What are the Andean Colombian anurans? Empirical regionalization proposals vs. observed patterns of compositional dissimilarity (#78830)

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What are the Andean Colombian anurans? Empirical regionalization proposals vs. observed patterns of compositional dissimilarity

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Andean anurans are of great interest as ecological models with which to understand the effects of climate change on the persistence of tropical species and communities along elevation gradients. However, for the northern Andes (Ecuador, Colombia and Venezuela), there is no consensus regarding the elevation interval that hosts and defines the Andean anurofauna and it is consequently unclear whether the Andean anurans constitute a taxonomically and biogeographically coherent group. For the Colombian Andes (~66% of the northern Andes), there are at least three proposals for the differentiation of "Andean anurans" from "lowland anurans", and at least one to distinguish “Andean anurans” from "high mountain anurans". However, the first three proposals differ at least in their original objectives, taxonomic coverage and lower elevation limits, while none of the proposals specify intra-Andean differences, or fully consider the fauna associated with the inter-Andean valleys of Colombia. From 5776 elevation bands for 593 species, 72 genera and 14 families of Colombian anurans, we evaluated the consistency of these four proposals based on an analysis of elevation patterns and species compositional dissimilarity among eight Andean entities (combinations of slopes and inter-Andean valleys). About a 30% of the species and 90% of the families, presented an elevation distribution that did not coincide with that expected for the delimitation between Andean and lowland anurans. Moreover, between 1-15% of the species presented an elevation distribution that did not coincide with the delimitation between Andean and highland anurans. Our results suggest that the four proposals should not be used in a generalized way to define the Colombian Andes anurans. The implications of the generalized use of these proposals are discussed and some general guidelines are presented in order to address the theoretical and applied

challenge of delimiting the Colombian Andes anurans.

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Abstract

Andean anurans are of great interest as ecological models with which to understand the effects of climate change on the persistence of tropical species and communities along elevation gradients. However, for the northern Andes (Ecuador, Colombia and Venezuela), there is no consensus regarding the elevation interval that hosts and defines the Andean anurofauna and it is consequently unclear whether the Andean anurans constitute a taxonomically and biogeographically coherent group. For the Colombian Andes (~66% of the northern Andes), there are at least three proposals for the differentiation of "Andean anurans" from "lowland anurans", and at least one to distinguish “Andean anurans” from "high mountain anurans". However, the first three proposals differ at least in their original objectives, taxonomic coverage and lower elevation limits, while none of the proposals specify intra-Andean differences, or fully consider the fauna associated with the inter-Andean valleys of Colombia. From 5776 elevation bands for 593 species, 72 genera and 14 families of Colombian anurans, we evaluated the consistency of these four proposals based on an analysis of elevation patterns and species compositional dissimilarity among eight Andean entities (combinations of slopes and inter-

Andean valleys). About 30% of the species and 90% of the families, presented an elevation distribution that did not coincide with that expected for the delimitation between Andean and lowland anurans. Moreover, between 1-15% of the species presented an elevation distribution that did not coincide with the delimitation between Andean and highland anurans. Our results suggest that the four proposals should not be used in a generalized way to define the Colombian Andes anurans. The implications of the generalized use of these proposals are discussed and some general guidelines are presented in order to address the theoretical and applied challenge of delimiting the Colombian Andes anurans.

Introduction

The Colombian Andes belong to the "northern Andes" region, which extends from the Amotape-Huancabamba depression between Peru, and Ecuador (5 °S), to Caribbean plate contact point, in the Mérida mountain range in Venezuela (*ca*. 12 °N) (Graham, 2009). The Colombian Andes comprise *ca*. 66% of the "northern Andes" and, given the topographic complexity, represent one of the most diverse regions in the world. In particular, the northern Andes host 27.6% of the South American anuran species, with 73% of this richness concentrated in Colombia, ranking the country as the second richest in anuran species worldwide (Cochran & Goin, 1970; Armesto & Señaris, 2017; Frost, 2018; Acosta Galvis, 2019). Despite the high species richness of the region, the definition of which should be considered an Andean anuran is unclear. Historically, at least four empirical definitions have been postulated to circumscribe Andean anurans. Three have defined minimum elevation limits to differentiate Andean from lowland anurans, and a fourth has been postulated to separate Andean anurans from those that are exclusive to high mountain ecosystems (high mountain anurans). All of them have been used to delimit Andean anurans in regional species lists, studies of response to climate change scenarios and local species lists, but their indiscriminate use can have repercussions for decision-making and knowledge of the fauna of the region (Péfaur & Rivero, 2000; Bernal & Lynch, 2008; Armesto & Señaris, 2017). And although, in practical terms, trying to define complex communities within arbitrary geographic boundaries brings us back to Clements and Gleason's discussion of whether communities are open or closed systems (see Begon, Townsend & Harper, 2006), the truth is that in practical terms the use of arbitrary delimitation for a group, (understanding the advantages and limitations of these), can make it easier to obtain general responses to specific scenarios.

