

# AVIAN DISTRIBUTION IN THE HIGHLANDS OF CENTRAL AMERICA

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## Introduction

One of the main goals of historical biogeography is to detect causal relationships between changes in the earth history and distribution patterns of living biotas. Central America has received a considerable attention by biogeographers. Several authors have analyzed the distribution of particular taxa in Central America, especially fishes (Miller, 1966; Bussing, 1976), and reptiles (Savage, 1982). In this aspect birds have received considerably less attention (but see Howell, 1969). Nevertheless Central America is included in the analysis of avian taxa widely distributed in the neotropics (Cracraft and Prum, 1988; Haffer, 1985). Biogeographical studies of the Central American highlands have been limited to particular taxa, like plethodontid salamanders (Wake, 1987). For taxa with reduce abilities to disperse either over water or over unsuitable habitat, vicariant events seems the most plausible explanation for patterns of speciation and radiation. Wake (1987) suggests that plethodontid salamanders have coevolved with particular habitats in Central America for a very long time, possibly through the Tertiary (Wake, 1987). Haffer (1985) and Cracraft (1985) have proposed a similar explanation for selected taxa of the neotropical avifauna. The major differences between Haffer and Cracraft models is in the time scale and the relative importance of several vicariant events for processes of speciation and radiation. Haffer invokes

climatic fluctuations during the Pleistocene, and subsequent fragmentation and contraction of habitats (forest refugia) as the major cause of the high degree of diversification in the neotropical avifauna (Haffer, 1985). Cracraft (1985) has analyzed areas of endemism in South American lowland birds, and suggests that some of the refugia proposed by Haffer are considerably older, with hierarchical patterns of endemism established prior to that epoch. He invokes that the physiographic evolution of South America was probably as crucial in the formation of avian taxa as were habitat changes caused by climatic changes in the Pleistocene.

In this paper I present a preliminary analysis of the endemic avifauna of Central America restricted to land masses above 1000 m. I hope that this analysis can provide some insights on the processes that have shaped actual distributions. I set my framework using geological and paleoecological information to explain actual distributions. Finally I suggest new approaches to test the validity of a vicariant explanation for the distribution of the montane avifauna of Central America. I assume that vicariant events are responsible for present distributions as a framework to answer three basic questions:

1.- Is there a common pattern in the distribution of endemic avian taxa through all the Central American highlands? For example, are there several taxa with a concordant presence/absence pattern of endemic representatives?

2.- Is there a correlation between geological stability and degree of endemism? If there is any relation I predict a higher number of endemics in geologically more stable areas, other things being equal.

3.- Can we explain the actual diversification of all avian taxa in the highlands of Central America as a result of Pleistocene climatic cycles exclusively? For this comparison I assume similar rates of evolution in different taxa along the entire region. If the diversification of all taxa happened during the Pleistocene, I predict similar degrees of endemism along the entire region.

#### **The study area**

The vegetation in the highlands of Central America is dominated by a mixture of cloud forest and pine-oak forest. Extensive pine forest still cover vast areas of Guatemala and Honduras reaching the southern limit of its range in the highlands of Nicaragua. In the highest parts of Cordillera de Talamanca the paramo is the dominant formation. Much of the original forest has been transformed into pasture and agricultural land, but none of the endemic species has become extinct (with the exception of the Atitlan Grebe Podilymbus gigas, of Guatemala, not included in this analysis). Hartshorn (1988) presents an overview of the major vegetation formations, and Weyl (1980) summarizes the geology of the region.

The effect on climatic oscillations on the vegetation has been documented in several localities and appears to be a generalized

phenomenon (Toledo, 1982; Markgraf, 1989). Current evidence shows that between 35,000 and 12,000 years B.P., climates throughout Central and South America were cooler than today by 4<sup>0</sup> to 5<sup>0</sup> C (Markgraf, 1989, Bratlett and Barghoorn, 1973). Sea level was as much as 120 m below current sea level at about 17,000 years B. P. during the maximum extension of the glaciers. Fossil pollen in Panama and Guatemala suggest that montane trees grew at elevations 500 to 1,000 m below the present altitudinal limit (Bratlett and Barghoorn, 1973; Leyden, 1984).

### **Methods**

I conduct my analysis using a checklist of Central American highland birds. I consider highland species those who breed and spend most of the year above 1000 m elevation in Central America. Thus I include species that further North breed at lower elevations but in Central America are restricted to the highlands. In general highland avifauna tend to range lower (700-800 m) in the more humid Caribbean slope than in the Pacific slope, but these populations are also considered highland species for this analysis. Field guides and other similar sources were used to build species lists: I use the A.O.U. checklist of North American birds (A.O.U., 1983) for general distributions and systematic arrangement of the taxa, and more specific sources for avifaunas of particular countries: Guatemala, Land (1970); Honduras, Monroe (1968); El Salvador, Dickey and van Rosen (1938); Costa Rica, Stiles and Skutch (1989); Panama, Ridgely and Gwynne (1989), and South America, Hilty and Brown (1986). For Nicaragua I used my personal records and the information of specimens in several museums.

