THE NORTHERN ANDES: AN EVENT-BASED BIOGEOGRAPHIC RECONSTRUCTION

El Norte de los Andes: una reconstrucción biogeográfica basada en eventos

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Trabajo de grado presentado como requisito para optar al título de Bióloga

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Ph.D en ciencias biológicas

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PALABRAS CLAVE: Dispersión, DIVA, Máxima Vicarianza, Neotrópico, biota Nor-Andina, Norte de los Andes, vicarianza

CONTENIDO: El Norte de los Andes comprende las zonas de alta montaña desde el Norte de Colombia y Venezuela hasta el Norte de Perú. La gran diversidad de esta porción de los Andes ha sido estudiada en base a pocos grupos o desde perspectivas narrativas. Con el fin de elucidar las relaciones históricas de las áreas de endemismo del Norte de los Ande, se reunieron a partir de la literatura 37 filogenias pertenecientes a diferentes taxones distribuidas en 19 áreas Neotropicales. El grupo de áreas internas está compuesto por la Cordillera de Mérida, la Cordillera oriental de Colombia, el Complejo de cordilleras central y occidental de Colombia, el Sur de Colombia, el Norte de Ecuador, el Centro y Sur de Ecuador y el Norte de Perú. Se realizó un análisis biogeográfico, en donde se identificaron los patrones generales de áreas, los eventos más comunes, y se evaluó su significancia. Adicionalmente, mediante un análisis de re-muestreo se evaluó la estabilidad de la reconstrucción general. Los resultados soportan la idea de un origen híbrido de la biota del Norte de los andes, ya que incluye componentes de áreas como el Centro de los Andes y la Amazonia. Tres relaciones de áreas sugieren el origen híbrido: (1) La relación del Sur de Colombia con un gran grupo de áreas Neotropicales, (2) el Norte de Perú está estrechamente relacionado con la Amazonia, y (3) el Centro de los Andes esta dentro del grupo Andino, conformado por los Andes Ecuatorianos, Colombianos y Venezolanos. Dentro del grupo Andino las depresiones geológicas parecen haber jugado un papel importante en la diversificación de la biota, por ejemplo, la depresión del Táchira en Venezuela en la separación de la Cordillera de Mérida, el Valle del Magdalena en la diversificación en las cordilleras de Colombia y el Valle Interandino en Ecuador.

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[1] Proyecto de grado.

[**] Facultad: Ciencias. Escuela: Biología. Director: Daniel Rafael Miranda Esquivel.

ABSTRACT

TITLE: The Northern Andes: an event-based biogeographic reconstruction[1]

AUTHOR: Erika Jazmín Parada-Vargas[**]

KEYWORDS: Dispersal, DIVA, event-based treefitting, Maximum Vicariance, Neotropic, North Andean biota, North Andes, vicariance.

ABSTRACT

The Northern-Andes ranges from the high mountains in northern Colombia and Venezuela to the mountains in northern Peru. This portion of the Andes harbours a high diversity that has been studied based on few groups or a narrative perspective. In order to elucidate the historical relationships among the North-Andean areas, we performed a biogeographic analysis based on events. 37 phylogenies from different taxa ranged in 19 Neotropical areas were taken from the literature. The set of in-group areas is composed by the Merida Cordillera (CM), the Eastern Cordillera of Colombia (CE), the Western and Central Cordilleras of Colombia (CW), the South of Colombia (SC), the North of Ecuador (NE), Central and South Ecuador (SE) and the North of Peru (NP). We identified the general patterns of area relationships, the most common events, and evaluated their significance. Additionally, we evaluated the stability of the general reconstructions using a resampling test. Our results support the idea of a composite origin for the North Andean biota, which includes components from areas as the Central Andes and Amazonia. Three area relationships suggest the composite origin: (1) the relationship of the Macizo Colombiano with a majour group of Neotropical areas, (2) the North of Peru is more closely related to Amazonia and (3) the Central Andes is clustered together with a group conformed by the Ecuadorian, Colombian and Venezuelan Andes. In the group conformed by some North Andean areas of endemism and the Central Andes, tectonic depressions seem to have played an important role on the biotic diversification, for example, the Táchira depression in the split of the Merida Cordillera, the Magdalena Valley in the diversification of Colombian biotas, and the Valle Interandino in the diversification of the Ecuadorian biota.

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[1] Bachelor's thesis.

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INTRODUCTION

The Andean Cordillera extends for ~7000 km along the western coast of South America. According to Cabrera and Willink (1973), all the high mountains of the Andean mountain range, from Venezuela to Tierra del Fuego in Argentina, belong to the High-Andean Province and the Paramo Province. From a geological point of view, the Andes are not a single entity, and the timing of uplift most likely varied from north to south and from east to west (Gregory-Wodzicki, 2000). The Andean Cordillera reached its current configuration between the late Miocene and the Holocene, and "the late Miocene marked the start of a paroxysm in the uplift of the north-eastern Andes and represents the most dynamic episode during the entire Miocene" (Hoorn et al., 1995, p. 239). These important geological changes are reflected in the highly diverse Andean biota (Dinerstein *et al*., 1995; Palminteri *et al*., 2001; Albert *et al*., 2006; Brumfield & Edwards, 2007; Alzate *et al*., 2008; Elias *et al*., 2009), which varies along and across the continent and is not the by-product of a single history (Crisci *et al*., 1991; Katinas *et al*., 1999). The Andean cordillera is divided into three domains (Ganser, 1973; Morain, 1984; Taylor, 1991), which, in general, coincide with the volcanic zones. The three Andean domains are: the Southern, the Central, and the Northern. These zones reflect the changing plate geometry along the pacific margin (Gregory-Wodzicki, 2000).