First, Duellman (1979) considered Andean anurans to be distributed above 1000 m asl in elevation, thus excluding the species mainly distributed in lowlands and with only peripheral occurrence above this elevation. This delimitation was formulated for the single purpose of compiling the first list of anurans of South America. Although this proposal is not justified in any formal theory or observation, later authors accepted and used it as an approach for delimiting Andean anurans (e.g. Bernal & Lynch, 2008; Armesto & Señaris, 2017). On the other hand, based on the distribution of the ancient genus Eleutherodactylus in the Colombian Andes (currently the families Craugastoridae, Stabomantidae and Eleutherodactylidae, in part), Lynch (1999) proposed a vertical classification, where anurans were considered Andean in elevational distributions above 900 m asl. Although this classification was proposed considering a portion of the diversity of the northern Andes region, the author suggested that the proposal could also apply to other anuran groups. Some authors have therefore used the classification to distinguish Andean anurans according to elevation (e.g. Armesto & Señaris, 2017).

Meanwhile, and almost concurrently with Lynch (1999) proposal, Péfaur & Rivero (2000) analyzed the spatial distribution of the anurans of Venezuela, and defined the elevation limit between lowland and Andean anurans at 500 m asl. Again, although this proposal was not justified in any formal theory or observations, some authors have adopted it as a criterion for differentiating Andean anurans (e.g. Anderson et al., 2011; Meza-Joya & Torres, 2016). In addition, these three proposals for a low elevation limit for Andean anurans exclude a portion of the anuran species that live in the inter-Andean valleys (i.e. Cauca River valley and Magdalena River valley).

At the other extreme, authors such as Lynch (1999) and Navas (2002) have proposed an upper elevation limit for Andean anurans. These proposals establish the elevation limit between Andean anurans and high mountain anurans (= High Andean anurans) at nearly 3000 m asl. The approach by Lynch (1999) and Navas (2002) is linked to the idea that mountain peaks "behave as islands", and is based on the distribution of the ancient genus *Eleutherodactylus* in the western Colombian mountain range (Lynch, 1999), or on ecophysiological observations on species of anurans in the Andes (Navas, 2002). This delimitation has been used in the subsequent literature to define high mountain species and conduct vulnerability studies in the face of climate change scenarios (e.g. Acosta-Galvis, 2015; Agudelo-Hz, Urbina-Cardona & Armenteras-Pascual, 2019). Despite the apparent differences between the four delimitation proposals mentioned above, there is still no consensus regarding which is the most appropriate and all of them continue to be used interchangeably and extensively to define Andean anurans, when it is in fact unclear whether it is appropriate to use such a generalized definition of Andean anurans.

Compositional dissimilarity (beta diversity) has been used as a tool for the delimitation of biogeographic units (e.g. Hernández-Camacho, 1992; Lynch, Ruiz-Carranza & Ardila-Robayo, 1997; Lynch, 1999; Morrone, 2014; Rahbek et al., 2019a). Such delimitations are frequently used to explain the patterns of distribution and diversification of species on a large scale, as well as to delimit priority conservation areas and regions of radiation and endemism (e.g. Whitehead, Bowman & Tideman, 1992; Whiting et al., 2000; Chen & Bi, 2007; Rahbek et al., 2019b). In amphibians and reptiles, compositional dissimilarity has been used to delimit biogeographic regions, model endemism zones and test the consistency of biogeographic proposals (Lynch, Ruiz-Carranza & Ardila-Robayo, 1997; Nori, Díaz Gómez & Leynaud, 2011; Vasconcelos et al., 2019). In this sense, amphibians have been used as model organisms in climate change scenarios and biogeographic regions used to model their responses against environmental changes (Chen & Bi, 2007; Acosta-Galvis, 2015; Agudelo-Hz, Urbina-Cardona & Armenteras-Pascual, 2019). There are no studies at the regional level that test the consistency of the different delimitation proposals for Andean anurans with the observed distribution of the group although, according to the delimitation proposal used, different results can be obtained in studies of species lists or the response of particular species to climate change scenarios, on which conservation management decisions are based.

Many authors have found variations in the elevations at which different ecosystems occur within the same mountain system slopes (Rahbek et al., 2019a,b). This phenomenon is explained by changes in physical variables (i.e. wind, humidity, cloudiness) among different slopes, causing units of the same mountain system to behave differently and, consequently, to differ in terms of the associated biota on each slope (Narváez-Bravo & León-Aristízabal, 2001; Kattan et al., 2004; Rahbek et al., 2019b). These differences are enough to consider each range as a biologically independent sample within the same topographic region (Kattan & Franco, 2004). The northern portion of the Andes in Colombia is considered the most bioclimatically and topographically complex of the Andean system (Kattan et al., 2004). However, the proposals for delimiting Andean anurans do not consider these variations between the entities that compose the Andes (i.e., each of the mountain ranges and the inter-Andean valleys).

We evaluated the consistency between the four delimitation proposals for Andean anurans and the current distributions of this assemblage in the Andes of Colombia by analyzing beta diversity patterns built from occurrence data. Considering that these delimitation proposals do not differ substantially in their lower limits (i.e. 500, 900 and 1000 m asl), if these models are adequate, we would expect to obtain the following three different groups of anurans along elevation gradients across the Andes of Colombia: (1) lowland anuran species (approximately between 500 and 1000 m asl), (2) Andean anuran species (at least between 1,000 m to 3000 m asl) and (3) high Andean anuran species (> 3000 m asl). In addition, the conformation of these elevation groups should be consistent or similar across different Andean slopes in Colombia.

