul.</i> 0.1 <i>A. geo.</i> 0.1 <i>C. bre.</i> 0.8 <i>S. ery.</i> 1.0 <i>S. bid.</i> 1.0 <i>S. lil.</i> 1.0 <b>(4.0)</b>	<i>S. bog.</i> 1.0 <i>S. lud.</i> 1.0 <b>(2.0)</b>	<i>S. ara.</i> 1.0 <b>(1.0)</b>		
Nectarivores	6.9	<b>2.2</b>		<i>A. cau.</i> 0.4 <i>A. lat.</i> 0.4 <i>A. lui.</i> 0.4 <b>(1.2)</b>	<i>A. cul.</i> 0.4 <i>A. geo.</i> 0.4 <i>D. gla.</i> 0.1 <b>(0.9)</b>		<i>A. lit.</i> 0.1 <b>(0.1)</b>		
<b>TOTALS</b>	<b>99.9</b>	<b>32</b>	<b>2</b>	<b>8</b>	<b>14</b>	<b>4</b>	<b>4</b>		

Piscivory is an impossible feeding strategy in these forests due both physical and resource impediments. Fast water currents make it impossible for piscivorous bats to capture their prey (fish and aquatic insects), despite the fact that they may be available in sufficient quantities, since their fishing method is only suitable to calm waters. Additionally, of the two *Noctilio* species (the only piscivorous genus in tropical America) only *N. leporinus* really feeds on fish, since observations by Hooper and Brown (1968) and Howell and Burch (1974) suggest that insects constitute the fundamental items of *N. albiventris*'s diet. Low density and diversity of prey species may be limiting factors.

The presence of hematophages does not have a simple explanation, since an absence of vampires would be expected in high montane environments, based on two important considerations, the first being of physical nature; the second depends on the availability of a sufficient volume of blood to maintain the populations. McNab (1973) showed evidence that vampires are physiologically incapable of maintaining populations above 2000 m due to their diet, which is composed mainly of proteins and void of sugars. Therefore, their metabolic rates are too low to compensate for the heat losses caused by environmental conditions, meaning that they are unable to maintain a positive energy budget. In consequence, their presence at high elevations is the product of an artifact produced by anthropic activities; the rare captures of vampires above 2000 m are consistently associated with cattle ranches, which artificially increase the availability of blood for these bats. Given the flight capacity of *Desmodus rotundus*, which can cover distances of over 5 km from roost to prey (Lew 1987), it may be postulated that this species is not a genuine member of the cloud forests; but rather that it raids them from lesser altitude environments, such as seasonal forests in which colonies have been observed (P.J. Soriano pers. observ.).

Insectivores are the functional group most affected by altitude. To explain this phenomenon, I will examine two possible hypotheses: decrease of food resources and decrease in environmental temperature.

**i) Decrease in food resources.** Scarcity of food supplies is the most simplistic explanation. However, if this explanation were true, there would be an equal altitudinal reduction in number of bat species affecting all insect-eating taxa in a similar

way. In this case, the bat families distribution should be as that presented in Table 5 (expected values), obtained from the mean distribution in lowland rainforests. However, the real distribution observed in Andean cloud forests does not agree with that expected if the decrease were equal for all species ( $\chi^2$ , significant difference  $\alpha < 0.001$ ).

In any lowland Neotropical bat community, the insectivore guild may contain a relatively high number of sympatric species (between 31 and 42), explicable by the way in which available food resources are partitioned. At least three alternative non-exclusive ways may be distinguished whose adequate combination allows an integrated and efficient exploitation of such resources (Norberg and Rayner 1987): i) vertical stratification in the activity areas, ii) size variation of bat species within each stratum, so that each bat species preferentially consumes prey within certain size limits, and iii) variation of anatomical characteristics linked to mastication and toughness of the prey, so that in each stratum each size group may consume prey of different degrees of toughness. Although there is no work from lowland forests which illustrates this, in the semiarid inter-Andean enclave of Lagunillas (Mérida state, Venezuela) the vespertilionid bat *Rhogeessa minutilla*, whose body mass is no more than three g, selects very small size insects of soft texture, which is in agreement with its poorly-developed masticatory musculature (Sosa *et al.* 1996).