The Northern Andes

The Northern Andes range from the Mérida Cordillera in Venezuela to southern Ecuador, where the transition between Central and Northern Andes is the Amotape-Huancabamba zone (Berry, 1982; Weigend, 2002). According to Morrone, the Northern Andes belong to the Paramo province (2002), which in turn is contained within the South American transition zone (2006). Different authors have assessed the North Andean patterns of endemism based on few groups' distributions (e.g. Cracraft, 1985; Morrone, 1994c; Quijano-Abril *et al*., 2006; Sánchez-González *et al*., 2008). In contrast, Bolivar-Leguizamón & Miranda-Esquivel (pers comm.) defined seven areas of endemism for the Northern Andes based on approximately 26,000 species (the largest data set available for the domain) and found two new endemic regions in the Colombian Andes, while the other areas were congruent with previous studies (Haffer, 1969; Brown, 1979; Cracraft, 1985; Morrone & Urtubey, 1997; Quijano-Abril *et al*., 2006; Sánchez-González *et al*., 2008). These seven areas are: 1) Sierra Nevada of Santa Marta, an isolated mountain range located in the Caribbean coast of Colombia. 2) Serranía of Mérida, located in the Venezuelan Andes, and separated from the Eastern Cordillera of Colombia by the Táchira depression. 3) Colombian Eastern Andes, this area goes from the Táchira depression to the Paramo de Sumapaz. 4) Central-Western cordilleras Complex, this area comprises the Cauca river valley and limits in the north with the Nudo de Paramillo and in the south with the Macizo Colombiano; in the easternmost part it is separated from the Eastern cordillera by the Magdalena valley. 5) Northern Ecuador, this area spreads from the Southwest Colombia (2° 15’ N) to Central Ecuador (1° 30’ S) and corresponds mainly to the Macizo Colombiano; Northern Ecuador has two nested areas of endemism, one that corresponds to the southernmost part of Colombian Andes (1.5'- 0.75'N) and a second that corresponds to the northernmost part of Ecuador (0° 75' N - 0° 75' S). 6) Southern Ecuador, this area is placed between the Central Ecuador (1° 30’ S) and the northernmost part of Peru (5° 45' S). And finally, 7) Northern Peru, defined by different authors as the “transitional zone” between the Northern and the Central Andes (Berry, 1982; Morrone and Urtubey, 1997; Weigend, 2002), it is comprised between 6° 30' S to 10° S.

Historical Biogeography

The basic idea in historical biogeography is that general patterns of area relationships (i.e. general area cladograms) may be elucidated by comparing monophyletic groups and their distributional data, that is, taxon-area cladograms (Rosen, 1978; Platnick & Nelson, 1978; Wiley, 1980; 1988; Page, 1994b; Sanmartín & Ronquist, 2002). Pattern-based methods search for general pattern(s) of area relationship(s), allegedly, without making any assumptions about evolutionary processes (Ronquist, 2003). As such, pattern-based methods do not have an explicit model, which hampers a clear event evaluation and makes necessary the use of *ad hoc* procedures to handle with incongruence between the general area cladogram and the taxon-area cladograms (Wiley, 1988; Page, 1994b; Ronquist, 1997, 1998b, Sanmartín *et al*., 2001; Sanmartín & Ronquist, 2002). Event-based methods explicitly derive from models so the optimal reconstruction specifies the biogeographic events responsible for biotic distributions and no *a posteriori* interpretation is necessary (Ronquist, 1998a; Sanmartín *et al*., 2001, 2007; Sanmartín & Ronquist, 2002). Most event-based methods consider four events or processes: vicariance, allopatric speciation in response to a general dispersal barrier (i.e. a mountain uplifting); duplication, allopatric speciation due, for example, a temporary dispersal barrier affecting only a single taxon; extinction, when a taxon disappears from an area; and dispersal, speciation due to colonisation of a new area (Page, 1994b; Sanmartín & Ronquist, 2002; Ronquist, 2003; Sanmartín *et al*., 2007). Tree fitting is an event-based approach which has as objective to find the general reconstruction with the minimum cost (Ronquist, 2003). As the solution tree fitting finds depends on the cost values of each event, and it is not possible to estimate such values directly from the data set, different cost assignments can be combined in different ways in order to evaluate different historical scenarios (Ronquist, 2003; Sanmartín *et al*., 2007).

Common biogeographic models include: Maximum Vicariance (Page, 1994b; Ronquist, 1998a, 1998b), which optimises cospeciation events; Reconciliation (Page, 1994a), which prohibits a relevant event like dispersion; and Ronquist's model (i.e. default set of costs in the program TreeFitter 1.3; Ronquist, 2002, 2003), in which the two events that generate phylogenetically conserved patterns, vicariance and duplication, are maximised over the other two events, extinction and dispersion, allowing the researcher to find phylogenetically constrained patterns (Ronquist & Nylin, 1990; Sanmartín & Ronquist, 2002; Ronquist, 2003; Sanmartín et al., 2007).

Previous biogeographic studies in the Northern Andes

Alzate *et al*. (2008) postulated that the Andean *Bomarea* (Alstroemeriaceae) biota has been fragmented by vicariant events due to the uplift of the Andean mountain chain. Elias *et al*. (2009) showed that the Andes act as a physical barrier for the genera *Napeogenes* and *Ithomia*. Based on the genus *Proctoporus* (Gymnophthalmidae), Doan (2003) showed a South-to-North speciation pattern along the Andes, even though a more complex pattern(s) in the northern region (Ecuador, Colombia and Venezuela) was observed, suggesting a dynamic model that includes both vicariance and dispersal across barriers. Brumfield & Edwards (2007), based on phylogenetic and distributional data from the genus *Thamnophilus* (Passeriformes), concluded that although the initial Andean uplift resulted in the diversification of some trans- and cis- Andean taxa, the subsequent climatic fluctuations and/or marine transgressions that periodically interrupted and reconnected dispersal corridors around the Northern Andes also played an important role. Using the areas of endemism defined by Morrone (1994c), a pattern-based study by Morrone & Urtubey (1997) concluded that the North Andes is not a single unit and that southern Ecuador could be more related to the Central Andes than to the Northern Andes. The idea of a composite origin for the North Andean biota is in accordance with Quijano-Abril's *et al*. (2007) finding of a connection between the Andean region and both the Caribbean and Amazonian subregions.

