BIOGEOGRAPHIC PATTERNS OF COLOMBIAN FROGS AND TOADS

por

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Resumen

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Con base en los datos de **Ruiz-Carranza** et al. (1996), la distribución de 540 especies de ranas y sapos registradas en Colombia se ubican en diez entidades basadas en la elevación y la precipitación pluvial. Unas de las áreas de tierras bajas (del Pacífico y la Amazonia) muestran alta diversidad (85-94 spp.) pero en general las zonas de tierras bajas parecen pobres (30-52 especies), en contrastando con las áreas de tierras altas. En la Cordillera Central se han registrado121 especies de ranas y sapos, en la Occidental 118, y la Oriental 87, con lo que se muestra que la mayor biodiversidad de Colombia se encuentra en las áreas montañosas y no en las selvas de tierras bajas. Al separar el endemismo biológico del endemismo político, aparecen cinco áreas con alto endemismo (las tres cordilleras andinas, la Sierra Nevada de Santa Marta, y las tierras bajas del Pacífico). Mediante el análisis cladístico en varios grupos de leptodactílidos se trata de mostrar este patrón; la diversificación obedece a un patrón horizontal (especiación alopátrica) con contribuciones menores de diversificación vertical.

Palabras claves: Anura, biodiversidad, biogeografía, especiación alopátrica.

Abstract

Using the data provided in **Ruiz-Carranza** et al. (1996) the distributions of the 540 species of frogs and toads are partitioned among ten ecogeographic units of Colombia defined on the basis of precipitation and elevation. Some lowlands areas (Pacific lowlands, Amazonia) exhibit high diversity (85-94 species) but lowlands areas in general are impoverished (30-52 species), especially when contrasted with upland areas. The three Andean cordilleras harbor between 87 and 121 species of frogs and toads, demonstrating that the biodiversity of Colombia resides primarily in its montane components, not in its lowland rainforests. When biological endemicity is separated from political endemicity, five areas of high endemicity remain (the three Andean

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cordilleras, the Sierra Nevada de Santa Marta, and the Pacific lowlands). We endeavor to explain this description by recourse to cladistic analyses of several groups of leptodactylid frogs where we find that the general pattern of diversification is by means of horizontal diversification (allopatric speciation) with a minor contribution from vertical diversification.

Key words: Anura, biodiversity, biogeography, allopatric speciation.

Introduction

Ruiz-Carranza et al. (1996) provided a listing of the species of amphibians known from Colombia, substantially altering the currency of **Cochran & Goin** (1970) or **Duellman** (1979). Our investigations over the past twenty years have established Colombia as the country richest in amphibian species on the planet, especially as concerns frogs and toads. It is believed widely, especially by non-specialists, that biotic richness is related to the proportion of the tropical lowlands included in some political unit. However, the data provided by **Ruiz-Carranza** et al. (1996) contradict that belief and establish that the Andean fauna is what makes the Colombian biota so distinctive and rich. The purposes of the present contribution are to set the data provided by **Ruiz-Carranza** et al. (1996) into a biogeographic context and to emphasize the major points of those data as concerns the geographic distribution of biodiversity. The more than 540 species[3] of frogs and toads found within the geographic limits of the Republic of Colombia are partitioned among thirteen family-groups, as follows: Bufonidae (60), Centrolenidae (63), Dendrobatidae (54), Hylidae [128, subfamilies — Hemiphractinae (26), Hylinae (86), Phyllomedusinae (16)], Leptodactylidae [212, subfamilies — Ceratophryinae (2), Leptodactylinae (34), Telmatobiinae (176)], Microhylidae (14), Pipidae (4), Pseudidae (1), and Ranidae (3).

The frogs and toads found in Colombia exhibit a wide variety of reproductive modes representing adaptations, presumably, to the availability of moisture and as protection for the embryonic stages from predation. Some areas of Colombia are notably dry, and therefore unsuitable for most frog species (thorn forests, > 5 months per year without rains), whereas others are among the wettest places on the planet. In general, the republic can be described as a moist region with abundant supplies of precipitation. The lowland units consist of rainforests (Amazonia and Chocó), grasslands (Llanos), and the relatively dry thorn forests of the Caribbean lowlands and the interior river drainages (ríos Cauca and Magdalena). In addition to these lowland areas, there is a large isolated massif (La Sierra Nevada de Santa Marta) located on the Caribbean coast and a series of andean chains separated by the Cauca and Magdalena river valleys. The three Andean cordilleras are united in the Macizo de Pasto, just north of the Republic of Ecuador. Each of the montane regions has individual

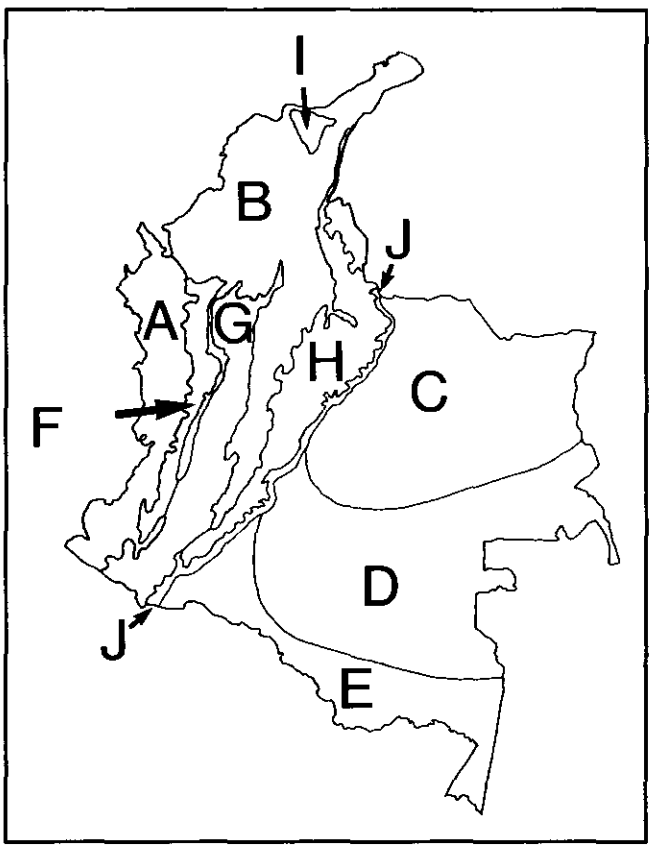

Figure 1. Map of Colombia showing the ten ecogeographic units mentioned in the text and referenced in Tables 1-3.