Although members of eight of the nine bat families found in the Neotropics show strictly or primarily insectivorous feeding habits, only two of them (Vespertilionidae and Molossidae) are represented in high mountain communities, in agreement with the fact that these families are also the only ones whose geographical distribution extends widely beyond the tropical limits in North and South America (Koopman, 1981, McNab 1982). The absence of families such as Emballonuridae, Mormoopidae, Thyropteridae, Furipteridae and Natalidae, whose distribution is restricted to the intertropical belt, makes the absence or low abundance of food resources (insects) an unsatisfactory explanation.

Although there is no doubt that in high montane environments there are less food sources than those in the lowlands (Terborgh 1971), it does not seem logical to suppose that this is the determining factor for the taxonomic bias observed, since the representatives of the rest of the families show the whole spectrum of adaptive possibilities already described. Considering these facts, we would also

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**Table 5.** Species number of insectivore bats from Andean cloud forests and its expected values according to its distribution by family in lowland forests.

Families of Chiroptera	Lowland rainforests										Andean cloud forests			
	Manapiare Vzla.	Imataga Vzla.	Frech Guiana	Manú Perú	Loreto Perú	BCI Panamá	La Selva Costa Rica	Chiapas México	Aver.No spp.	Distribution (%)	Mérida Vzla.	Vilcabamba Perú	Observed distribution (%)	expected distribution (%)
Emballonuridae	10	9	7	5	4	7	8	6	7,0	17,3	0	0	0	1,8
Noctilionidae	1	2	0	2	1	2	2	2	1,5	3,7	0	0	0	0,5
Mormoopidae	1	1	3	0	1	2	2	4	1,8	4,4	0	0	0	0,4
Phyllostomidae	19	18	24	15	14	16	19	15	17,5	43,2	1	2	1,5	4,5
Thyropteridae	0	1	2	1	1	2	1	1	1,1	2,7	0	0	0	0,3
Natalidae	0	0	0	0	0	1	0	1	0,3	0,7	0	0	0	0,1
Furipteridae	0	0	1	1	1	0	1	0	0,5	1,2	0	0	0	0,1
Vespertilionidae	5	6	4	6	5	5	7	9	5,9	14,6	9	8	8,5	1,5
Molossidae	6	9	6	2	4	6	2	4	4,9	12,1	1	0	0,5	1,3
TOTALS	42	46	47	32	31	41	42	42	40,5	99,9	11	10	10,5	10,5

Source of data: see Table 2. The Andean cloud forests show significant differences between observed and expected values of insectivores ( $\chi^2$  calculated = 38,4;  $\chi^2 = 20,5$ ; for  $\alpha = 0,001$ ).

expect the presence of species from some of the families of Neotropical origin and distribution. Alvarez and Alvarez (1994) and Narváez and Soriano (1996) found that the moths of the Sphingidae family in Mérida cloud forests show a 40% reduction in number of species and certain changes in the distribution of body sizes, compared with those from lowland regions. Considering that a similar phenomenon is observed in other insect groups, it does not appear probable that only the prey types consumed by representatives of absent families disappear.

**ii) Decrease of temperature.** Altitude is not the direct factor leading to those changes in functional structure of the montane bat assemblages; nevertheless temperature decrease with altitude is shown to be the most important environmental factor in the majority of altitudinal changes in plants and animals. In the Andes, the thermic altitudinal gradient is 0.6 °C per 100 m (Sarmiento 1986); it could thus act as the restrictive environmental factor for some species, including phylogenetically related groups. It has been pointed out that the variations in metabolism observed in bats are mainly related to body mass and trophic habit (McNab 1969, 1970, 1982, 1983, 1984, 1986). Thus, bats with insectivorous or hematophagous diets have low metabolic rates, bats with combined diets (frugivore-carnivore) have low to intermediate metabolic rates, frugivores have high metabolic rates, and those for nectarivores are very high. The

capacity to regulate body temperature is associated with base metabolic rates. Therefore, within the same feeding habit, large bats regulate their temperature better than small ones. Similarly, for bats of a given body mass, the insectivores maintain lower body temperatures and are more dependent on environmental temperature variations than frugivores.