In general, previous studies in the Northern Andes have been focused on its role as barrier (Brumfield & Edwards, 2007), or in the biogeographical history of one taxon or few taxa (Vuilleumier, 1968; Fjeldså, 1995; Morrone & Urtubey, 1997; Doan 2003; Weir, 2006; Quijano-Abril *et al*., 2007; Alzate *et al*., 2008; Elias *et al*., 2009; Wiens *et al*.,2009). From an event-based perspective, our main goal was to elucidate the historical relationships of the North Andean areas of endemism and to identify the most influential biogeographic events based on several groups of taxa.

MATERIAL AND METHODS

Compilation and data handling

We used phylogenies from different groups, all with species, “subspecies”, or haplotypes as terminals, following Sanmartín *et al*. (2001) criteria. Thus, for each phylogeny: (a) the group must be monophyletic and must exhibit predominantly North Andean distribution; the organisms present in external areas are useful to test whether the origin of the Northern Andes is unique. (b) It must have at least three terminals occurring in the ingroup areas of endemism (see fig 1). (c) It must comprise at least three tips. (d) It cannot have more than one tetratomy or more than two trichotomies. Additionally, we used two criteria of our own: (1) when terminals were haplotypes (not species), constituted a monophyletic group, and belonged to the same locality they were reduced (i.e. collapsed) into a single terminal. (2) In order to avoid dubious phylogenetic signals, trees product of majority rule consensus (see Sharkey & Leathers, 2001; Pickett & Randle, 2005; Goloboff & Pol, 2005; Yang, 2008) were reanalysed using parsimony, and the results were summarised by a strict consensus. The selected groups, references, and areagrams are listed in Table 1. We ended up with 37 phylogenies representing 28 groups of animals and seven groups of plants.

Areas of endemism

Although there are previous approaches to the Northern Andes' areas of endemism (Darlington, 1957; Cracraft, 1985; Morrone, 1994c; Morrone, 2001; Quijano-Abril *et al*., 2006; Sánchez-Gonzáles *et al*., 2008), in this study we used a modification of the areas of endemism identified by Bolivar-Leguizamón & Miranda-Esquivel (pers comm.). We preferred this study because its large data set, and its methodological approach (Szumik *et al*., 2002; Szumik & Goloboff, 2004), as implemented in NDM (Goloboff, 2005), which outperforms other techniques in the identification of areas of endemism (Carine *et al*., 2008).

Bolivar-Leguizamón & Miranda-Esquivel (pers comm.) identified seven areas of endemism: the Sierrra Nevada of Santa Marta (SN), the Serrania of Merida (MC), Eastern Colombian Andes (EC), Central-West cordilleras Complex (CWC), Northern Ecuador (NE), Southern Ecuado (SE), and Northern Peru (NP). Intending to include the distributional information at hand that did not correspond to any of the aforementioned areas of endemism, the Macizo Colombiano (MZC) at Southern Colombia was also included in the areas used for this analysis. Additionally, we used ten external areas in order to evaluated if the North Andes is a biogeographic unit; those areas were Central America (CAM), Caribe (CAB), Choco (CHO), Orinoquia (OQ), Amazonia (AZ), Central Andes (CA), Chaco (CHA), North-East Brazil (NEB), Serra do Mar (SDM) and Southern Andes (SA). All areas are shown in Figure 1.

Biogeographic analyses

Terminals

We generated all possible dichotomous resolutions of polytomous cladograms. Each alternative dichotomous cladogram was weighted such that the sum of the alternatives corresponded to the value of the single fully resolved cladogram (Sanmartín *et al*., 2001). In all tree fitting analyses we treated widespread taxa with the recent option. Sanmartín *et al*. (2001) showed that this option has advantages over the free and ancient options in finding common patterns and inferring vicariant events (See also Sanmartín & Ronquist, 2002).

Historical relationships between the North Andean areas.

To find a general biogeographic pattern for the North Andes, we searched for the best general area cladogram using the parsimony-based tree fitting approach, as is implemented in the program TreeFitter 1.3 (Ronquist, 2002), under the default (Ronquist, 2002; Ronquist, 2003) and Maximum Vicariance costs values (Page, 1994b; Ronquist, 1998a, 1998b). We conducted heuristic searches including all areas, holding 100 trees in each step and using a neighbourhood of 30 nodes.