Materials & Methods

Study area

The Colombian Andes are divided into three mountain ranges: the western, central and eastern ranges, which diverge from a high rising massif (Macizo Central Colombiano) in Colombian southwest (Irving, 1975; Kattan et al., 2004). The western range is separated from the Pacific Ocean by a narrow strip of rainforest (Kattan et al., 2004). The western and central ranges are separated by the Cauca River valley with an approximate elevation of 1000 m asl in its middle zone and elevation decrease in both northern and southern valley zones to about 200 m asl (Kattan et al., 2004). The central and eastern ranges are separated by the Magdalena River valley, which has an elevation in its middle zone of 500 m asl, decreasing in the north of the valley to approximately 80 m asl (Duellman, 1979; Hernández-Camacho, 1992; Kattan & Franco, 2004), the eastern slope of the Eastern Range is connected to the Orinoco and Amazon regions. In this study, we considered a lower elevation limit of the western slope of the western range and eastern slope of the eastern range at 300 m asl. This delimitation is lower than the one used in the proposals evaluated here; however, it remains an arbitrary delimitation used only for the practical purposes of the analysis. The inter-Andean valleys were associated with their closest mountain range, taking into account the divisions represented by the Cauca and

Magdalena Rivers. A straight line from the Serranía de San Lucas in Antioquia to the Jagua de Ibirico at the base of the Serranía del Perijá in Cesar was considered the northern limit of the Magdalena valley (Fig. 1).

Figure 1. Extent of the Colombian Andes considered in this study. Blue lines: Colombia's main rivers, Gray dashed line: extent of the Andean area considered in this work, White lines: Division of the Andean entities.

We therefore divided the Colombian Andes into the following parts (modified from Kattan & Franco, 2004): (i) Occidental Cordillera, as the western range of the Colombian Andes and the western portion of the Cauca River valley, with the extreme north of the hydrographic basin of the Patía River as its southern limit, (ii) Central Cordillera, as the portion that includes the Colombian central range, the eastern portion of the Cauca River valley, and the western portion of the Magdalena River valley, with the northern intersection of the hydrographic basins of the Patía and Caquetá Rivers as its southern limit, (iii) Oriental Cordillera, as the eastern range of the Colombian Andes including the Perijá mountain range in the northern region and the eastern portion of the Magdalena River valley, with the extreme north of hydrographic basin of the Caquetá River as its southern limit, and (iv) the southern block of the Colombian Andes, as the portion that contains the Colombian Central Massif and the "*Nudo de los Pastos*", which has the extreme north of the hydrographic basins of the Patía and Caquetá Rivers as its northern limit. All of these parts were divided into western and eastern slopes throughout the watershed of each of them, each separate part will be referred to as an "entity" (Fig. 1).

Colombian Andean Anurans species data

Anuran species were compiled from the following sources: (i) original descriptions of the species, (ii) papers published in scientific journals specifying museum codes and collection sites, (iii) short notes published in scientific journals in which the distribution range of some species is extended with the support of a museum number and, (iv) databases from the Instituto de Ciencias Naturales of the Universidad Nacional de Colombia (ICN, 2004), Instituto Alexander von Humboldt (IAvH, 2018), Universidad del Valle (Colección de Herpetología de la Universidad del Valle, 2016) and the Museo de Historia Natural of the Universidad de Caldas MNH-UCa (Serna-Botero & Ramírez-Castaño, 2017). For records in which the coordinates were imprecise or not available, an approximation to the nearest town (municipality, township or village) was made with the program Google Earth Pro (Google Earth, 2018). We followed the taxonomic classification proposed by Frost (2018). We assign the elevation to each species record using an Digital elevation model (DEM) obtained from Consortium for Spatial Information database (Jarvis et al., 2008) and Qgis (QGIS.org, 2022). All taxonomic nomenclature and species are updated to December 2018.

Data analyses

To evaluate the biotic consistency of the four proposals in terms of delimiting Andean anurans (i.e. Duellman, 1979; Lynch, 1999; Péfaur & Rivero, 2000; Navas, 2002), we analyzed compositional dissimilarity patterns throughout the defined Andean entities and across the entire region. For this, the species were grouped into 200 m elevational bands per Andean entity to build clusters based on the UPGMA method (Suzuki, Terada & Shimodaira, 2019) and the Jaccard dissimilarity index (Carvalho et al., 2013); the same procedure was performed for the entire region. Support for each cluster was evaluated by Jaccard bootstrap (1000 replicates) (Legendre & Legendre, 2012). With this information, we identified unambiguous grouping patterns reflecting the division of the anuran fauna at the elevation thresholds suggested in each proposal: 500 m asl Duellman (1979), 900 m asl Lynch (1999), 1000 m asl Péfaur and Rivero (2000), and above 3000 m asl Lynch (1999) and Navas (2002). Elevation range graphs were used to visualize: (i) the percentage of splitted species (defined as those species with a minimum distribution below a delimitation limit and maximum distribution above a delimitation limit), and (ii) the elevational distribution of the species through the elevation gradient of each entity and across the entire region. The elevation range graphs were built from the minimum and maximum elevation records for each species. All analyses were performed using R environment and the package pvclust (Suzuki, Terada & Shimodaira, 2019; R Core Team, 2021).