The Andean cloud forests reach altitudes between 2000 and 3000 m, and show a reduction in mean ambient temperature, which ranges between 7 and 10 °C higher than lowland rainforests. Therefore, the low temperatures of montane environments may impose important physiological restrictions on the possession of an adequate energetic balance. Members of the Emballonuridae, Mormoopidae, Thyropteridae, Furipteridae and Natalidae families are never or rarely found above 1000 m. It was shown that the Mormoopidae (*Pteronotus davyi*, *P. parnelli*, *P. personatus* and *Mormoops megalophylla*), exhibit: low metabolic rates, which are slightly lower than those expected for their body mass; high values of thermal conductance; no resistance to temperatures below 15 °C; and no capacity to enter into torpor (Bonaccorso *et al.* 1992). Similar results were found in the Natalidae—*Natalus tumidirostris* (Genoud *et al.* 1990); however, in the Emballonuridae, *Peropteryx macrotis* was shown to be more tolerant of cooler conditions, which explains its presence in environments with mesic

temperatures.

These data lead to the postulation that bats of tropical origin have a low degree of adaptation to environments with low mean temperatures. Therefore, they would require metabolic rates beyond their physiological limits; thus all these bat species have strictly insectivorous habits and reduced size. Another argument which supports this interpretation is the fact that many of the Vespertilionidae from cloud forests, such as *Myotis oxyotus*, *Histiotus montanus*, *Eptesicus fuscus* and *E. montosus*, are associated with the Andean region of the intertropical belt; and some of them have wide distributions over both hemispheres of the continent (Koopman 1982).

In the case of aerial insectivores, despite the fact that in lowland localities they show relatively large internal variation, their differences are less than those found in cloud forests (Table 2). This could be due to the fact that the members of this guild are mainly strict insectivores, which means that they are physiologically restricted from environments where thermal regulation requires higher metabolic rates than those permitted by their energy budget. In contrast, the majority of species associated with the foliage gleaner guild could complement their diet with fruit, as it is the case of many Phyllostomatidae (Gardner 1977), increasing their basal metabolism rate as a consequence of their higher phenotypic plasticity, and overcoming the physiological restriction of the previous group. This could be the reason for the few differences observed for this group between montane cloud forests and lowland forests.

When considering frugivory, the dependence of tropical evergreen forests, including cloud forests, on vertebrates as seed dispersers are well known, especially the participation of certain group of flying vertebrates (birds and bats). In this case, it is noteworthy that a reduction to half the mean number of frugivores found in cloud forests (Table 2) is almost wholly due to the nomadic frugivore guild. In addition, there is almost a total absence of species in the small size category, represented by the genera *Platyrrhinus*, *Artibeus* (*Dermanura*), *Ectophylla*, *Uroderma*, *Vampyressa* and *Chiroderma*. On the contrary, the number of representatives of sedentary frugivores does not change substantially, but there is an almost total replacement of lowland species by those exclusive to these environments. The high diversification of the *Sturnira* genus is remarkable, represented by some species exclusively associated with these

environments and showing up to five sympatric species (Soriano *et al.* 1999).

The drastic reduction of representatives with small size in the most important guilds seems to be an indicator that the determining factor is the physiological limitation which these animals must face in order to colonize cold environments. Similarly, the altitudinal substitution suggests that species of the highlands must possess certain adaptive features to these environments, which at the same time make their presence incompatible with the prevalent conditions in the low levels of the altitudinal gradient, resulting in the existence of species characteristic of high regions and *viceversa*. It is probable that in this case the determining factor is of a physiological nature and linked to thermoregulatory capacity, since the types of food consumed in one or other of the environments are basically the same and the other conditions of the physical environment are also similar.

Based on the physiological considerations mentioned above, one would expect the nectar-polinivores to have the greatest advantage in such environmental conditions. The nectarivores potentially have the lower physiological restrictions; however, in this case it is the plants, which seem to encounter limitations. Stiles (1978) showed that the lowest temperatures at higher elevations limit nectar production, and he presented the example of *Inga vera*, which at low elevations shows peak nectar production at the beginning of the night. However, as the altitude increases, the optimal temperature for the secretion of nectar is observed earlier, and above 1000 m nectar production occurs mid-afternoon making it inaccessible to bats, but not to hummingbirds. However, the reduction in this guild is not so large as the preceding ones, and the presence of several species of the genus *Anoura* is noteworthy, seeming similar to the case of the *Sturnira* genus described above.