Dispersal-Vicariance analysis

We conducted a Dispersal-Vicariance analysis, as is implemented in DIVA 1.2 (Ronquist, 1996, 1997), to calculate the rate of the most frequent dispersal events among the areas. Because the program allows a maximum of 15 areas and our initial data set consisted of 18 areas, based on the default set of costs' results from the tree fitting analysis we reduced three pairs of areas into three single areas: (orinoquia, Southern Andes), (Choco, Caribe), and (Serra do mar, Chaco). Because DIVA's result summary only allows including the first eight areas in the data set, we performed runs handling the areas in three different ways: 1) we treated all external areas (hereafter ExA) as a single one in order to evaluate which were the North Andean areas with more influence of external biota, and which areas presented more dispersion out of the Northern Andes. 2) We treated all ingroup areas (hereafter IgA) as a single area in order to evaluate which external area has contributed more to the North Andean biota and which external areas have received more North Andean biota. 3) We considered external areas individually and did four summaries including: the eight ingroup areas, Central Andes (CA), Amazonia (AZ), and Choco and Caribbean (CHO/CAB). We chose CA and AZ because they are the external areas with a closer relationship to the Northern Andes' areas of endemism (see tree fitting results), and CHO/CAB because its geographic closeness. We merged the four summaries into one list, organised it from most to least frequent dispersal events, and calculated the percentage based on the total number of dispersions. We did all searches using an heuristic strategy holding 100 trees. The ‘maxareas’ option of the command optimize impose a maximum number of unit areas allowed in ancestral distributions (Sanmartín, 2003; Mico *et al*., 2008). We evaluated different values of ‘maxareas’ and preferred the answer obtained when we set the value to equal the number of areas present in the distribution of each clade, because this value minimised the number of dispersions and increased the number of vicariance events.

Significance analysis

With the purpose of evaluating if the patterns found in the searches were constrained to the phylogenetic information in the data set, we performed a permutation test (Ronquist, 2002) by random shuffling of the organism's distributions 1000 times. If the randomised data had a total cost equal or lower than the observed cost less than 5% of the times, the reconstruction was considered significant. Additionally, we calculated the frequency and significance of the events necessary to explain the reconstructions.

Stability analysis

For any hypothesis of area relationships, future stability is a desirable property. Data perturbations (e.g., jackknifing) could be interpreted as stability measures, because they derive from changing the structure of the original dataset and finding the elements that persist under such changes (Hovenkamp, 2009). So, in order to assess the stability of the reconstructions (Siddall, 1995; Hovenkamp, 2009) obtained with the default set of costs, we submitted the data set to resampling permutations. We did 25 pseudoreplicates by randomly removing 13 areagrams from the original data set and then we analysed each pseudoreplicate to obtain its general reconstruction. Then, we counted the number of times each group in the original reconstruction was recovered in the pseudoreplicates, and only those groups found more than 50% of the times were considered strong (for stability and support in phylogeny reconstruction see Farris *et al*., 1996; Farris, 1998; Goloboff *et al*., 2003).

RESULTS

We found 5001 significant reconstructions with the Maximum Vicariance set of costs, while the default set of costs generated 15 significant reconstructions. Figure 2 shows the strict consensus of the biogeographic reconstructions for the two models used. (a) Shows the reconstruction under the default set of costs and (b) the reconstruction under the Maximum Vicariance set of costs. These results show the North Andean composite origin, since some of its areas are more related to external areas than to other North Andean areas of endemism. It is worth mentioning that because this study was focused on the Northern Andes, relationships among external areas were based on lesser quality data, and thus were misleading in some cases (e.g., node L).

The permutations of the terminals' associations showed no significant vicariant events in the Maximum Vicariance reconstruction, but with the default set of costs four vicariant events involving North Andean areas were significant; these events are summarized in figure 2b (square marks). The resampling test recovered three most stable groups associations (fig 2b, circle marks), one involving external areas and two of them involving North Andean areas of endemism; those associations are EC- CWC and NE- SE.

In the tree fitting analyses all dispersal events were neither significant nor considerably frequent, and in the DIVA analysis no dispersal event between single areas surpassed the 10% of the total frequency of dispersal events. The most frequent event was (IgA -> CA) followed by (IgA -> CHO/CAB) and (IgA -> AZ) with percentages of 9.98%, 9.32% and 6.37% respectively. These results suggest that dispersal has not contributed importantly in shaping current North Andean distributional patterns, as have been alleged by some authors (e.g. Fjeldså, 1995; Heindl & Schuchmann, 1998; Doan, 2003; Weir, 2006; Wiens *et al*., 2009). This analysis also suggests that although a flow between Central and Northern Andes exists, there is not a dispersion-based history between the regions. (DIVA dispersion results are summarized on table 2).

In the DIVA analysis, the most frequent event involving at least two areas was (NE,ExA)-SE. In the summaries including the Central Andes and the Amazonia this vicariant event was recovered with each area (i.e (NE,AZ)-SE and (NE,CA)-SE); this finding suggests that the external areas could be Amazonia and Central Andes. The DIVA analysis showed the relationship between Ecuadorian areas as the result of a vicariant event rather than a dispersal event.

DISCUSSION

The biogeographic patterns we recovered in the tree fitting analyses indicate that the Northern Andes' areas of endemism do not conform a biogeographic unit. This scenario is congruent with previous studies (Morrone & Urtubey, 1997; Porzecanski & Cracraft, 2005; Hughes & Eastwood, 2006) which have evidenced a close relationship between Northern and Central Andes. The DIVA analysis showed that the North Andean biota presents a predominant flow to external areas (Weir, 2006), especially to the Central Andes, Amazonia, and Choco/Caribbean, rather than dispersion from external areas to the Northern Andes (Table 2). This result agrees with the idea that the North Andean biota has a Paleo-Andean origin, and not a lowland origin (Navas, 2006; Hedges *et al*., 2008; Elias *et al*., 2009)

As is expected with some data sets, the analysis based on Maximum Vicariance costs yielded a poorly resolved general hierarchical pattern (see Ronquist, 2003), and the vicariant events were not significant. We recovered a group in the Maximum Vicariance strict consensus (fig 2b) that joins North Ecuador with the Macizo Colombiano. The DIVA analysis also showed a flow in both directions between MZC and NE. This relationship may be explained by the finding that the southernmost part of the Macizo Colombiano and the northernmost part of Ecuador have been included in a unique area of endemism (Morrone 1994c; Morrone & Urtubey, 1997; Bolivar-Leguizamón & Miranda-Esquivel, pers comm.). Furthermore, Vuilleumier (1968) placed the Nariño (South Colombia) biota closer to the Ecuadorian biota than to the Eastern and Central Colombian cordilleras; he also recognised a well-marked morphological gap between north and south Colombian species. The Macizo Colombiano in the analysis under the default set of costs appeared as the sister area of a group of Andean and non-Andean areas (fig 2a, node A); this relationship could be the outcome of an area where remnant fragments of different ancient biotas have been in contact (Alzate *et al*., 2008; see also Berry, 1982).