The following terminology is employed for present land areas:

- North America (NA), the continental land mass lying West and North of the Isthmus of Tehuantepec.
- South America (SA), the continental land mass extending east and south the Isthmus of Panama.
- Central America, the region running southeast from the Isthmus of Tehuantepec to the Isthmus of Panama.
- Nuclear Central America, the northern portion of Central America from the Isthmus of Tehuantepec to the upland of Northern Nicaragua.
- Lower Central America, the southern part of Central America between Southern Nicaragua and eastern Panama.
- Central American Highlands, are those areas above 1000 m elevation.

For analytical purposes, I have group them into seven subunits (Map 1):

- Chiapas-Guatemala (Ch & G), it includes all Sierra Madre de Chiapas, the altiplano of Central Guatemala, and the volcanic chain along the Pacific coast of Chiapas and Guatemala.
- Western Honduras-El Salvador (WH & ES), includes highlands of El Salvador and Honduras West of Comayagua and Sula valleys.
- Central Honduras-Northern Nicaragua (CH & NN), comprises the rest of Honduras and the highlands in Northern Nicaragua north of parallel 12° 50'N.
- Southern Nicaragua-Northern Costa Rica (SN & CR), extends between parallels 12° 50'N and 10° 30'N, including all the volcanic peaks of Western Nicaragua and Cordillera de Guanacaste in Costa Rica.
- Central Costa Rica (CCR), includes Cordilleras de Tilarán and Central, between parallels 10° 30'N and 9° 50'N.

- Southern Costa Rica-Western Panama (SCR & WP), comprises Cordillera de Talamanca and the highlands of Panama West of meridian 81° 30'W.

- Eastern Panama (EP), including Cerros Sapo, Serranía de Pirre and Serranía de Tacarcuna, both in the frontier between Panama and Colombia.

## Results

I present the distribution of Central American birds subdivided in 7 biogeographical areas (Table 1). Of a total of 874 species of breeding birds, 25% (220) are restricted to the highlands. Of this subset, 38% (83) are Central American endemics. This contrasts sharply with the percentage of lowland endemics: 5% (33) of the total lowland breeding birds (654 spp). Map 1 shows the number of endemics by geographic subunits, although my arbitrary subdivision of Nuclear Central America (3 subunits), and Lower Central America (4 subunits) hide the distribution of many of them. It is more useful to display a map superimposing ranges of endemic species, like Haffer (1985) presents for lowland birds (Map 2). Notice the high degree of endemism among the highland birds of Lower Central America (Map 1). Forty eight non endemics (35% of the total) are present in both sides of the Nicaraguan Gap. However, only 6 endemics (7% of the total) have similar distribution. This suggest that the endemic avifauna of the Central American highlands have poor dispersal abilities compared with the non endemic avifauna.

The high degree of endemism in the highlands of Lower Central America may be the result of an old isolation (older than Pleistocene) and subsequent speciation. More surprisingly, birds in the contiguous lowlands have also many endemic species (Map 2), and the ratio highland/lowland endemics is almost identical for Nuclear Central America (2.14) and Lower Central America (2.17). Do these numbers mean anything? At the time of the Glacial/Interglacial climatic changes in the Pleistocene, the Central American lowlands were interconnected and served as corridors for the faunal interchange between North and South America. Why didn't these endemics disperse further North or South? There are several possibilities: They are species of recent formation and they have not had enough time to disperse. Or they have been restricted in their ranges by specific habitat requirements, or by competitive exclusion with other species. These explanations are not mutually exclusive and not all the species must fit the same one. The origin of the endemic avifauna of the highlands could be in sister taxa of the lowlands. When the mountains became appropriated habitat, they occupied this empty niche. Climatic oscillations isolated some populations that evolved in new species. Other possibility is that the sister taxa are in other highlands further North or South. Cooler temperatures during the glacial periods in the Pleistocene expanded the range of some montane species that become isolated during subsequent warmer periods. If lowland and highland endemics are sister taxa, this could explain why I get similar ratios between Nuclear Central America and Southern Central America.

