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Authors: Anthelme, Fabien, Jacobsen, Dean, Macek, Petr, Meneses, Rosa I., Moret, Pierre, et al.

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# Biodiversity patterns and continental insularity in the tropical High Andes

Fabien Anthelme\*†‡+

Dean Jacobsen‡

Petr Macek§#

Rosa I. Meneses@ &

Pierre Moret%

Stephan Beck@† and

Olivier Dangles^†+

\*Institut de Recherche pour le Développement (IRD), UMR AMAP (Botanique et Bioinformatique de l'Architecture des Plantes), Boulevard de la Lironde, TA A-51/PS2, F-34398 Montpellier Cedex 5, France

†Universidad Mayor San Andrés, Instituto de Ecología, Calle 27 – Cota Cota, Campus Universitario, La Paz, Bolivia

‡Freshwater Biological Section, Department of Biology, University of Copenhagen, Helsingørsgade 51, DK-3400 Hillerød, Denmark

§ LINCGlobal, Estación Experimental de Zonas Áridas, Consejo Superior de Investigaciones Científicas, Ctra. Sacramento s/n, E-04120 La Cañada de San Urbano, Almería, Spain

#Department of Botany, Faculty of Science, University of South Bohemia, Na Zlaté stoce 1, CZ-37005 České Budějovice, Czech Republic

@Herbario Nacional de Bolivia, Calle 27 - Cota Cota, Campus Universitario, La Paz, Bolivia

%Université de Toulouse–CNRS, UMR 5608 TRACES, Maison de la Recherche, 5 allées Antonio Machado, F-31058 Toulouse, France

^Institut de Recherche pour le Développement (IRD), UR 072, Laboratoire Evolution, Génomes et Spéciation, UPR 9034, Centre National de la Recherche Scientifique (CNRS), 91198 Gif-sur-Yvette Cedex, France, et Université Paris-Sud 11, 91405 Orsay Cedex, France

&Museo Nacional de Historia Natural, Cota Cota, Calle 26, La Paz, Bolivia

+Corresponding authors: Anthelme (fabien.anthelme@ird.fr), Dangles (olivier.dangles@ird.fr)

## Abstract

Alpine areas of the tropical Andes constitute the largest of all tropical alpine regions worldwide. They experience a particularly harsh climate, and they are fragmented into tropical alpine islands at various spatial scales. These factors generate unique patterns of continental insularity, whose impacts on biodiversity remain to be examined precisely. By reviewing existing literature and by presenting unpublished data on beta-diversity and endemism for a wide array of taxonomic groups, we aimed at providing a clear, overall picture of the isolation-biodiversity relationship in the tropical alpine environments of the Andes. Our analyses showed that (1) taxa with better dispersal capacities and wider distributions (e.g., grasses and birds) were less restricted to alpine areas at local scale; (2) similarity among communities decreased with spatial distance between isolated alpine areas; and (3) endemism reached a peak in small alpine areas strongly isolated from main alpine islands. These results pinpoint continental insularity as a powerful driver of biodiversity in the tropical High Andes. A combination of human activities and warming is expected to increase the effects of continental insularity in the next decades, especially by amplifying the resistance of the lowland matrix that surrounds tropical alpine islands.

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## Introduction

Tropical alpine environments (TAEs) represent as much as 10% of alpine systems worldwide and display unique environmental characteristics among alpine regions (Rundel et al., 1994; Körner, 2003). Among them, low seasonality, inverted rainfall gradients above 3000–3500 m, and the high frequency of freeze-thaw cycles (see Anthelme and Dangles, 2012) set up a peculiar pool of environmental conditions that have shaped the evolution of species assemblages substantially different from those that live in extratropical alpine systems (Hedberg and Hedberg, 1979; Ramsay and Oxley, 1997; Navas, 2003; Jacobsen et al., 2010). For instance, plant growth forms like giant rosettes, giant cushions (Fig. 1, parts A and C), and tussock grasses are more abundant under the tropics than anywhere else in alpine regions (Hedberg and Hedberg, 1979; Körner, 2003). Another specificity of TAE is that they develop at higher elevation than any other alpine ecosystem (Körner, 2003), maybe with the exception of dry subtropical regions (Halloy, 1991; Macek et al., 2012). This argument has been commonly cited to generate a higher isolation of alpine systems under the tropics, with fragmented TAE constituting an archipelago of continental islands (Smith and Young, 1987; Luteyn, 1999; Hughes and Eastwood, 2006; Sklenář et al., 2014).