In the tree fitting analysis based on the default set of costs, we found that five North Andean areas are grouped together with Central Andes and thus behave as a single unit (fig 2a, node D); also, this group of areas has a relationship with a group that contains Amazonia and the North of Peru (fig 2a, node C). The general pattern recovered was significant ($p < 0.05$), as well as four vicariant events (figure 2a, nodes B-D). Nodes A and B (figure 2a) on this reconstruction showed a closer relationship between the Andes (North and Central) and Amazonia, instead of areas to which the Andes has been traditionally related to (e.g. Caribbean and Choco; Quijano-Abril *et al*., 2006). The reactivation of the uplifting in Central Andes ~20 Myr (Yuan *et al*., 2000; Garzione *et al*., 2008) might have marked the split of the Andes from the K group. The appearance of the Colombian Eastern Cordillera as a continuous range at ~11.8 Myr marked the shift of the sediments through the Amazonas River (Hoorn *et al*., 1995), and could have caused the vicariance among Amazonian and Andean areas (fig 2a, node B). Our result joins Amazonia and Northern Peru in a biogeographic unit (fig 2a, node J). This scenario is in accordance with Berry's idea (1923; see also Gregory-Wodzicki 2000) that the flora of Northern Peru was tropical in nature. The current lack of similarity in terms of biotic composition between Amazonia and Northern Peru may be attributed to a widespread compressive deformation in Peruvian Andes between 7 and 9 Myr (Rousse *et al*., 2005; Wesselingh & Salo, 2006). Alternatively, Elias *et al*. (2009) attribute the *Ithomia* and *Napeogenes* lineages, present in the Amazonia, to dispersions from the Andes ~7 Myr when middle Miocene marine incursions stopped. This idea matches DIVA’s result that showed dispersions from the North Andes to the Amazonia, especially from South Ecuador.

The Central Andes and five ingroup areas MC (Mérida Cordillera), NE (North Ecuador), SE (South Ecuador), CWC (Western and Central Colombian cordilleras), and EC (Eastern Colombian Cordillera) conform the group C (fig 2a). This biogeographic unit matches the generalized tracks found by Alzate *et al*. (2008). These authors argued that such tracks represent the ancestral distribution of the genus *Bomarea*. The group C also supports the idea that most highland Anurans and some Lepidoptera came from an ancestral biota which lived at moderate tropical elevations during middle Miocene and suffered vicariance due to the irregular accretion of the mountain chain (Navas, 2006; Hedges *et al*., 2008; Elias *et al*., 2009). Thus, we could place the vicariant event that originated this biota in the middle-late Miocene. In discordance with the idea presented above, Ribas *et al*. (2007), based on DNA information of the genus *Pionus*, placed the common origin of the montane biotas around 4.4 Myr, while Hughes & Eastwood (2006) placed the radiation of the Andean *Lupinus* ~1.5 Myr. The cause of the differences between the approximations on the putative date of origin of the biotas may be due to the data source and the tool of analysis used in each case. In our point of view, geological events have to be considered the starting point of a vicariant event whereas dates based on fossil records and DNA divergence is the minimum age of a speciation event (Heads, 2005) (i.e. a taxon does not speciate due to the split of an island in a time x, but it does when the islands answered in different ways to a climatic change in a time x+1). Although direct correspondence between geological events and speciation events may not be accurately inferred for various reasons, this practice may be preferred because the basic conceptual expectation that some biotas, sooner or later, answer to such geological events. Additionally, the question to be solved is about area relationships rather than individual taxon history.

The first area split from the biogeographic group C was the MC and was the result of the uplift of the Merida mountain chain ~8 Myr (Albert *et al*., 2006; Backe *et al*., 2006). According to Berry (1982), the Táchira depression constitutes a secondary dispersal barrier between Venezuelan and Colombian Andes; based on our findings, such assertion allows to propose the Táchira depression as a barrier between the MC and our group E (fig 2a), which is constituted by NE, SE, EC, CWC, and the Central Andes. Furthermore, from a biotic point of view, the Mérida Andes seems not to be an extension of the EC in Venezuela (see Mario *et al*., 2001).

Although we do not have a geological event which matches the group E (fig 2a), it could however, based on the adjacent dated nodes, be placed as a biogeographic unit which originated somewhere in the late Miocene (8-5? Myr). The main vicariant event inside this group is one that divided the Central and Ecuadorian Andes (fig 2a, group F) from the Colombian cordilleras (fig 2a, group H). This result shows the Macizo Colombiano as a barrier that might have caused the vicariance between these two groups of areas, rather than a dispersal corridor as Berry (1982) stated. Another valid explanation could be that during the Plio-Pleistocene glaciations the Paramo islands came "closer together" and thus led to a homogenization of the biotas, allowing a subsequent differentiation of the biotas during global warms (Simpson-Vuilleumier, 1971; Fjeldså *et al*., 1999; Weir, 2006; *contra* Elias *et al*., 2009).