Results

From 34388 anuran records, 5776 unique occurrence data points were curated and incorporated into the analysis, bringing together 593 species, 72 genera and 14 families (Table 1). This study thus covered 76%, 84%, and 100% of the species, genera and families, respectively, of native anurans known from Colombia. 59% of the data was extracted from scientific papers and the remaining 49% corresponds to data available in biological databases (Table S1). The Andean entity with the highest species richness was the western slope of the Occidental Cordillera (210 spp.), followed by the eastern slope of the Oriental Cordillera (169 spp.) and the eastern slope of the Central Cordillera (168 spp.) (Table 1). We found the greatest family richness on the eastern slope of the Oriental Cordillera (13 families; Table 1).

Table 1. Total number of species, genera and families included in the analysis. The geographic definition of each Andean entity is provided in the text.

Cluster analysis at the Andean region level detected three main groups (Figure 2A). The first group held all the bands distributed between 200–2600 m asl (JI = 0.75), the second grouped all the bands between 2800–4000 m asl (JI = 0.86) and the third grouped the bands between 4200–4400 m asl (JI = 0.81).

For the Occidental Cordillera's western slope, the cluster analysis showed four main groups (Fig. 2B). The first grouped bands between 400–2600 m asl (JI = 0.60), the second grouped bands between 2800–3200 m asl (JI = 0.88), third grouped bands between 3000–4000 m asl (JI = 0.85) and finally fourth grouped bands over 4200 m asl (JI = 0.86). For Occidental Cordillera's eastern slope, the compositional dissimilarity analysis detected five main elevation groups (Fig. 2C). The first one was represented by the 400 m asl elevation band (JI = 0.62), the second grouped the 600 and 1000 m asl bands (JI = 0.62), the third contained the 800 m asl band (JI = 0.84), the fourth grouped the bands between 1200–3000 m asl (JI = 0.67), and finally the fifth contained the 3600 m asl band (JI = 0.66).

Figure 2. Detected grouping of elevation bands. A. Complete Andes region. B. Western slope of Occidental Cordillera. C. Eastern slope of Occidental Cordillera. D. Western slope of Central Cordillera. E. Eastern slope of Central Cordillera. F. Western slope of Oriental Cordillera. G. Eastern slope of Oriental Cordillera. H. Western slope of the South block of the Colombian Andes. I. Eastern slope of the South block of the Colombian Andes. Values above each group correspond to their support using Jaccard's Bootstrap (1000 replicates).

In the Central Cordillera, we also detected a different number of elevation groups between slopes. On the western slope, were detected five elevation groups (JI: 0.77–0.86; Fig. 2D): (1) 200 and 800 m asl; (2) 400–600 m asl; (3) 1000–1400 m asl; (4) 1600–3800 m asl, and (5) 4000-4200 m asl. In contrast, for the eastern slope, three groups were detected (JI: 0.70–0.78; Fig. 2E): (1) 200–1400 m asl and 2400 m asl, (2) 1600–2200 m asl and 2600–3800 m asl; (3) 4000–4400 m asl.

For the Oriental Cordillera, we detected three and two elevation groups on the western and eastern slopes, respectively. On the western slope, the first elevation group included bands between 200–1200 m asl (JI = 0.83), the second grouped the elevation bands between 1400–3800 m asl (JI = 0.87) and finally, the third grouped by the 4,000 and 4,400 m asl elevation bands (JI =0.86; Fig. 2F). For the eastern slope, the two groups where: (1) 400–2400 m asl and (2) 2600–4000 m asl (JI = 0.92 for both groups; Fig. 2G).

For the western slope of the Andean southern block, four groups were detected (JI = 0.63–0.84). The first group grouped elevation bands between 400–1600 m asl; the second grouped those of 1800–2200 m asl, and the 2800–4000 m asl bands; the third grouped the 2400 m asl band and the fourth was contained the 2,600 m asl band (Fig. 2H). For the eastern slope of the southern block, three groups were detected. The first grouped bands between 400–1200 m asl and the 1600 m asl band (JI = 0.92); the second contained the 1400 m asl band (JI =0.87) and the third grouped the elevation bands between 1800–3600 m asl (JI = 0.63; Fig. 2I).

Table 2. Percentages of species and families of Andean anurans for which distribution is splitted by the delimitation proposals evaluated in this work. The geographic definition of each Andean entity is provided in the text.

Around one third of the anuran species had distribution ranges with minimum values below 1000 meters and maximum values above this same elevation for the Complete Andes, Occidental Cordillera western slope and Oriental Cordillera eastern slope (Table 2 and Fig. 3). For the inter-Andean valleys (i.e. Occidental Cordillera eastern slope, Central Cordillera slopes and Oriental Cordillera eastern slope) and the southern block of Colombian Andes, the proportion of species with distribution ranges with minimum values below 1000 meters and maximum values above this same elevation, were less than one-fourth of the total number of species (Table 2). Only the family Ceratophryidae had elevation distribution ranges located below 500 m asl, which was the lowest limit evaluated in this study. Around 15% of total species for complete Andes had distribution ranges with minimum values below 3000 meters and maximum values above this same elevation. For the rest of the Andean entities, the percentage of species splitted by the limit of 3000 m asl varied between 0.8–23% (Table 2). There were no families with altitudinal distribution exclusive above 3000 m asl.

Figure 3. Elevation range profiles for species through Colombian Andes. A. Complete Andes region. B. Western slope of Occidental Cordillera. C. Eastern slope of Occidental Cordillera. D. Western slope of Central Cordillera. E. Eastern slope of Central Cordillera. F. Western slope of Oriental Cordillera. G. Eastern slope of Oriental Cordillera. H. Western slope of the South block of the Colombian Andes. I. Eastern slope of the South block of the Colombian Andes.