[3] **Ruiz-Carranza** et al. (1996) reported 540 species and we use those figures. However, additional species are described from Colombia at an astonishing rate; in this journal, nine additional species of *Eleutherodactylus* were described in two articles appearing in the March 1997 issue, **Lynch & Duellman** (1997) described two additional species found in Nariño, Colombia (and Ecuador), and **Lynch & Ruiz** (1996) described a new *Cochranella*.

peaks reaching 4000 or more meters and is described generally as having substantial areas above 2000 meters.

Results

For convenience, Colombia can be divided into ten ecogeographic units (Fig. 1), based on the amount and distribution of precipitation. These include four elevated regions (the three Andean cordilleras and the Sierra Nevada de Santa Marta) and six lowlands regions. Using the data provided in **Ruiz-Carranza** et al. (1996), one may tabulate the numbers of species from each family-group found in each of the ten regions, ranging from a low value of 17 species to a high value of 121 species (Table 1). Some family-groups are found in all ten regions whereas others are restricted to some lowlands regions. When a species occurs in more than one ecogeographic region, it is counted for each region (hence, the totals across regions exceed 540 species). The number of species found in a region is one measure of a group's importance. A second measure of a group's importance is concerned with how exclusive are the species making up the group (endemicity). Areas B-J (Table 1) have low endemicities, whether or not there are many or few species present in the area.

Tabla 1. Números de especies de ranas colombianas en diez zonas ecogeográficas. Letras identifican áreas (vease Fig. 1).

	A	B	C	D	E	J	F	G	H	I
Bufonidae	11	3	4	4	5	3	12	14	7	7
Centrolenidae	9	2			1	3	25	17	15	1
Dendrobatidae	16	1		3	7	2	9	13	7	(2)[4]
Phyllomedusinae	6	2	1	1	4	4	1		2	
Hemiphractinae	3				2	2	7	10	8	1
Hylinae	17	17	15	18	29	17	5	8	15	
Ceratophryinae		1		1	1					
Leptodactylinae	5	8	7	12	16	8	1	1	1	
Eleutherodactylini	23	6		4	13	14	57	47	31	8
Pipidae	1		1	1	2					
Pseudidae		1	1	1						
Microhylidae	2	3	1	6	5	1	1	1	1	
Ranidae	1	1		1	1	1				
TOTAL	94	45	30	52	85	55	118	121	87	17
% endémicas	71	36	33	25	37	29	74	62	84	94

[4] The two dendrobatid species from the Sierra Nevada de Santa Marta are undescribed species of *Colostethus*. Because they are undescribed, and not listed in **Ruiz-Carranza** et al (1996), they are included in this table in parentheses (as well as in Table 2).

Discussion

Descriptive biogeography of Colombian frogs and toads. Historically, most biologists have believed that tropical diversity was a simple function of the presence (and extent) of the biota of lowland rainforests. The lowlands of western Colombia harbor 94 species of frogs and toads and the southeastern fringe of Colombia, residing in Amazonia, harbors 85 species. A few widespread species (e.g., *Bufo marinus, B. "typhonius", Hyla boans,* and *Scinax rubra*) are held in common by these two regions, but these two areas contain "only" approximately 175 species (only 32% of the frog fauna of the Republic). This is one of our major points – that although these lowland rainforest areas exhibit prominent diversity, the presence of such forests in Colombia explains only part of the diversity of its frogs and toads.

Other lowlands regions are less richly endowed with species of frogs and toads and also have fewer endemics (Table 1). The Caribbean lowlands (including the interandean valleys), with their mediterranean climate and dry, scrub forests, harbor 45 species and the llanos of the Orinoquia harbor only 30 species. Another eastern lowlands region (triángulo guayanés), between the llanos and the Amazonian selva, is peculiar because, although forested, it has a pronounced dry season, and harbors 52 species of frogs and toads. This unit is perhaps best viewed as an ecotone between the llanos of the Orinoco and the selvas of Amazonia. Along the eastern base of the Andes is another ecotonal region (piedemonte) extending from Venezuela to Ecuador and harboring 55 species. This unit is forested and very narrow.

The Caribbean lowlands and the Orinoco grasslands are vast regions but are relatively species-poor. This is accentuated by noting that endemicity is low for each region. The only lowlands region to have substantial numbers of species and appreciable endemicity is the Pacific lowlands of western Colombia (Table 1). The comparably rich Amazonia does not exhibit a comparable level of endemicity. Twenty-five years ago (**Cochran & Goin**, 1970), the Andes seemed unimportant biogeographically but discoveries in the past twenty years have revealed that the previous (and currently popular) view is a myth. When we began our investigations, there were only eight

centrolenid species and only 35 eleutherodactyline species known for Colombia (see Table 1) – and, each group has its diversity centered in the northern Andes.

Our second major point is that more than half of the species of frogs and toads of Colombia occur in the relatively small geographic area occupied by the Andean cordilleras. In fact, the two richest regions of Colombia are the two western Cordilleras, the narrow Cordillera Occidental with 118 species, and the Cordillera Central with 121. The Cordillera Oriental is somewhat less rich ("only" 87 species), roughly comparable to the diversity of the Chocó or of Amazonia.

To summarize this introduction to the pattern of biodiversity of the frogs and toads of Colombia, species richness does not correlate with endemicity (Table 1, Fig. 2). Rather, five areas exhibit high levels of endemicity (62-94%) and five areas exhibit low endemicity (25-37%). All areas of low endemcity are lowland faunas and all highlands areas exhibit high endemicity as does one lowland region (Chocó).