The group G contains the relationship between the Central Andes and Ecuador areas of endemism. This split might be due to the Amotape-Huancabamba deflection (Vuilleumier, 1968; see also Weigend, 2002) and might be chronologically placed at late Miocene-Pliocene. The Amotape-Huancabamba deflection has been largely considered as the major transitional zone between the species of the Northern and Central Andes (Berry, 1982; Morrone & Urtubey, 1997), or as a dispersal barrier between the zones (Vuilleumier, 1968; Weigend, 2002). In our results, neither the vicariant nor the dispersal event between the Central Andes and Ecuadorian areas was significant, or stable in the resampling test. Thus, the role of the Amotape-Huancabamba deflection in the relationship of the Central and Ecuadorian Andes seems open to interpretation. Despite this fact, the differentiation of the Central and North Andean biotas could be product of the continuous uplift of the Central Andes' Puna segment until the late Pliocene (1-2 Myr) (Allmendiger *et al*., 1997). The relationship between the two Ecuadorian areas of endemism is enclosed in the group G (fig 2a), was stable in the resampling test, and was not a significant vicariant event. The limit between NE and SE partly corresponds with Alzate's *et al*. (2008) node 2, which represents the lowest altitude for Ecuadorian Andes (Valle Interandino), and is assumed to be a barrier for *Bomarea glaucescens* and *Bomarea pauciflora*. On the other hand, Vuilleumier

(1968, p. 13) suggested "only a slight restriction in gene flow" due to the Valle interandino. This depression in Ecuadorian Cordilleras could have been generating differentiation of the biotas of NE and SE areas of endemism depending on the group. This idea is supported by the minimum number of duplications (8.980) and vicariances (16.980) required for the reconstruction in this node and the duplications for each area, North Ecuador (12.000) and South Ecuador (11.600). This node has the higher number of duplications of any node, and the duplications into the terminal areas are the highest for any ingroup areas.

The last relationship is group D (fig 2a) conformed by the Colombian Cordilleras, the areas of endemism CWC and EC. The similarity of these biotas rather than to other North Andean areas was recognised by Vuilleumier (1968). Its separation could be associated with the final and quick upheaval of the Eastern Colombian Cordillera between 2 and 5 Myr, and the formation of the Magdalena Valley; it has been shown that this emergence allowed different climatic belts, which caused high levels of autochthonous speciation and therefore the diversification of the biota (Simpson & Todzia, 1990; Hoorn *et al*., 1995; Hooghiemstra *et al*., 2002).

In the treefitting analyses the relationship of the SNS with other areas remained unsolved. However, the DIVA analysis showed a dispersion event from the SNS to EC in a low frequency compared with the remaining dispersion events because of the nature of the data set and the poor sampling of the zone (Carbono & Lozano-Contreras, 1997).

CONCLUSION

The biogeographic reconstructions obtained in the tree fitting analysis support a hybrid origin for the North Andean biota (Crisci *et al*., 1991; Morrone & Urtubey, 1997; Katinas et al., 1999; Quijano-Abril *et al*., 2006; Alzate *et al*., 2008). Three events suggest the composite origin: (1) the Macizo Colombiano is more related to a majour group of Neotropical areas (fig 2a group B) and seems to represent a zone where remnant fragments of different biotas were in contact (Alzate *et al*., 2008). (2) The outcome of the uplift of the Eastern Cordillera ~11.8 Myr could explain the split of the Amazonia from the Andes, while the homogenizing biota effect of the marine incursions could account for the relationship between the North of Peru and Amazonia. (3) The Central Andes is inside a group of areas conformed by the Ecuadorian, Colombian, and Venezuelan Andes; inside this group the depressions seem to have played an important role on the biotic diversification (e.g among Ecuadorian areas, from South Ecuador to Amazonia). The Táchira depression, formed after the uplift of the Mérida Cordillera, seems to be an effective barrier between the Venezuelan Andes and the Central and Northern Andes. The vicariant event between the Colombian Cordilleras and Central-Ecuadorian Andes might address the Macizo Colombiando as a possible barrier. The Huancabamaba deflection, based on our results, is neither a dispersion corridor nor a barrier. Finally, The Magdalena Valley and the Valle Interandino seem to be barriers of modern activity (Plio-Pleistocene) that could have induced vicariant events in the biota.

ACKNOWLEDGMENTS

We thank I. Garzón, S. Arias, M. Ebach, J. J. Morrone, J. Villabona and S. Bolivar for their constructive comments. The first author is much indebted to Federico López-Osorio for his encouragement and improvement discussions. This study was supported by the Direccion de Investigaciones y Extensión (DIEF), Universidad industrial de Santander, grant 3152.

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Table 1. Overview of taxa, areagrams and case studies from which we assembled the phylogenies used. Ingroup areas: SNS, Sierra Nevada de Santa Marta; MC, Merida cordillera; EC, Eastern cordillera; CWC, Central Western cordilleras complex; MZC, Macizo Colombiano; NE, Northern Ecuador; SE, Southern Ecuador; NP, Northern Peru. External areas: CAM, Central America, CAB, Caribbean; CHO, Choco; CA, Central Andes; SA, Southern Andes; SDM, Serra do Mar; CHA, Chaco; NEB, North-East Brazil; AZ, Amazonia; OQ, Orinoquia