Discussion

This study is the first numerical effort to evaluate the empirical proposals to delimit the anuran fauna of the Andes in Colombia. We present an exhaustive analysis that included 76% of the species and 100% of the frog families present in the country. However, we were unable to detect patterns that were consistent with the delimitation proposals frequently used for anurans of the Andes (i.e. Duellman, 1979; Lynch, 1999; Péfaur & Rivero, 2000; Navas, 2002) and our results therefore suggest that these proposals do not reflect the natural differentiation in species composition along the vertical gradient of the mountains, and may indeed be unsuitable for directing conservation decisions for anurans. The elevation range graphs showed that the empirical proposals split the elevation distribution of around one third of the anuran species in the Colombian Andes region (i.e. 93% of the anuran families in the Colombian Andes). The remaining two thirds had their elevation distributions ranges above or below these empirical elevation limits.

Duellman (1979, p. 372) proposed to consider as Andean those species of anurans with an elevation distribution above 1,000 m asl, excluding species "primarily from lowlands" and with a peripheral distribution on the Andean slopes. At Andean level, there was not a single grouping for bands below 1000 m asl, but these were associated with bands of mid-elevation and the high mountains up to 3800 m asl (Fig. 2A). Moreover, about one third of the anuran species richness in the Andean region had its minimum elevation distribution below 1000 m asl and its maximum above this elevation. For the western slope of the Occidental Cordillera and eastern slope of the Oriental Cordillera (i.e., colombian Andes external slopes), bands below 1000 m asl grouped with mid-elevations bands (400–2600 m asl and 400–2400 m asl, respectively), contrasting with Duellman's (1979) delimitation. In addition, 31% species richness for the Occidental Cordillera western slope and 34% species richness for Oriental Cordillera eastern slope had a minimum elevation distribution of below 1000 m asl and a maximum above this elevation. This is a clear example of how the proposed elevation limits are not appropriate for at least one third of the anuran species considered to be Andean.

On the Cordillera Occidental eastern slope and Cordillera Central western slope, which are connected by Cauca river valley, the lowland grouping (<1000 m) did not seem consistent with Duellman's (1979) propposal. In the first case, the elevation bands of 400–1000 m asl were separated between groups with support greater than 60%, while in the second case, the elevation bands lower than 1000 m asl were ordered in three groups with support greater than 80% (Fig 2C-D). Moreover, the species percentages in these two groups with minimum elevation distribution below Duellman delimitation and maximum elevation distribution above the same delimitation were 11% and 9%, respectively. However, it is important to consider that the Cauca River valley has an average elevation of 1000 m asl that tends to decrease in the northern and southern regions (Kattan and Franco, 2004). Therefore, it is possible that a lower percentage of split species by Duellman's proposal in the Cauca river valley than in the Occidental Cordillera western slope may be simply an effect of the valley's topography.

The Central Cordillera eastern slope and Oriental Cordillera western slope, which are connected by Magdalena river valley. For his valley the clusters showed that for the Central Cordillera eastern slope the elevation bands lower than 1000 m asl were grouped with the bands up to 1400 m asl. In the case of the Oriental Cordillera western slope the elevation bands of below 1000 m asl were grouped with the mid-elevational bands of up to 1,200 m asl. Additionally, 24% of the species, for both Central Cordillera eastern slope and Oriental Cordillera western slope, had elevational distribution ranges splitted by Duellman's (1979) proposed delimitation. These percentages were lower than those observed in the external slopes of the Andean region, which can be explained considering that the average elevation of the Magdalena valley is 500 m asl and tends to decrease across its northern region (Kattan & Franco, 2004). Therefore, it is possible that a lower percentage of split species by Duellman's proposal in the Magdalena river valley than in the Oriental Cordillera eastern slope may be simply an effect of the valley's topography.

In the case of the southern block of the Colombian Andes, the clusters showed that <1000 m asl elevation bands grouped with mid-range elevation bands up to 1600 m asl. In addition, the species percentage whose elevation distribution was split by Duellman's (1979) proposal were between 7–12%, similar to observed in the inter-Andean valleys. Both the band elevation clusters and the species percentage should be interpreted carefully since the southern block of the Colombian Andes was the entity with the lowest species number and elevation bands, even so, despite the low percentage of species split by the Duellman's (1979) proposal and the low representation within the elevation gradient, the "lowland" bands (<1000) and "medium-high lands" (>1000) do not behave as a distinct groups.

Based on anurans of the ancient genus *Eleutherodactylus* (Currently reassigned between the families Craugastoridae, Eleutherodactylidae and Strabomantidae) of the Colombian Occidental Cordillera, Lynch (1999, p. 152) proposed that the distribution of the anurofauna could be divided in five different categories, being the lower limit of the Andean species at 900 m asl. This division was based on the hypothesis that anurans of this group (and other families such as the Centrolenidae family) were distributed across equivalent bands on the Andean slopes. Our results suggest that elevation bands lower than 900 m do not constitute a clearly distinct group of species, with the exception of the Cauca river valley components due to its topographical features (as discussed in the previous lines). Moreover, our data suggest that the elevation distributional ranges of the species vary widely between Andean components across different families in the region. Thus, the expected species separation if the division proposed by Lynch (1999) were adequate is not supported by our data.