The indicators which lead us to presume that low temperatures constitute the determinant factor for the structural features of the bat assemblages of montane cloud forests may be summarized as follows: i) reduction in the number of small sized species (Table 4), ii) altitudinal substitution in the frugivore species, iii) absence of insectivorous families whose distribution is restricted to the Neotropical region, iv) presence of Vespertilionidae and Molossidae species with wide geographical distribution of which the majority extend beyond the tropical limits and in many cases their tropical distribution is

restricted to mountainous regions. Such is the case of *Lasiurus cinereus*, *L. blossevillii*, *Histiotus* spp., *Eptesicus fuscus*, *Myotis oxyotus*, *M. keaysi* and *Tadarida brasiliensis*, which implies the possession of adaptations to cold environmental conditions.

For the hypothesis of physiological responses to be true, the representatives of each guild should show certain differential metabolic features, which should affect their thermoregulatory capacity and should allow them to adapt their physiologies to the low temperatures. Among these modifications, one expects the metabolic activity of the inhabitants of cloud forests to be characterized by one or several of the following distinctive features: i) a displacement of the thermoneutral zone towards lower temperature values; and concomitant increase in their insulation would be expected, which translates into a decrease in thermal conductance values; or if not ii) an increase of the basal metabolic rate and thermal conductance, maintaining the same thermoneutral zone; iii) an intermediate response, which involves an increase of the basal metabolic rate, displacement of the thermoneutral zone toward lower temperature values, leaving terminal conductance constant. An other alternative that could contribute to maintaining the energetic balance is the circadian loss of endothermy, which means that during the resting hours the animals would not invest energy in thermoregulation, letting their body temperature fluctuate according to that of the environment (daily torpor). According to the species, torpor could be facultative or obligate.

The absence of studies on the metabolic characterization of montane species in the Neotropics, as well as small sized species of lowland rainforests, means that these hypotheses cannot be tested yet. However, it opens an interesting field for future investigations in this direction. This essay has aimed to show that the key to understanding the changes in functional structure of high montane forest bat communities lies in the metabolic behavior of its species, which have been able to overcome the resistance imposed by the temperature as a restrictive force of the first order.

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**Appendix 1.** Bat species that integrate all lists used in the analysis. Numbers in columns represent the trophic values of each species by guild: C = carnivores, P = piscivores, S = sanguivores, Fg = foliage gleaners, Ai = aerial insectivores, Nf = nomadic frugivores, Sf = sedentary frugivores, and N = nectarivores. Localities represented by number are: 1 = Montes Azules, Chiapas (tropical rainforest), México; 2 = La Selva (tropical rainforest), Costa Rica; 3 = Barro Colorado Island (tropical deciduous forest), Panamá; 4 = Sn Juan de Manapiare (tropical rainforest), Venezuela; 5 = Imataca Forestry Reserve (tropical rainforest), Venezuela; 6 = Manú (tropical rainforest), Perú; 7 = Loreto (tropical rainforest), Perú; 8 = French Guiana (tropical rainforest); 9 = Cordillera de Mérida (cloud forests), Venezuela; 10 = Cordillera de Vilcabamba (cloud forests), Perú; 11 = Cordillera de Mérida (seasonal forests), Venezuela; 12 = Curazao (thorn shrub); 13 = Aruba (thorn shrub); 14 = El Frío (gallery forests), Venezuela; 15 = Capatárida (dry forest), Venezuela; 16 = Paraguaná (thorn shrub), Venezuela.

Species by family	Guilds								Localities																
	C	P	S	Fg	Ai	Nf	Sf	N	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
<b>Emballonuridae</b>																									
<i>Balantiopteryx io</i>					1				X																
<i>B. plicata</i>					1				X																
<i>Centronycteris maximiliani</i>					1					X	X														
<i>Cormura brevirostris</i>					1					X	X	X	X	X		X									
<i>Cyttarops alecto</i>					1					X						X									
<i>Diclidurus albus</i>					1					X	X	X	X												
<i>D. ingens</i>					1							X													
<i>D. isabellus</i>					1							X													
<i>D. scutatus</i>					1							X	X			X									
<i>Peropteryx kappleri</i>					1				X	X			X	X	X				X						
<i>P. macrotis</i>					1				X			X	X			X					X	X			
<i>Peropteryx</i> sp.					1						X														
<i>Rhynchonycteris naso</i>					1				X	X	X	X	X	X	X	X							X		
<i>Saccopteryx bilineata</i>					1				X	X	X	X	X	X	X	X							X		
<i>S. canescens</i>					1						X	X											X		
<i>S. leptura</i>					1					X	X	X	X	X	X	X							X		
<b>Noctilionidae</b>																									
<i>Noctilio albiventris</i>		0.3	0.4	0.3					X	X	X	X	X	X	X									X	
<i>N. leporinus</i>		0.5	0.3	0.2					X	X	X		X	X					X				X		
<b>Mormoopidae</b>																									
<i>Mormoops megalophylla</i>					1				X										X	X	X			X	
<i>Pteronotus davyi</i>					1				X	X					X									X	
<i>P. gymnotus</i>					1				X		X					X									
<i>P. personatus</i>					1											X									
<i>Pteronotus parnelli</i>					1				X	X	X	X	X			X			X					X	
<b>Phyllostomidae</b>																									
<i>Chrotopterus auritus</i>	0.8		0.1			0.1			X	X	X	X	X	X		X			X				X		
<i>Lonchorhina aurita</i>			1						X				X										X		
<i>Lonchorhina inusitata</i>			1													X									