Four groups of frogs and toads (Ceratophryinae, Pipidae, Pseudidae, and Ranidae) are depauperate in Colombia (1-4 species) and are confined to lowlands regions. The first three of these are groups of small to modest diversity on a global scale whereas the last is diverse in Africa, Asia, and North America, and reaches a distributional limit in northwestern South America (presumably as a Pliocene entrant to the continent). Three other groups (Phyllomedusinae, Leptodactylinae, and Microhylidae) are more speciose (14-34 species) but are scarcely represented in the Andean fauna (three endemic phyllomedusines, one endemic *Leptodactylus*, and one nonendemic microhylid). The remaining six groups (Bufonidae, Centrolenidae, Dendrobatidae, Hemiphractinae, Hylinae, and Telmatobiinae [tribe Eleutherodactylini]) have significant numbers of species in the Andes and in the fauna of Colombia. Two of these groups are represented across all regions and the other four are poorly, or not, represented in drier regions (Table 2).

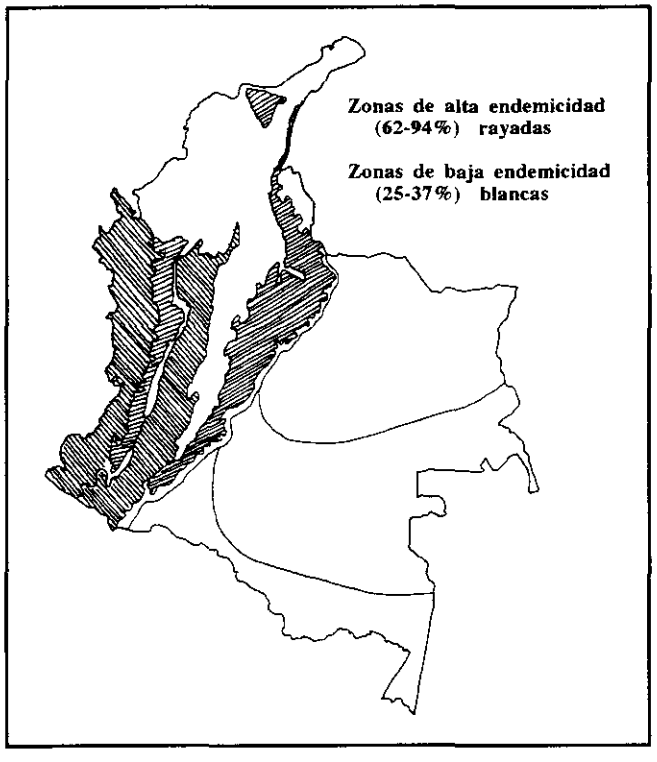

Figure 2. Levels of endemicity among the ten ecogeographic units; hatched areas exhibit high endemicity.

The general pattern of diversity described previously is reflected in these data as well but is less obvious in some groups than for others because percentages do not reveal differences in numbers of species. However, all of the data presented thus far incorporate artificial endemicity. A frog species might be endemic to area E (Colombian Amazonia) but is found as well in Brasil, Ecuador, and Peru. It is not biologically endemic to the Amazonia of Colombia, only politically endemic. If one makes an effort to distinguish biological and political endemicity, the apparent high endemicity of Colombian frogs and toads (to ecogeographic regions) is reduced dramatically. The chocoan lowlands of western Colombia share much of their distinctive fauna with Ecuador and Panamá. Nearly all species found in the Caribbean lowlands of Colombia are shared by Venezuela and/or Panamá. The Orinocoan fauna is shared with Venezuela. The triángulo guayenés shares its fauna with Brasil and Venezuela. The

Tabla 2. Porcentaje de especies endémicas de seis familias de ranas colombianas en las zonas geográficas. Las áreas son identificadas por letras (vease Fig. 1). El símbolo * indica que 100% de las especies son endémicas.

	A	B	C	D	E	J	F	G	H	I
Bufonidae	82	33	25	25	40	33	92	93	86	86
Hylinae	53	41	40	17	31	6	60	62	93	
Centrolenidae	50	0			*	*	63	62	87	*
Dendrobatidae	*	*		33	57	50	89	62	86	(*)
Hemiphractinae	67				*	0	43	70	50	*
Eleutherodactylini	70	20		50	31	50	77	56	93	*

piedemonte shares most of its species with Ecuador or Venezuela. The Cordillera Central represents the northern extension of the Cordillera Real of Ecuador and many Andean species are shared by Colombia and Ecuador and/or Venezuela. Only the Sierra Nevada de Santa Marta preserves its high endemicity when political endemicity is eliminated from the equation.

Over the past twenty years, two groups of frogs and toads have formed central foci for us, in part because each is well represented in Colombia. However, part of these foci reflect systematic and taxonomic interests of the authors. The family Centrolenidae (63 species) has been a major focus of JDL and PMR while the tribe Eleutherodactylini (176 species) is an obsession of JDL. Because we have devoted so much time to the study of these groups documenting their taxonomies and distributions, we are most confident of the data sets for these two groups, and will use these two groups to examine biological endemicity and its pattern among the ecogeographic units making up the Colombian biota. We suspect that we are approaching a complete knowledge of the centrolenids of Colombia. By that, we mean that we think we have found most of the species to be found in Colombia (although several of these have not yet been named formally). Our estimate is that we have placed names on 90% of the centrolenid species found in the Republic. For most areas of Colombia, we are confident of the 90% figure but there exist a few areas where novelties surely remain. Our knowledge of eleutherodactyline frogs is less complete (in our estimate). For eleutherodactyline frogs, we think that 90% (or better) knowledge exists for many regions, even large and complex ones (western lowlands, Cordillera Occidental), but for other regions the discovery phase is far from complete. For example, in the cloud forests of the northern Cordillera Central, names can be placed on less than 40% of species that we recognized (**Ruiz-C.** et al., 1996). In that biota, we found eight species of centrolenids and 28 species of eleutherodactylines. Aside from these caveats, these two groups of organisms are taken as representative groups for a general description of the biogeographic pattern of Colombian frogs.