Yet, the effects of such pronounced continental insularity on biodiversity patterns and dynamics are not straightforward. Some authors argue that continental insularity is one of the main drivers of the high proportion of endemism observed

in TAE (Luteyn, 1999), especially because topographical barriers may be more effective than in extratropical regions (Janzen, 1967; Richter et al., 2009). Other authors tend to reduce its influence because the lowlands located between TAE are not only a matrix resistant to the dispersion of alpine taxa, but they may act instead as a source of colonization during climatic fluctuations (e.g., Smith and Young, 1987). The extent to which continental insularity explains patterns of diversity in tropical alpine systems in comparison with oceanic insularity is a topical question that has been poorly addressed so far and certainly deserves more attention given the high levels of biodiversity found in TAE and their high sensitivity to current global changes (Luteyn, 1999; Bradley et al., 2006).

The tropical High Andes represent an ideal study region to examine the effects of continental insularity on biodiversity patterns for several reasons. First, they are particularly representative of TAEs as they gather more than 90% of their area worldwide (Jacobsen, 2008a). Second, they shelter a wide latitudinal range of environmental conditions from the humid páramos in the north to the dry puna in the south. Third, they display both highly fragmented alpine areas, as in Colombia and Venezuela (Vuilleumier, 1970), and continuous alpine areas in the central Andes, as found in the Peruvian and Bolivian altiplano (Fig. 2). Also, by encompassing Colombia, Venezuela, Ecuador, Peru, Bolivia, North Chile, and North Argentina, tropical Andes are the largest tropical mountain range worldwide, providing opportunities for tropical alpine biodiversity to diverge not only because of habitat fragmentation, but also because of the effects of geographical



**FIGURE 1.** The elements of biodiversity characteristic of the tropical High Andes. (A) *Espeletia pycnophylla* (páramo El Angel, Ecuador), a giant rosette-like species adapted to the harsh climate of the páramo; (B) *Theristicus melanopis* (páramo del Antisana, Ecuador), a bird restricted to high-elevation wetlands; (C) *Azorella compacta* (Sajama National Park, Bolivia), a giant cushion-like species adapted to the dry climate of the puna; and (D) *Telmantobius culeus* (Bolivia), a frog endemic to Titicaca Lake. Photos taken by Olivier Dangles.

distance along a continuous topographical unit (Hughes and Eastwood, 2006; Sklenář et al., 2014).

Continental insularity in the tropical Andes not only is a matter of single isolated summits but also is effective at a coarser, regional scale, with entire mountain ranges being separated from the main cordillera (e.g., Cordillera del Condor in Ecuador, Cordillera Apolobamba in Bolivia, and Sierra Nevada de Santa Marta in Colombia). The most important interruption of Andean tropical alpine regions is the Huancabamba deflection in northern Peru (Fig. 2; Lauer, 1968; Simpson, 1975). There, both the Eastern and the Central Cordillera are entirely interrupted and the only mountain chain providing continuous elevation above 2150 m a.s.l. is the very dry mountain range of the Western Cordillera, which may have contributed to increasing contemporary isolation between the southern and the northern tropical Andes, thus being likely a driver of dissimilarities in floristic elements between these two regions (Smith and Cleef, 1988; Sklenář et al., 2011). However, current patterns of community dissimilarity between Central and Northern Andes are also indebted to more ancient biogeographical processes, including the effects of a former lowland corridor invaded by wetlands, termed the “Western Andean Portal” at this location (Antonelli and Sanmartín, 2011).