TROPICAL RAINFOREST AND ANDEAN CLOUD FOREST BAT COMMUNITIES

Appendix 1. Continued

Species by family	Guilds					Localities																			
	C	P	S	Fg	Ai	Nf	Sf	N	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
<i>Macrotus waterhousii</i>				0.9			0.1		X																
<i>Macrophyllum macrophyllum</i> 1									X	X	X	X	X	X		X									
<i>Micronycteris brachyotis</i>				0.8			0.2		X	X	X														
<i>M. daviesi</i>				0.8			0.2		X				X												
<i>M. hirsuta</i>				0.8			0.2		X	X	X			X						X					
<i>M. megalotis</i>				0.8			0.2		X			X	X	X	X	X		X	X				X	X	
<i>M. microtis</i>				0.8			0.2		X	X			X				X	X							
<i>M. minuta</i>				0.8			0.2		X		X	X	X			X			X				X		
<i>M. nicefori</i>				0.8			0.2		X	X	X	X			X	X									
<i>M. schmidtorum</i>				0.8			0.2		X	X	X	X		X	X									X	
<i>M. sylvestris</i>				0.8			0.2		X			X					X								
<i>Mimon benetti</i>				0.8		0.2			X	X															
<i>M. crenulatum</i>				0.8		0.2			X	X	X	X	X	X	X	X									
<i>Phylloderma stenops</i>	0.2			0.4			0.4		X	X	X	X	X	X	X	X		X							
<i>Phyllostomus discolor</i>				0.4			0.3	0.3	X	X	X	X	X			X	X			X			X	X	
<i>P. elongatus</i>	0.1			0.4			0.3	0.2				X	X	X	X	X							X		
<i>P. hastatus</i>	0.2			0.3			0.3	0.2		X	X	X	X	X	X	X				X			X		
<i>P. latifolius</i>				0.4			0.3	0.2										X							
<i>Tonatia bidens</i>				0.8			0.2									X	X								
<i>T. brasiliensis</i>				0.8			0.2		X	X	X	X	X	X	X	X				X			X		
<i>T. carrikeri</i>				0.8			0.2					X				X									
<i>T. evotis</i>				0.8			0.2		X																
<i>T. saurophila</i>				0.8			0.2		X	X	X	X	X	X						X					
<i>T. schultzi</i>				0.8			0.2										X								
<i>T. silvicola</i>				0.8			0.2			X	X	X	X	X	X	X									
<i>Trachops cirrhosus</i>	0.7			0.2			0.1		X	X	X	X	X	X	X	X							X		
<i>Vampyrum spectrum</i>	0.8			0.1			0.1			X	X	X	X	X	X	X									
<i>Anoura caudifera</i>				0.5			0.1	0.4						X	X	X	X	X							
<i>A. cultrata</i>				0.1			0.4	0.5									X	X	X						
<i>A. geoffroyi</i>				0.1			0.4	0.5				X	X			X	X	X	X						
<i>A. latidens</i>				0.1			0.4	0.5					X			X		X							
<i>A. luismanueli</i>				0.1			0.4	0.5								X		X							
<i>Choeroniscus intermedius</i>				0.1			0.1	0.8							X	X									
<i>C. godmani</i>				0.1			0.1	0.8		X			X										X		
<i>C. minor</i>				0.1			0.1	0.8					X	X											
<i>Glossophaga commissarisi</i>				0.2			0.3	0.5	X	X	X			X											
<i>G. longirostris</i>				0.1			0.5	0.4				X								X	X	X	X	X	X
<i>G. soricina</i>				0.2			0.2	0.6	X	X	X	X	X	X	X	X				X			X		
<i>Hylonycteris underwoodi</i>				0.1			0.1	0.8	X	X															
<i>Leptonycteris curasoae</i>				0.1			0.5	0.4													X		X	X	
<i>Lichonycteris obscura</i>							0.1	0.9		X			X												
<i>Lionycteris spurelli</i>				0.1			0.1	0.8				X	X				X								
<i>Lonchophylla mordax</i>				0.1			0.1	0.8								X									
<i>L. robusta</i>				0.1			0.1	0.8		X	X									X					
<i>L. thomasi</i>				0.1			0.1	0.8				X	X	X	X	X									
<i>Carollia breviceauda</i>				0.2			0.8		X	X	X	X	X	X	X	X	X	X	X	X					
<i>C. castanea</i>				0.2			0.8			X	X			X	X										
<i>C. perspicillata</i>				0.2			0.8		X	X	X	X	X	X	X	X				X			X		
<i>Rhinophylla fischeriae</i>				0.1			0.9									X									
<i>R. pumilio</i>				0.1			0.9						X	X	X	X									
<i>Ametrida centurio</i>							1				X	X	X			X	X								
<i>Artibeus amplus</i>				0.1			0.8	0.1									X			X					
<i>A. anderseni</i>				0.1			0.8	0.1						X	X										
<i>A. aztecus</i>				0.1			0.8	0.1	X																
<i>A. cinereus</i>				0.1			0.8	0.1					X	X						X					