Group	Reference	Areagram
Anelosimus (Arachnida, Araneae, Theridiidae)	Agnarsson *et al*., 2007	((SE,(NE,AZ)),(SE,(SE,(AZ,NE))))
Chimarra (Insecta, Trichoptera, Philopotamidae)	Blahnik, 2002	(CWC,((AZ CA,(CA,SE)),(NP,(CA,CA))))
Oleriina (Insecta, Lepidoptera, Nymphalidae)	Brower *et al*., 2006	(NP,((AZ,NE),(SE,(MZC NE,(AZ,AZ)))))
Dircenna (Insecta, Lepidoptera, Nymphalidae)	Brower *et al*., 2006	(SE,(MZC NE,(SDM,(NP,(AZ,AZ)))))
(***Pteronymia***; ***Ceratinia***; ***Episcada***) (Insecta, Lepidoptera, Nymphalidae)	Brower *et al*., 2006	(((MZC NE,SE),(CHO,(CA,(MZC NE,(MZC NE,MZC NE))))),((NE,CHO),((SDM,AZ),(MZC NE,(SDM,SDM)))))
Napeogenina (Insecta, Lepidoptera, Nymphalidae)	Brower *et al*., 2006	(((CA,AZ),(MZC NE,(AZ,(AZ,MZC NE)))),((AZ,(SE,CA)),(SDM,AZ)))
Thamnophilus (Aves, Passeriformes, Thamnophilidae)	Brumfield & Edwards, 2007	((CHA,(CA,CHA)),(SE,(EC,(SE,CA))))
Tangara (Aves, Passeriformes, Thraupidae)	Burns & Naoki, 2004	(AZ,(CA,(NE,SE)))
Buarremon (Aves, Passeriformes, Emberizidae)	Cadena *et al*., 2007	(CA,(NE SE CHO,(CHO CAB CA EC CWC MZC NE SE,CAB)))
B. torquatus (Aves, Passeriformes, Emberizidae)	Cadena *et al*., 2007	(CAB,((CHO,CWC),(CWC,(EC,(EC,EC)))))
B. torquatus assimilis; nigrifrons (Aves, Passeriformes, Emberizidae)	Cadena *et al*., 2007	((CWC,EC),(SE,(SE,CWC,(NE,(SE,SE)))))
Isidrogalvia (Monocotyledoneae, Liliales, Liliaceae)	Cruden, 1991	(CHO CA SE NP,(MC AZ OQ EC CWC,MC))
Rhodnius (Insecta, Heteroptera: Reduviidae),	de Paula *et al*., 2007	((SE NP,(CA,CAB)),((CAB AZ CWC,(AZ CAB,CHA)),(SN CAB,(SDM,((SDM NEB,CHA),(NEB,(CWC AZ CAB SN,(AZ CWC NP,SDM NEB))))))))
Ceresia (Monocotyledoneae, Poales, Poaceae)	Denham *et al*., 2002	((CA CHA,CAM CA EC CWC MZC NE SE NP MC CAB CHO SA),(CHA NEB CA EC CM,(NEB,NEB)))
Henicorhina leucophrys (Aves, Passeriformes, Troglodytidae)	Dingle *et al*., 2006	(SE,(SE,(CA,((NE,NE),(SE,NE)))))
Proctoporus (Reptilia, Squamata, Gymnophthalmidae)	Doan, 2003	((SE,SE),((NE,((NE SE,(CAB,CHO NE)),(SE,(EC CWC,NE CHO)))),(CWC,((CA,(CM,(CAB,CAB))),(NE SE,((SE,(NE,(SE,NE))),(SE,((MZC NE,MZC),(NE,NE SE NP)))))))))
Hyloscirtus (Amphibia, Anura, Hylidae)	Faivovich *et al*., 2005	((EC CWC,CWC),((CA,CHA CA),(E,(MZC NE SE,MZC NE SE))))
Physalaemus petersi (Amphibia, Anura, Leptodactylidae)	Funk *et al*., 2007	(AZ,(NE,SE))
Colostethus; Epipedobates (Amphibia, Anura, Dendrobatidae)	Graham *et al*., 2004	(CHO NE,(NE,(NE SE,(CHO SE,CHO SE))))
Phrynopus; Eleutherodactylus (Amphibia, Anura, Leptodactylidae)	Lehr *et al*., 2005	(AZ CHO MZC NE SE,((NE,MZC),((NP,NP),(NE,(MZC,NE)))))
Ithomia (Insecta, Lepidoptera, Nymphalidae)	Mallarino *et al*., 2005	((SE,CAM),((CWC,(MZC NE,(CA,(CA,CA)))),((CWC,CAM),(NE,(CAM,(CHO,(SE,(CHO,SE))))))))
Pyrrhobryum mnioides (Bryopsida, Bryales, Rhizogoniaceae)	McDaniel & Shaw, 2003	(CA,(CAM,MC CWC MZC,(MZC,MZC NE))))