Tabla 3. Especies endémicas biológicamente en zonas ecogeográficas de Colombia. Areas son identificadas en Fig. 1.

	A	E	J	AF	F	FG	G	H	I
Centrolenidos	1	1		2	9	3	9	10	1
Eleutherodactylinos	4		1		27	9	22	24	8

Of the 63 species of centrolenids (Table 3) known from Colombia (**Ruiz-C.** et al., 1996), 36 are endemic (biologically) to Colombia (although we doubt the endemicity of *Cochranella ametarsia*). Nine species are endemic to the Cordillera Occidental, nine others to the Cordillera Central, three endemics are shared by those two cordilleras (otherwise endemic), ten are endemic to the Cordillera Oriental, and one is endemic to the Sierra Nevada de Santa Marta. The other four endemic species include one in the Pacific lowlands, two shared by the Pacific lowlands and the Cordillera Occidental, and one questionable endemic in Amazonia.

Of the 176 eleutherodactylines known from Colombia (listed in **Ruiz-C.** et al, 1996), 96 are endemic to Colombia (Table 3). Twenty-seven are endemic to the Cordillera Occidental, 22 to the Cordillera Central, nine are shared exclusively by those two cordilleras, 24 are endemic to the Cordillera Oriental, and eight are endemic to the Sierra Nevada de Santa Marta. The Pacific lowlands harbor four endemics.

These data tell us that four marked areas of endemism exist for the frogs of Colombia – each of the three Andean cordilleras and the Sierra Nevada de Santa Marta. They also suggest that a fifth area (Pacific lowlands) should be so identified as well. One curious pattern (FG) involves an array of species whose distributions are separated (fragmented) by the valley of the Río Cauca. This distributional patetrn suggests that the geological history of those two cordilleras will be found to be complex. These more precise data agree with the general trend (Table 1 and its description) identified using all species and ignoring the artifacts of political endemicity – that the richness of the frog fauna of Colombia is not an effect of lowland rainforests but of the highland areas. This conclusion suggests, but does not demonstrate, that the biological diversity of Colombia is due to Beta diversity rather than to Alpha diversity, that is, that the biodiversity is explained as a function of geographic replacements of species rather than ecological complexity.

Analytical biogeography of Colombian frogs and toads. Beta diversity corresponds to what is thought of as "normal" speciation (allopatric speciation). Using the data sets available to us, that pattern is nearly universal among them. The first author began to appreciate this pattern when he initiated his study of the frogs of the *Eleutherodactylus orcesi* group (Fig. 3). Six species are known at present, one of which is endemic to Ecuador, one is shared by Colombia and Ecuador, and four are endemic to the Cordillera Central of Colombia (**Lynch**, 1980, 1981, **Lynch** et