## SORIANO

## Appendix 1. Continued

Species by family	Guilds								Localities																
	C	P	S	Fg	Ai	Nf	Sf	N	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
<i>A. concolor</i>				0.1		0.8		0.1						X		X	X								
<i>A. glaucus</i>				0.1		0.8		0.1						X	X	X				X					
<i>A. gnomus</i>				0.1		0.8		0.1						X	X		X								
<i>A. jamaicensis</i>				0.1		0.8		0.1	X	X	X	X	X	X	X	X	X	X	X	X	X			X	
<i>A. lituratus</i>				0.1		0.8		0.1	X	X	X	X	X	X	X	X	X	X	X	X					
<i>A. obscurus</i>				0.1		0.8		0.1				X	X	X	X	X									
<i>A. phaeotis</i>				0.1		0.8		0.1	X	X	X							X		X					
<i>A. planirostris</i>				0.1		0.8		0.1						X											
<i>A. watsoni</i>				0.1		0.8		0.1	X	X	X														
<i>Centurio senex</i>								1		X	X														
<i>Chiroderma salvini</i>								1		X				X						X					
<i>C. trinitatum</i>								1				X	X	X	X	X				X					
<i>C. villosum</i>								1	X	X	X	X	X	X	X	X				X					
<i>Ectophylla alba</i>				0.1		0.9				X															
<i>Enchisthenes hartii</i>				0.1		0.9					X	X		X	X		X	X	X						
<i>Mesophylla macconnelli</i>				0.1		0.8		0.1			X	X	X	X		X									
<i>Platyrrhinus brachycephalus</i>								1					X	X	X									X	
<i>P. dorsalis</i>								1						X						X					
<i>P. helleri</i>								1	X	X	X	X	X	X	X	X				X					
<i>P. infuscus</i>								1						X											
<i>P. lineatus</i>								1						X						X					
<i>P. umbratus</i>								1									X		X						
<i>P. vittatus</i>								1									X	X	X						
<i>Sphaeronycteris toxophyllum</i>								1				X		X			X	X	X					X	
<i>Sturmira aratathomasi</i>								1									X			X					
<i>S. bidens</i>								1									X	X							
<i>S. bogotensis</i>								1									X	X							
<i>S. erythromos</i>								1									X	X	X						
<i>S. lilium</i>								1	X	X		X	X	X	X	X	X	X	X				X		
<i>S. ludovici</i>								1	X	X							X		X						
<i>S. luisi</i>								1			X														
<i>S. magna</i>								1						X	X				X						
<i>S. oporaphilum</i>								1						X											
<i>S. tildae</i>								1						X	X	X	X			X					
<i>Uroderma bilobatum</i>								1	X	X	X	X	X	X	X	X				X					
<i>U. magnirostrum</i>								1			X	X	X	X	X								X		
<i>Vampyressa bidens</i>								1				X	X	X		X									
<i>V. brocki</i>								1							X	X									
<i>V. macconnelli</i>								1							X										
<i>V. melissa</i>								1									X								
<i>V. nymphaea</i>								1			X	X		X											
<i>V. pusilla</i>								1	X	X	X	X	X	X	X	X				X					
<i>Vampyrodes caraccioli</i>								1		X	X	X	X	X		X									
<i>Vampyrodes major</i>								1		X															
<i>Desmodus rotundus</i>				1					X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	
<i>Diaemus youngi</i>				1					X			X												X	
<i>Diphylla ecaudata</i>				1					X					X						X					
<b>Natalidae</b>																									
<i>Natalus stramineus</i>								1	X		X														
<i>N. tumidirostris</i>								1												X					X
<b>Furipteridae</b>																									
<i>Furipterus horrens</i>								1		X				X	X	X									
<b>Thyropteridae</b>																									
<i>Thyroptera discifera</i>								1			X				X	X									
<i>T. tricolor</i>								1	X	X	X		X	X		X									