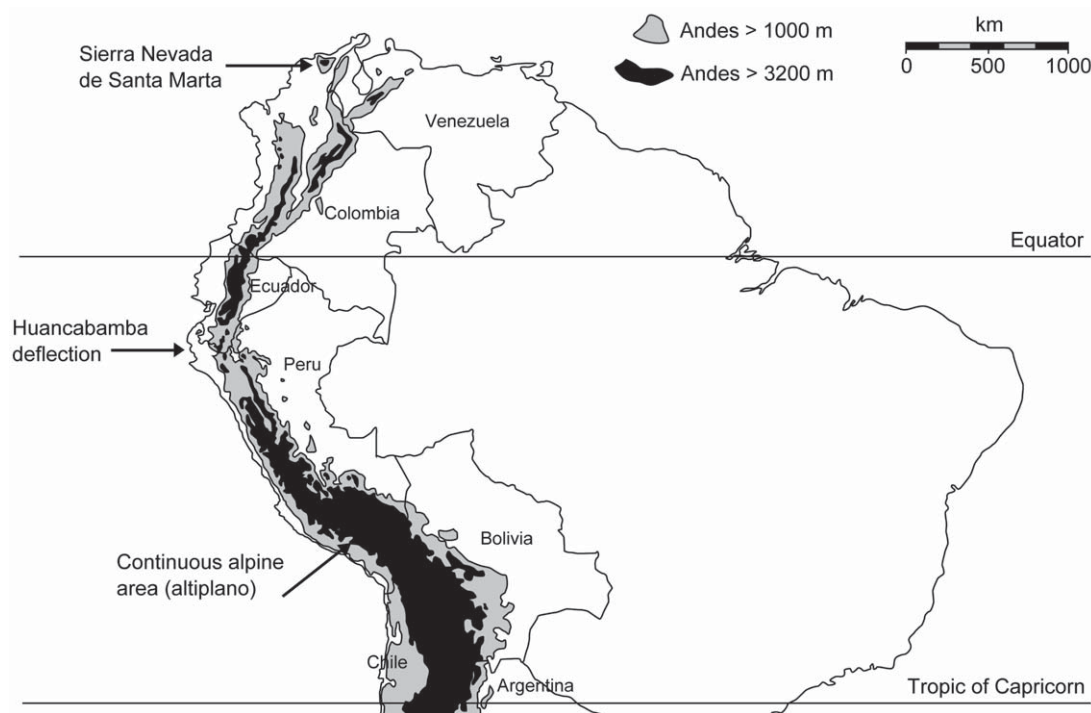
The tropical High Andes display three main features—harsh environmental conditions, large spatial extent, and strong habitat fragmentation—that are expected to greatly influence the organization of biodiversity at both local and regional scales. By analyzing variations in beta-diversity of different plant and animal groups at various spatial scales, the objective of our study is to describe general patterns in the organization and endemism of natural communities in the alpine areas of the tropical High Andes. Beta-diversity among sampling sites is indeed an important criterion for obtaining adequate representation of regional biodiversity (Kattan et al., 2006), an is-

sue that has been poorly considered at the scale of the tropical Andes (Kessler et al., 2011). We specifically intended to answer the following questions: (1) What proportions of the taxa that live in tropical alpine highlands are strictly restricted to this environment? (2) How does spatial distance between pairs of highlands affect community similarity? (3) How does the spatial configuration of tropical highlands influence the number of endemic species? It is not the objective of this paper to discuss the biogeographical/historical reasons for the present patterns of biodiversity found in tropical alpine islands of the Andes. Rather, our “ecological” approach, by providing an original insight from a different angle, may be used by biogeographers to provide a synthetic overview on these patterns.

## Methods

### STUDY AREA

The study area was limited to the tropical Andes *sensu stricto*, from Colombia (Sierra Nevada de Santa Marta; 11°N) to the Southern tropics (23°S; Fig. 1), thus excluding the tropical alpine regions of Central America. Most of the literature considers that the lower limit of TAE in the Andes occur between 3000 m and 3500 m a.s.l. (Vuilleumier, 1970; Smith and Cleef, 1988; Rundel et al., 1994; Luteyn, 1999; Körner, 2003). We arbitrarily used the elevation 3200 m as the lower limit of TAE, and focused on open environments in our review. However, given that Andean forest in some places develop at higher elevation, we eliminated data collected in mountain forests above 3200 m. As an exception, distribution data for terrestrial arthropods were only available from 3400 m upward (Moret, 2005, unpublished data), which sets the lower limit of alpine areas for this group.



**FIGURE 2.** Map of the tropical Andes, from Sierra Nevada de Santa Marta (Colombia, 11°N) to South Chile/Argentina (23°S). Tropical alpine regions displayed as areas above 3200 m.



Our database was extracted from the literature and unpublished data, and each study contributed one or several analyses (Table 1). Data in the literature had to fulfil two criteria: (1) to be located in tropical alpine regions of the Andes, and (2) to provide clear indices of beta-diversity, or at least raw data, to be considered in our meta-analyses. Among plants, information was provided for spermatophytes (wetland, terrestrial, and the specific group of grasses), pteridophytes, and bryophytes. Among animals, information was provided for aquatic (trichopteran) and terrestrial arthropods (carabids), frogs, reptiles, birds, and mammals. Most data were provided at species level, but some relevant data at genera level were also included in the analyses (Table 1).