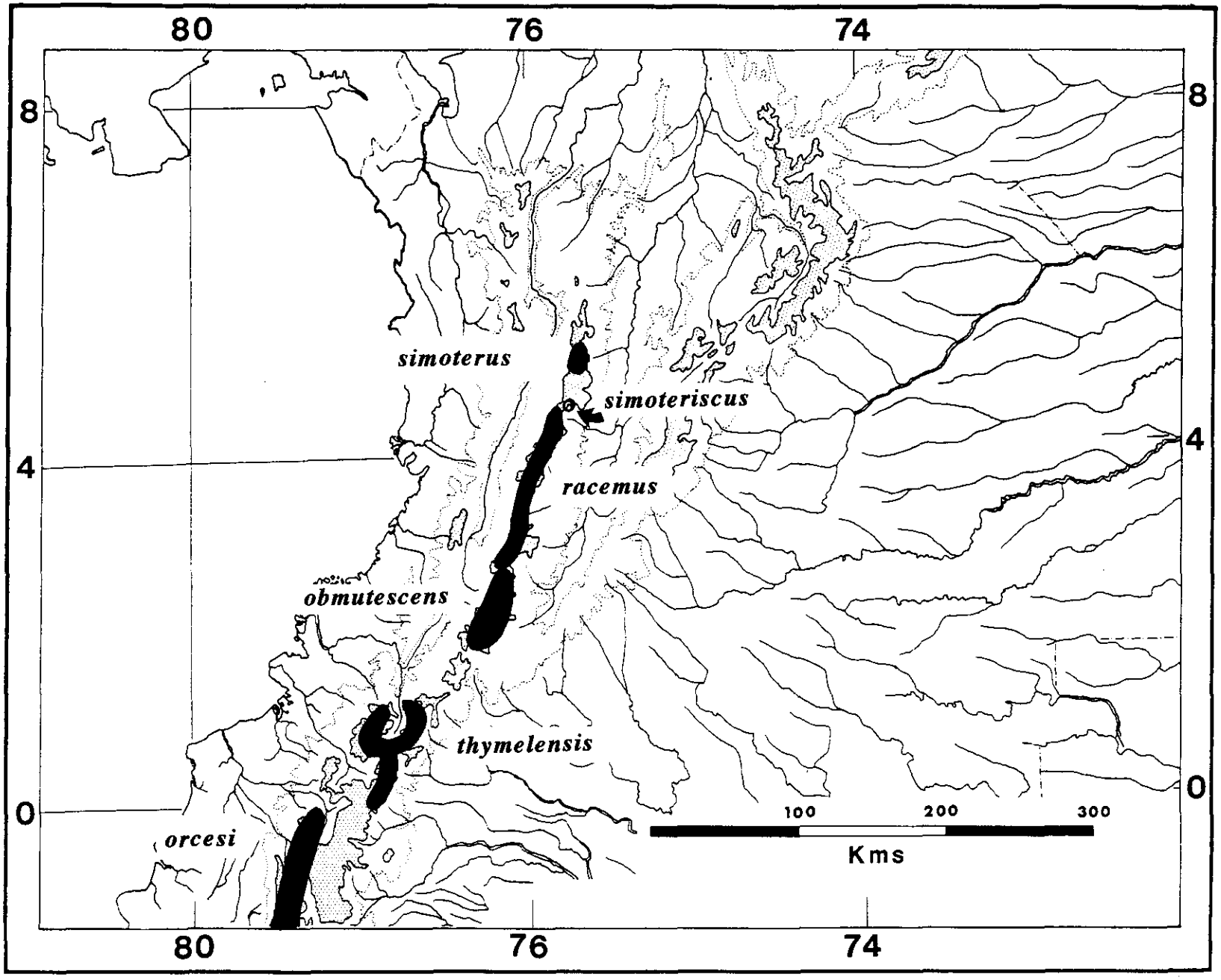

Figure 3. Distributions of the species of the *Eleutherodactylus orcesi* species group in Colombia and Ecuador.

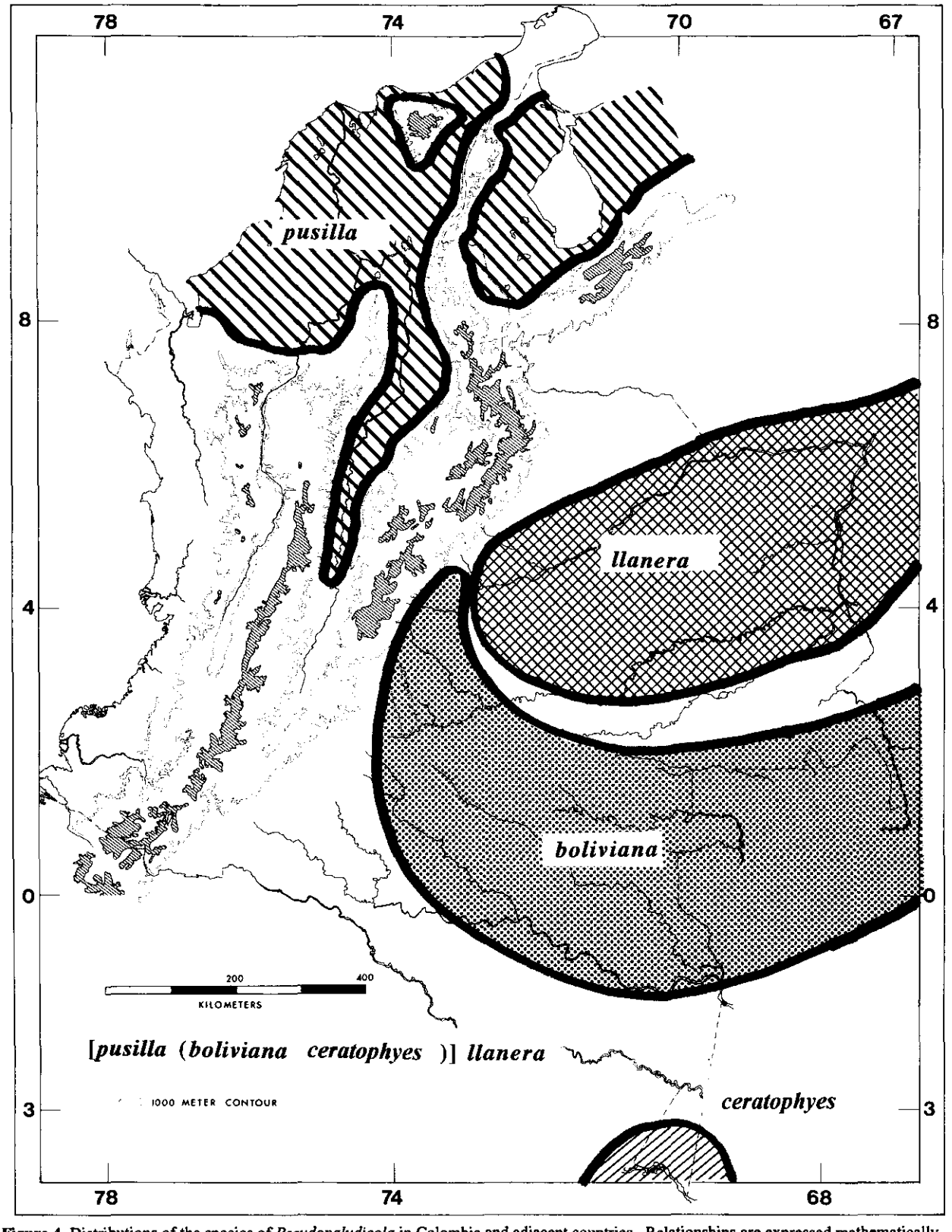

Figure 4. Distributions of the species of *Pseudopaludicola* in Colombia and adjacent countries. Relationships are expressed mathematically.