Péfaur and Rivero (2000, p. 45) proposed that species with an elevation distribution above 500 m asl could be considered Andean, and those with a distribution below this elevation could be considered as foothill species. For the Colombian Andes region, we found that elevation bands lower than 500 m asl do not constitute a differentiated group, but were associated with elevational bands of medium and higher elevations (see above). The elevation range graphs show that around 30% of the species on the external slopes of the Andean region had minimum elevation distributions below 500 m asl and maximum distribution above same elevation. For the inter-Andean Cauca River valley, the percentage of species with a distribution splitted by the delimitation of Péfaur and Rivero varied between 3–15%, possibly due to valley's topography features (Kattan & Franco, 2004). For the inter-Andean Magdalena River valley, with an average elevation of 500 m asl, the percentage of species with minimum distribution below 500 m asl and above this elevation varied between 22–25%. Cluster analysis showed that lowland elevation bands (≤1000 m asl) were associated with mid-elevation and highland bands (≥1400 m) in most cases. None of the groupings obtained are consistent with the groupings expected if the delimitation of Péfaur and Rivero (2000) were adequate, which suggests that the proposed historical delimitations do not reflect the natural elevational distribution patterns of frogs in the region.

In the case of the upper delimitation of the Andes (Lynch, 1999; Navas, 2002), it is observed for complete Andes that there were groups that differentiate the elevation bands above 2,800 m asl. However, at the slope level, this grouping did not behave consistently across all of the slopes. Only in the external slopes (Cordillera Occidental western slope and Cordillera Oriental eastern slope) the clustering is different from that observed for the complete Andes, and there were differentiation of elevation bands above 2600–2800 m asl. For the rest slopes, this grouping was not consistent, and just bands above 3600 m asl were clearly differentiated. It is important to highlight that, for all cases, more than 75% of the evaluated anuran species are distributed above or below the 3000 m asl elevation limit.

The results obtained from the elevation range graphs showed that all of the anuran families in the Colombian Andes are distributed across the entire elevation gradient (except for Ceratophryidae). Variation in the elevation distribution of species was more or less constant among families present in the region (Table 2). These patterns could be explained by the age of the Andean mountain range, which began to emerge during the early Miocene (~ 23 MA) and finally consolidated in Colombia in the Pliocene and Plestoic (~ 2.5-2 MA), when the mountains reached their current or slightly higher elevations (Hernández-Camacho, 1992; Guariguata & Kattán, 2002). On the other hand, the most recent anuran families diverged during the early Cenozoic in the middle of the Paleogene up to ~ 50 MA (Vitt & Caldwell, 2014) and the uprising of the Colombian Andes is therefore a relatively recent phenomenon compared to the history of anuran diversification, which could be the reason why most of the Colombian anuran families are distributed along the elevation gradient of the Andes. Moreover, authors such as Navas (2002) and Acosta-Galvis (2015) have suggested that the success of anurans in the Andes mountain range reflects physiological plasticity within species and that it seems to be a characteristic of this group across different families. Thus, the plasticity of anuran species could be another explanation for why most of the families are represented along the elevation gradients of the different Andean slopes.

Conclusions

In general, it was observed that the different empirical delimitations proposed for anurans of the Andes did not coincide with the elevational band groups detected in this study. The elevation range graphs showed that around one third of anuran species richness of the region of the colombian Andes had a minimum elevation distribution above delimitation proposals for the lower limit and a maximum elevation distribution above these delimitations, while less than a quarter had elevation distribution below a upper limit delimitation and a maximum elevational distribution above this limit. Our analysis suggests that the delimitation of lower limit proposals for Andean anurans are not applicable in the Colombian Andes, and that the upper limit proposal should be used with caution since it varies among Andean entities. We conclude that providing an absolute definition for “Andean anurans” based only on elevation delimitations is not informative, because the elevation distribution ranges of anuran species do not behave discretely but are distributed continuously along the entire elevation gradient. Moreover, it is important to highlight that inter-Andean valleys do not behave as distinct entities from the mountain ranges, and should therefore not be excluded in future studies of species lists or conservation. We propose three useful guidelines when conducting any studies with anurans of the Colombian Andes: (i) do not exclude inter Andean valleys, (ii) the distribution of anurans in Colombian Andes should be considered across their full distributional range, and not in a segmented way using arbitrary thresholds, and (iii) defining “Andean anurans” based only on an elevation delimitation is uninformative, and additional criteria such as natural history or phylogenetic relationships should be considered in order to make decisions regarding the limits of the study. Finally, although an absolute definition for "Andean anurans" appears not to be generalizable, it is possible to consider that Andean anuran species are simply those that occur in the Andes in a broad sense, which makes it necessary to consider what classification approach, in a biogeographic context, agrees with the observed distributional patterns of the anurans of the Andes.

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Table 1(on next page)

Total number of species, genera and families included in the analysis.

The geographic definition of each Andean entity is provided in the text.

Table 1. Total number of species, genera and families included in the analysis. The geographic definition of each Andean entity is provided in the text.