TROPICAL RAINFOREST AND ANDEAN CLOUD FOREST BAT COMMUNITIES

Appendix 1. Continued

Species by family	Guilds								Localities																		
	C	P	S	Fg	Ai	Nf	Sf	N	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16			
<b>Vespertilionidae</b>																											
<i>Bauerus dubiaquercus</i>					1					X																	
<i>Eptesicus andinus</i>					1						X		X						X								
<i>E. brasiliensis</i>					1							X	X		X		X	X	X								
<i>E. diminutus</i>					1																		X				
<i>E. furinalis</i>					1					X	X	X	X	X		X											
<i>E. fuscus</i>					1												X										
<i>E. montosus</i>					1												X										
<i>Histiotus humboldti</i>					1												X										
<i>H. macrotus</i>					1													X									
<i>H. montanus</i>					1												X	X									
<i>Lasiurus atratus</i>					1								X														
<i>L. blossevillii</i>					1					X		X					X	X									
<i>L. castaneus</i>					1											X											
<i>L. cinereus</i>					1												X	X	X						X		
<i>L. ega</i>					1					X		X		X			X	X									
<i>Lasiurus</i> sp.					1						X																
<i>Pipistrellus subflavus</i>					1					X																	
<i>Myotis albescens</i>					1					X	X	X	X		X	X							X				
<i>M. elegans</i>					1					X	X																
<i>M. fortidens</i>					1					X																	
<i>M. keaysi</i>					1					X				X				X	X								
<i>M. nigricans</i>					1					X	X		X	X	X	X		X	X	X			X				
<i>M. oxyotus</i>					1												X	X	X								
<i>M. riparius</i>					1					X			X	X	X	X			X								
<i>M. simus</i>					1									X	X												
<i>Rhogeessa tumida</i>					1					X	X												X				
<i>R. minutilla</i>					1																			X			
<b>Molossidae</b>																											
<i>Cynomops abrasus</i>					1								X														
<i>C. greenhalli</i>					1								X														
<i>C. parvus</i>					1								X														
<i>Eumops auripendulus</i>					1						X		X														
<i>E. bonariensis</i>					1																		X				
<i>E. dabbenei</i>					1																		X				
<i>E. glaucinus</i>					1							X											X				
<i>E. hansae</i>					1					X		X	X			X											
<i>Molossops greenhalli</i>					1					X							X										
<i>M. neglectus</i>					1								X		X												
<i>M. planirostris</i>					1							X				X							X				
<i>M. temminckii</i>					1																		X				
<i>Molossus ater</i>					1					X		X	X		X	X											
<i>M. bondae</i>					1						X	X															
<i>M. coibensis</i>					1						X																
<i>M. molossus</i>					1					X		X	X	X	X	X	X		X	X		X	X	X	X	X	
<i>M. pretiosus</i>					1																		X				
<i>M. sinaloae</i>					1						X	X															
<i>Nyctinomops laticaudatus</i>					1							X		X	X		X										
<i>N. macrotis</i>					1																		X				
<i>Promops centralis</i>					1										X							X					
<i>P. nasutus</i>					1							X															
<i>Tadarida brasiliensis</i>					1												X		X								
Total number of species by locality									64	65	64	67	78	71	61	75	32	24	53	8	4	34	10	7			