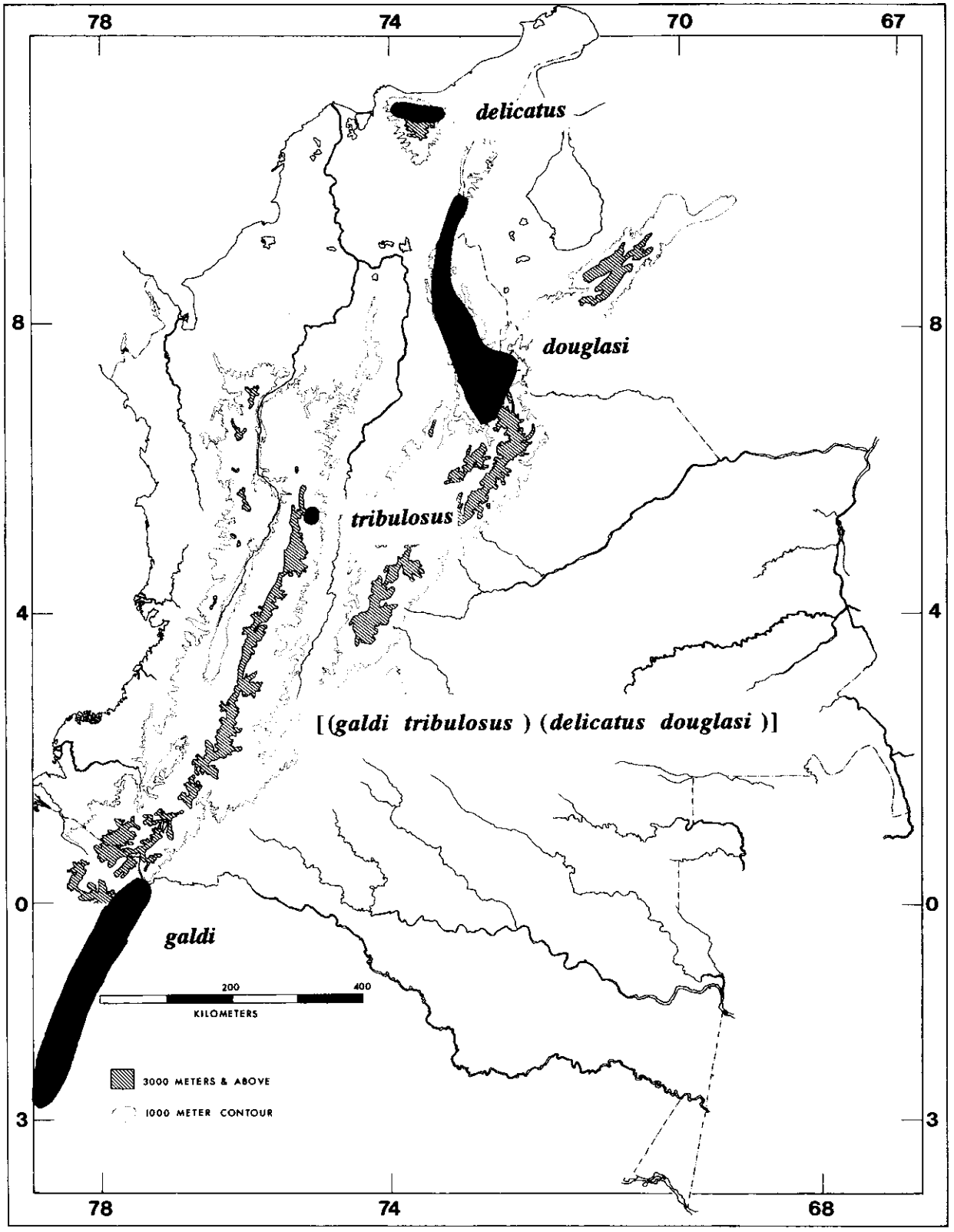

Figure 5. Distributions of the species of the *Eleutherodactylus galdi* clade in Colombia and Ecuador. Relationships are expressed mathematically.