Andean entity	Species number	Genera number	Family number
CA	593	71	14
OCW	210	40	11
OCE	121	32	11
CCW	136	39	12
CCE	168	44	12
ORW	129	42	12
ORE	169	49	13
SBE	95	31	10
SBE	102	32	11

Notes. CA: Complete Andes, OCW: Occidental Cordillera, western slope, OCE: Occidental Cordillera eastern slope, CCW: Central Cordillera western slope, CCE: Central cordillera eastern slope, ORW: Oriental Cordillera western slope, ORE: Oriental Cordillera eastern slope, SBW: Andean south block western slope, SBE: Andean south block eastern slope.

Table 2(on next page)

Percentages of species and families of Andean anurans for which distribution is splitted by the delimitation proposals evaluated in this work.

The geographic definition of each Andean entity is provided in the text.

Table 2. Percentages of species and families of Andean anurans for which distribution is splitted by the delimitation proposals evaluated in this work. The geographic definition of each Andean entity is provided in the text.

Andean entity	Species distribution splitted by delimitation proposal							
	Duellman (1979) / 1000 m asl		Lynch(1999) / 900 m asl		Préfaul and Rivero (2000) / 500 m asl		Navas (2002) / 4000 m asl	
	Species (%)	Families (%)	Species (%)	Families (%)	Species (%)	Families (%)	Species %	Families %
CA	30	93	30	93	29	93	15	50
OCW	31	100	32	100	31	91	1	9
OCE	13	64	11	55	15	45	0.8	9
CCW	9	58	4	42	3	25	23	50
CCE	24	92	24	100	25	100	14	42
ORW	24	75	23	92	22	92	16	50
ORE	34	85	34	85	34	85	9	31

SBW	7	50	7	50	8	60	9	30
SBE	12	55	13	55	15	72	12	18

Notes. CA: Complete Andes, OCW: Occidental Cordillera, western slope, OCE: Occidental Cordillera eastern slope, CCW: Central Cordillera western slope, CCE: Central cordillera eastern slope, ORW: Oriental Cordillera western slope, ORE: Oriental Cordillera eastern slope, SBW: Andean south block western slope, SBE: Andean south block eastern slope.

Figure 1

Extent of the Colombian Andes considered in this study.

Blue lines: Colombia's main rivers, Gray dashed line: extent of the Andean area considered in this work, White lines: Division of the Andean entities.

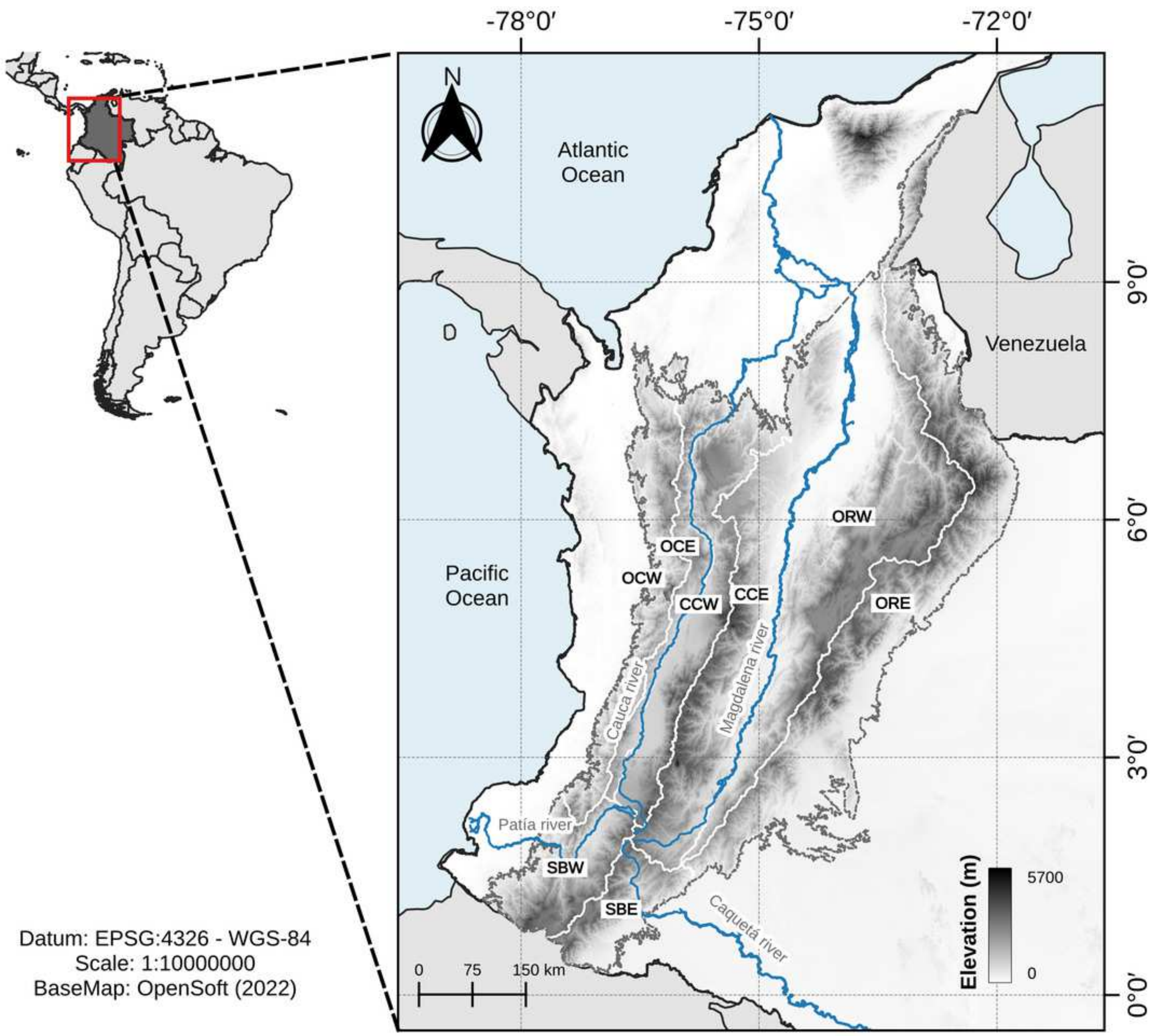

Figure 2

Detected grouping of elevation bands.