Cracraft (1985) has suggested that many taxa within the subtropical montane biota of South America have sister-group relationship with taxa restricted to other montane forests that lie either North or South, and not with the tropical biota of the adjacent lowlands. Using the taxonomic criteria of the A.O.U.(1983) I checked for sister taxa for the endemic avifauna of the Central American highlands. Thirteen species have their sister taxa in the Andes of South America, 21 species in the highlands of Central America, 6 in the highlands of North America, 1 in the South American lowlands, 1 in the North American lowlands, and none in the Central American lowlands. I was unable to find sister taxa for 26 species, including six monotypic, but numbers seems to indicate that highland endemics evolved from other highland avifauna.

### **Discussion**

I have been unable to explain the similar ratio highland/lowland endemics, the only pattern I detected. Endemic species seem to be a random subset of the local highland avifauna.

The geology of this region is extremely complex. Rosen (1985) has recognized 8 events of fragmentation and 7 of hybridization for Central America and the Caribbean. For this reason he suggests that it could be more useful to compare biological area cladograms with specific geological periods rather than try to match present distribution with features of the actual geography of the region. Map 4 shows the region in the early Miocene (21 Ma), according to Rosen (1985). Notice the



chain of volcanic islands between North and South America. All the volcanic centers appears to have a similar age. However, Weyl (1980) presents a geological map of the region with ages for the major geological formations (Map 3) with some interesting congruences between the degree of endemism and the age of major geological formations. I have highlighted in red those areas with Quaternary deposits of volcanic rocks. Almost all the highlands in the subunit Southern Nicaragua-Northern Costa Rica are covered with these volcanic rocks. No endemics have been recorded here, and the number of highland species is extremely poor. Are the highlands in this subunit too small or too low to provide enough habitat for highland birds? Highlands in the subunit East Panama are lower and less extended and still provide habitat for 10 endemic species. However, the region is composed by Mesozoic and Tertiary volcanic rocks, between 50 and 130 Ma. Volcanic rocks in the highlands of Southern Nicaragua-Northern Costa Rica are less than 1 Ma old (Weyl, 1980). Both Nuclear Central America (subunits Ch&G, WH&ES, and CH&NN) and Lower Central America (subunits CCN and SCR&WP) have extensive geological formations of Tertiary origin (50-65 Ma). The distribution of geologically "stable" areas match well with areas of high endemism in the highlands of Central America. This evidence support Cracraft's claims that areas of endemism can be explained prior to Pleistocene climatic changes (Cracraft, 1985), and it answers my second question on the correlation between geological stability and degree of endemism.

The third question on the power of Pleistocene events to fully explain actual differentiation of avian taxa cannot be answered with a simple comparison of checklists. We can use molecular techniques to

assess degrees of differentiation among isolated populations and sister species. Mitochondrial DNA is very useful to assess levels of differentiation between populations. This molecule is maternally inherited without recombination, and is highly conserved in function and gene arrangement across diverse taxonomic groups (Brown, 1983). Besides these characteristics, the molecule evolves very rapidly, and numerous studies have shown high levels of intraspecific heterogeneity (Ashley and Wills, 1987). MtDNA has been used for analyzing patterns of colonization and gene flow among insular and mainland populations (Ashley and Wills, 1987), island populations (Phillips et al, 1989), contiguous mainland populations (Ball et al, 1988) and isolated mainland populations (Riddle and Honeycutt, 1990).

Meanwhile a better knowledge of the geology of the region and a more complete fossil record will help us to understand mechanism of speciation and dispersion in the region. In Central America, ranges of many bird species are not well defined, especially in Nicaragua and Honduras. I cannot rule out the possibility that some of the patterns presented here are pure artifact of our incomplete knowledge of the ranges of many shy and secretive species.

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Map 1.- Endemism in the highlands of Central America. Areas in black indicate elevations above 1000 m. Dotted lines are the limits of zoogeographic subunits: NA, North America; Ch&G, Chiapas-Guatemala; WH&ES, Western Honduras-El Salvador; CH&NN, Central Honduras-Northern Nicaragua; SN&CR, Southern Nicaragua-Northern Costa Rica; CCR, Central Costa Rica; SCR&WP, Southern Costa Rica-Western Panama; EP, Eastern Panama; SA, South America. Numbers in parenthesis indicate endemics restricted to a particular subunit. Numbers underlined represent overlapping ranges of endemics restricted to the highlands, excluding 6 species with ranges in both sides of the Nicaraguan Gap.

Map 2.- Areas of endemism in the lowlands of Central America, with superimposed ranges of endemics species; numbers indicate how many species ranges overlap in a particular area. A, Caribbean Northern Central America; B, Caribbean Southern Central America; C, Pacific Southern Central America. Mountains above 1000 m elevation are indicated in black (From Haffer, 1985).

Map 4.- Central America and the Caribbean region in the early Miocene (21 Ma). Black dots represent primary sites of volcanism. Vertical hatching is land, and cross-hatching is shallow-water shelves with sedimentary deposits (from Rosen, 1985).