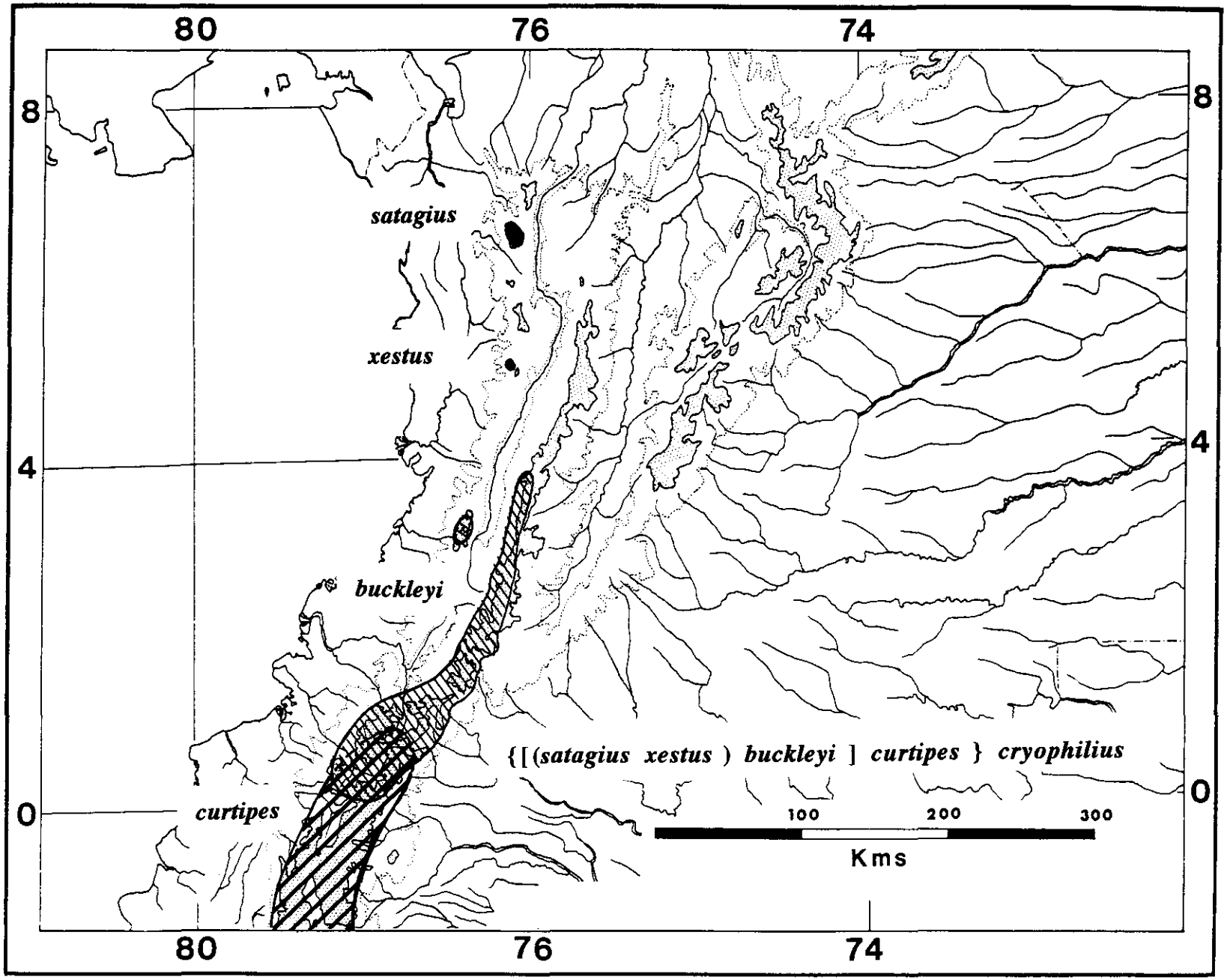

Figure 6. Distributions of four species of the *Eleutherodactylus curtipes* species group in Colombia and northern Ecuador. Relationships are expressed mathematically.

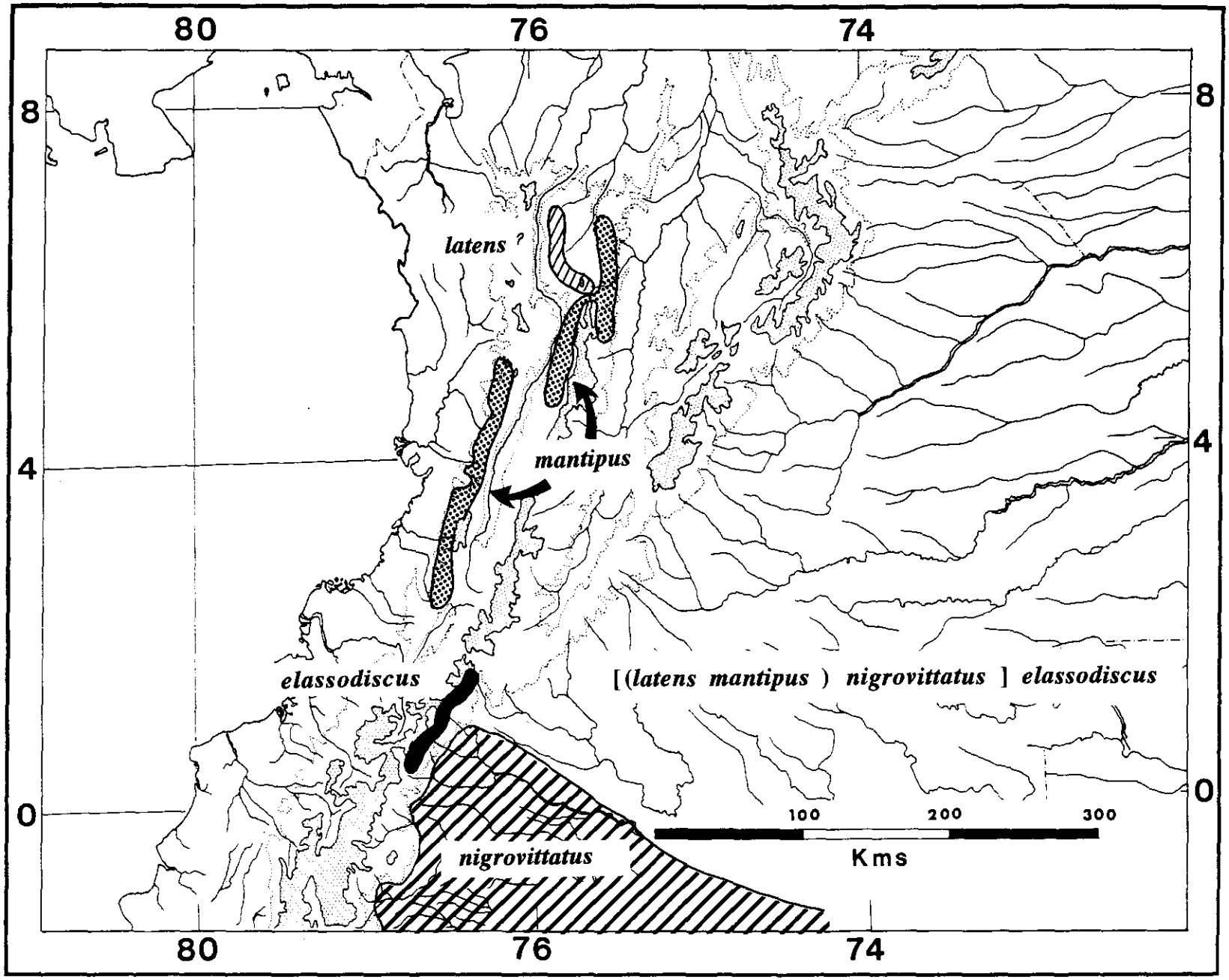

Figure 7. Distributions of the species of the *Eleutherodactylus nigrovittatus* species group in Colombia and Ecuador. Relationships are expressed mathematically.

al., 1996). The six species neatly replace one another along the geographic axis of the Cordillera Central and Cordillera Real with a single locality of apparent sympatry. All six species occupy paramo habitats (3000-4100 m) and it is unlikely that there are additional species in the complex or that the known distributions will be substantially altered by future collecting. Unfortunately, the relationships among the six species remain unknown. Frogs of the genus *Pseudopaludicola* (Fig. 4), a lowlands group found below 500 meters, demonstrate the same pattern but, in this case, the relationships are known (**Lynch**, 1989a). In the *galdi* group of *Eleutherodactylus*, the four species are allopatric (Fig. 5) and occur at comparable elevations (**Lynch & Rueda-A.**, 1997). In the *curtipes* group of *Eleutherodactylus* (**Lynch**, 1995), the five species are allopatric, except for the extremities of the distributions of *E. buckleyi* and *E. curtipes* (Fig. 6), and occur at comparable elevations (3200-4400 m).