(A) Complete Andes region. (B) Western slope of Occidental Cordillera. (C) Eastern slope of Occidental Cordillera. (D) Western slope of Central Cordillera. E. Eastern slope of Central Cordillera. (F) Western slope of Oriental Cordillera. (G) Eastern slope of Oriental Cordillera. (H) Western slope of the South block of the Colombian Andes. (I) Eastern slope of the South block of the Colombian Andes. Values above each group correspond to their support using Jaccard's Bootstrap (1000 replicates).

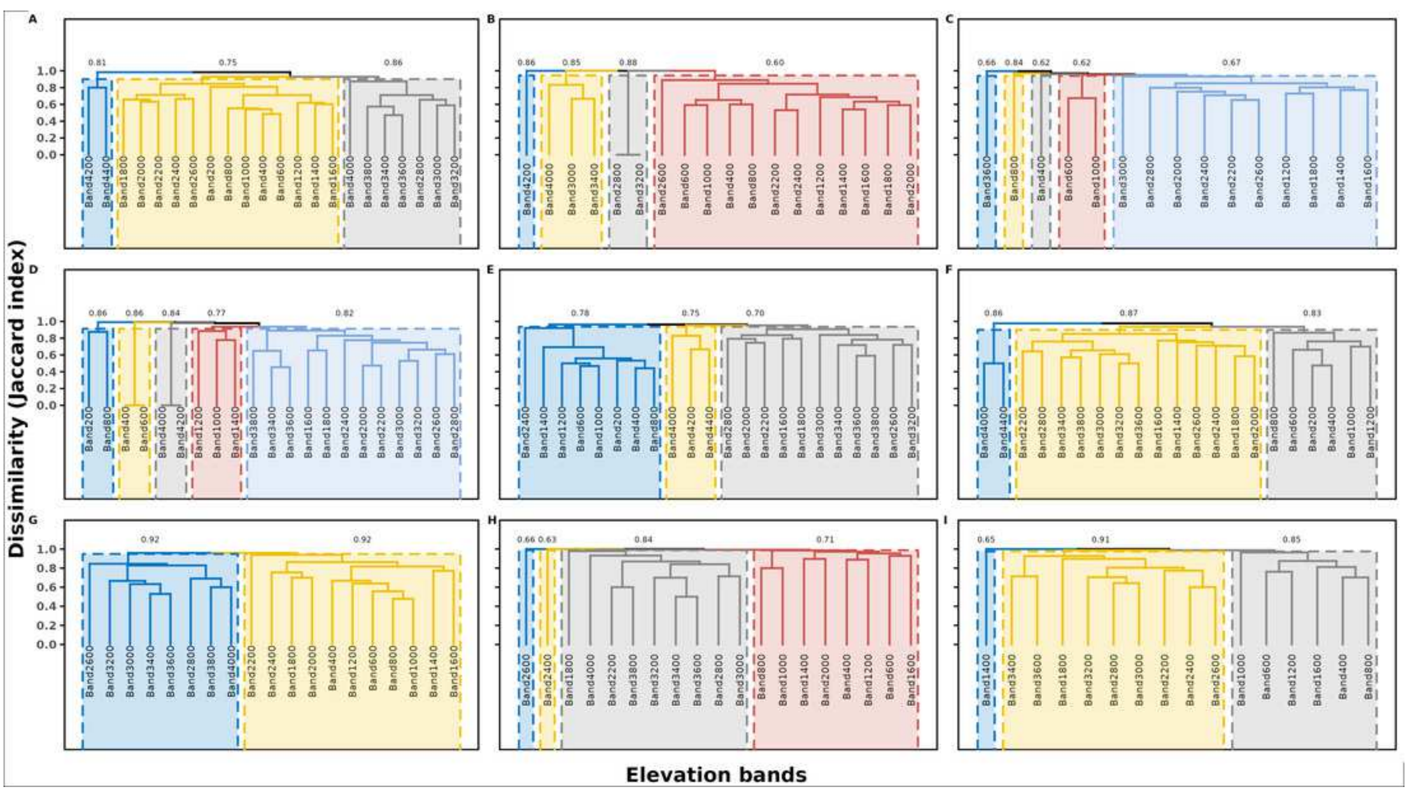

Figure 3

Elevation range profiles for species through Colombian Andes.

(A) Complete Andes region. (B) Western slope of Occidental Cordillera. (C) Eastern slope of Occidental Cordillera. (D) Western slope of Central Cordillera. (E) Eastern slope of Central Cordillera. (F) Western slope of Oriental Cordillera. (G) Eastern slope of Oriental Cordillera. (H) Western slope of the South block of the Colombian Andes. (I) Eastern slope of the South block of the Colombian Andes.