Simulium (Insecta, Diptera, Simuliidae)	Miranda-Esquivel & Coscaron, 2001	((EC,EC),(CA,(SDM,(NP CA,(SA,SA)))))
Simulium (Insecta, Diptera, Simuliidae)	Miranda-Esquivel & Coscaron, 2001	(EC CWC MC CHO CAM,(MC,CAM))
Stigmatopteris (Pteropsida, Filicales, Dryopteridaceae)	Moran, 1991	(SDM,(CA AZ CAB CWC NP,((CHO NE SE,CHO CAM),(CAB SN,(SN AZ MZC NE,CAM CHO AZ CWC NE SE)))))
Macrostyphlus (Insecta, Coleoptera, Curculionidae)	Morrone, 1994a	(CA,((EC CWC,(NE,NE)),((MZC,NE),(MC,(CWC,(MZC,SE))))))
Nacodius (Insecta, Coleoptera, Curculionidae)	Morrone, 1994b	(SE,(NE,(AZ,NP))
Crax; Nothocrax; Mitu; Pauxi (Aves, Galliformes, Cracidae)	Pereira & Baker, 2004	(AZ MZC NE,((CAB MC,(NEB,(AZ OQ EC,(AZ SE,(AZ CA,AZ CHA CA NP))))),(CAM CHO,((CAB OQ,SE EC CWC CHO),((AZ CHA,SDM),(AZ CHA NEB,AZ OQ))))))
Myioborus (Aves, Passeriformes, Parulidae)	Pérez-Emán, 2005	(MC,((CA,AZ),(SE,CWC,EC)))
Coeligena (Aves, Apodiformes, Trochilidae)	Sánchez-Osés, 2003	(EC CWC MZC NE SE AZ CHO,(CA SE NP,MC))
Coeligena (Aves, Apodiformes, Trochilidae)	Sánchez-Osés, 2003	(CA MC MZC NE SE NP,(((CA EC CWC MZC NE SE NP,(SN,EC)),(CWC MZC NE SE,(MC,EC CWC))),(CA SE NP,((SE NP,SE NP),(EC,(CHO MZC NE SE,CA AZ CAB EC CWC MZC NE SE NP))))))
Onoseris (Magnoliopsida, Asterales, Asteraceae)	Sancho, 2004	(SE,(((CHO,CA SE NP),(SE,(NP,AZ NE SE NP,SE))),(CA SE,(SE NP,((CA NP,CHO),(NP CA,(CA,CA)))))))
Onoseris (Magnoliopsida, Asterales, Asteraceae)	Sancho, 2004	(MZC,CA,(AZ,CA SE AZ,CA)))
Barnadesia (Magnoliopsida, Asterales, Asteraceae)	Urtubey, 1999	(NE SE NP,CA EC CWC MZC,(NP,CA))
Hyalenna (Insecta, Lepidoptera, Nymphalidae)	Willmott & Lamas, 2006	((CA CWC NE SE NP,(CA,CA AZ CWC MZC NE SE NP)),(NE SE NP,(SDM,CA AZ MC CHO EC CWC MZC NE SE NP,CWC NE SE NP)))

Table 2. Most frequent dispersion events of each summary in DIVA analysis.

Ingroup areas treated as a single one (IgA)

From	To	% Frequency
IgA	CA	99.751
IgA	CHO/CAB	93.171
IgA	AZ	63.675
CA	IgA	47.661
CHO/CAB	IgA	37.449

External areas treated as a single one (ExA)

From	To	% Frequency
ExA	SE	36.848
SE	NE	34.794
SE	ExA	32.098
ExA	NE	29.374
MZC	NE	29.230

Summary with all ingroup areas, and three external areas.

From	To	% Frequency
SE	AZ	3.889
SE	NE	3.189
MZC	NE	2.789
NE	MZC	2.509
MC	CHO/CAB	1.484
SE	CHO/CAB	1.412
NE	SE	1.261
SE	NP	1.088
CA	NP	0.851
CA	SE	0.833

Figure 1. Summary map of the area set used in this analysis. External areas are colourless: CAM, Central America, CAB, Caribbean; CHO, Choco; CA, Central Andes; SA, Southern Andes; SDM, Serra do Mar; CHA, Chaco; NEB, North-East Brazil; AZ, Amazonia; OQ, Orinoquia. Ingroup areas are coloured with gray: SNS, Sierra Nevada de Santa Marta; MC, Merida cordillera; EC, Eastern cordillera; CWC, Central Western cordilleras complex; MZC, Macizo Colombiano; NE, Northern Ecuador; SE, Southern Ecuador; NP, Northern Peru.

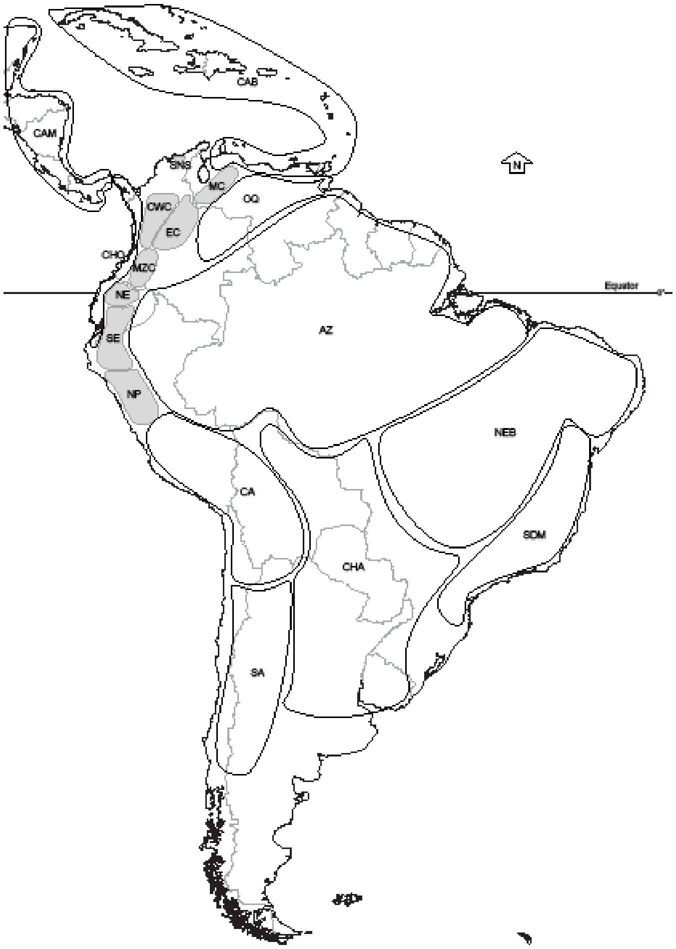

Figure 2. General area cladograms produced by the Tree fitter analyses. a) This tree represents the strict consensus of 15 optimal trees obtained under the default set of costs. Nodes are label with capital letters from A to N, squares indicate significant groups in the randomization test, and circles stable groups in the resampling test. b) This tree represents the strict consensus of 5001 optimal trees obtained under the Maximum Vicariance set of costs.