Three other species groups depart from this pattern (geographic replacement within the same elevational belt). In the *nigrovittatus* group (Fig. 7), three of the four species occupy upland habitats but the fourth is a lowlands species (**Lynch**, 1989b). Each is allopatric but the lowlands species belongs to a clade found in the Andes, suggesting that some dispersal has occurred after speciation. In the *loustes* group of *Eleutherodactylus* (**Lynch**, 1992), two species occur in cloud forests but the third (*E. hybotragus*) is a lowlands species, most closely related to one of the upland species. In the *sulcatus* group of *Eleutherodactylus* (**Lynch**, 1997), the seven Andean species (cloud forests 500-2500 m) form a clade. All sister species pairs are allopatric to one another but less closely related pairs of species may be partially (or wholly) sympatric.

Thus, the general pattern is that nearest relatives occur in the same elevational station but allopatrically. In addition to these cases, we can cite about a dozen additional cases, all distributed within the Cordillera Occidental, but involving only pairs of sister species. A variation on that general pattern is that one species of a clade (or an entire subclade) exhibits altitudinal displacement relative to the rest of the clade (Fig. 8).

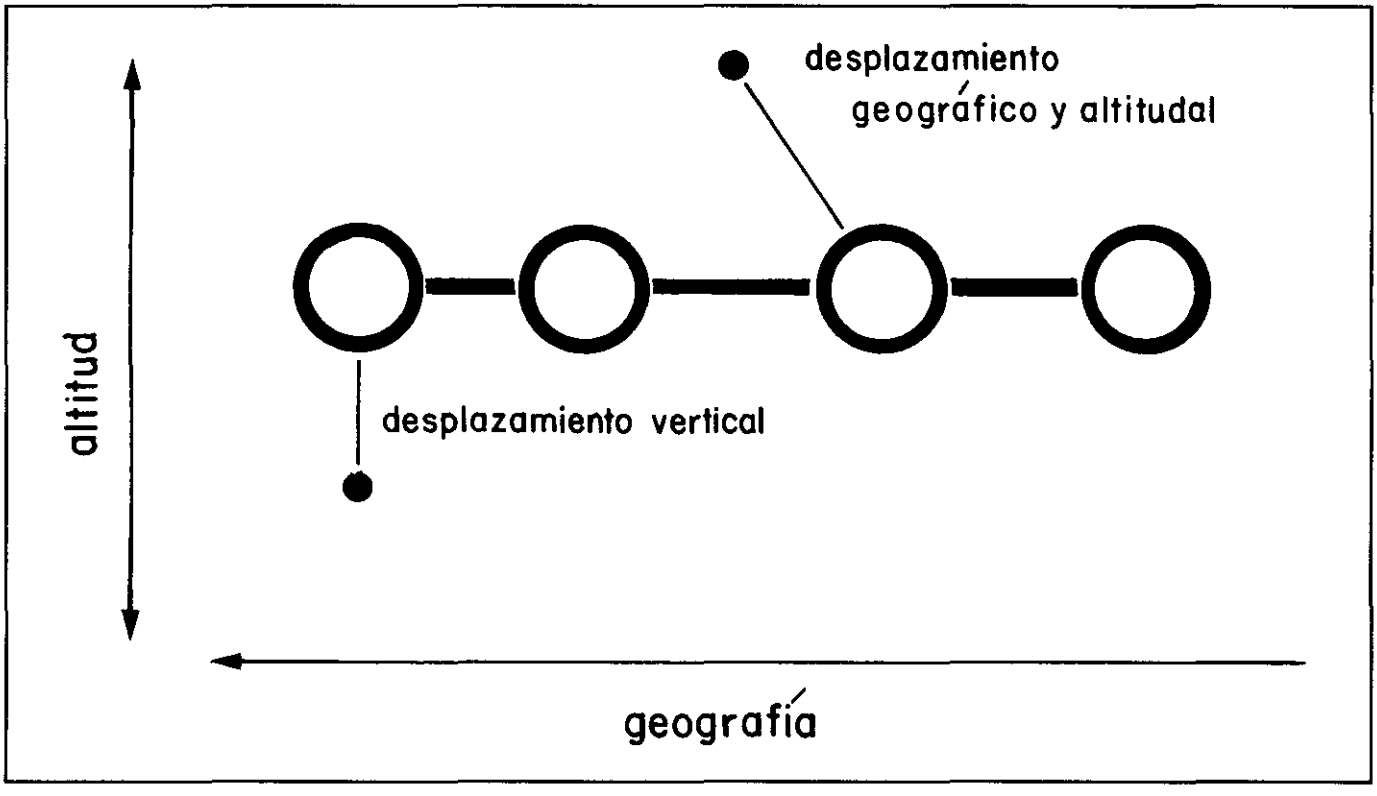

Figure 8. Distributional patterns for frog species in Colombia (heavy lines and circles reflect the major pattern; thin lines and solid circles reflect minor patterns).

We think that the emerging data set for Colombia is going to tell us that the Andean chains have played a critical role in the diversification of the Colombian frog fauna by fragmenting lowland populations (as in *Pseudopaludicola*) or by fragmenting populations by means of nonsynchronous uplifting of Andean blocks and providing topographic complexity that eliminates gene flow and promotes the development of allopatrically distributed species. At least two cases of upland groups are available where a lowland representative is positioned within the cladogram such that it is necessary to identify (postulate) dispersal as a means of explaining the geographic/cladistic relationships (*loustes* and *nigrovittatus* groups of *Eleutherodactylus*). Although very popular, Mayr's peripatric model of speciation (see **Mayr**, 1997) does not efficiently explain the pattern that we think characteristic of Colombian frogs. Our claim that horizontal diversification is the central pattern in these data (seven data sets) is contrary to **Funk**'s (1982) study of *Montanoa* (Asteraceae: Heliantheae) where vertical diversification appears to be the main pattern even though we have a few cases where vertical displacement appears to have been the case. Obviously, many more cladograms combined with detailed distributional data will be required to resolve the competing explanations.

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