We then performed three types of analyses. First, at local/country scale we calculated the proportion of taxa restricted to (or precinctive of) alpine areas as the total number of taxa found only above the lower elevational limit of the alpine area divided by the total number of taxa found in the alpine area. Depending on available data, this calculation was applied along specific elevation transects or along elevation transects at country scale (see Table 1).

Second, at regional scale we plotted the community similarity vs. geographical distance relationship among pairs of alpine areas separated by a non-alpine lowland matrix for six taxa in Bolivia (3) and in Ecuador (3; see number of sites and matrices in Appendix Table A1). Community similarity was quantified using the Sørensen's index of similarity  $S$  between two alpine communities as follows:

$$S = \frac{2C}{A + B} \quad (1)$$

where  $A$  is the number of species observed in one community,  $B$  is the number of species found in another community, and  $C$  is the number of species shared by the two communities. The distance between alpine areas was measured using the free software imageJ (<http://rsb.info.nih.gov/ij/>). When the alpine area was clearly dominated by a single summit, we chose this summit as the starting/ending point for the spatial distance. However, when no single summit was easily identified (e.g., Nudo de Cajas, Ecuador) or when several summits of similar importance coexisted in the same area (e.g., Antisana and Cotopaxi, Ecuador), then we selected the center or the equidistance between the summits of the alpine area to perform our measurement.

Third, we compiled data on "strict" endemic species of several alpine areas for three studies that provided particularly clean data (plants and birds in Colombia; Arthropods in Ecuador; 14, 15, and 15 sites, respectively, see Appendix Table A2). Strict endemism occurred as soon as one species was restricted to only one alpine area in the whole study area. Strict endemism was put in relation with the spatial extent of each alpine area (ranging from 0.73 km<sup>2</sup> to 3487 km<sup>2</sup>; see Appendix Table A2) and with the distance to nearest large alpine area (minimum 200 km<sup>2</sup> for plants and birds; 100 km<sup>2</sup> for carabid beetles), two of the best predictors of strict endemism as described in the literature (Vuilleumier, 1970; Simpson, 1975). Note that for beetles (Moret, 2005, unpublished data) the data set comes from Ecuador where alpine areas are much less fragmented than in Colombia (data on birds and plants; Vuilleumier, 1970; Simpson, 1975). Therefore, to make taxonomic groups comparable, we lifted the lower limit of alpine areas of arthropods to 4000 m, which resulted in a similar pattern of habitat fragmentation.

The different nomenclatures used in each of the five countries sampled may generate lists of species composition that are not

fully comparable (e.g., the genus *Deyeuxia* [Poaceae] in Bolivia is described as *Calamagrostis* in Peru). However, since our analyses did not compare species composition between countries, but rather within each country or each alpine site, this divergence did not affect our data.

## STATISTICAL ANALYSES

The similarity–geographic distance relationship was fitted with linear regressions and mean values of similarity were compared across two-sample T-tests. The proportion of animal vs. plant precinctive taxa was also inferred across two-sample T-tests. The relation between strict endemism and the two variables "area" and "distance to nearest large alpine area" was tested for each taxonomic group with stepwise regression (alpha to enter = 0.15; alpha to exit = 0.15;  $R^2$  adjusted when two explaining variables). Results are presented in the form of mean  $\pm$  standard error. Extrapolation provided by three-dimensional surface plot for strict endemism used the distance method (distance power: 2). All analyses were performed using MINITAB 15.

## Results

### BIODIVERSITY SPECIFIC TO ALPINE AREAS (FIG. 3)

The overall mean proportion of taxa precinctive to alpine areas was  $0.35 \pm 0.03$ , ranging from 0.09 (mammals and pteridophytes in Bolivia) to 0.71 (frogs in Bolivia). No significant differences were observed between animal and plant taxa (two-samples T-tests:  $p > 0.05$ ). Among animals, the most precinctive taxa were amphibians/reptiles (0.71 in Bolivia and 0.67 in Peru) and terrestrial arthropods (0.62 in Ecuador). In comparison, mammals and birds displayed lower precinctive scores, from 0.09 to 0.33. Among plants, the six most precinctive scores concerned spermatophytes, with proportions ranging from 0.50 to 0.56. The lowest value of precinctive taxa among spermatophytes was obtained for Poaceae (0.26). Pteridophytes were less restricted to alpine areas, but their proportion of precinctive taxa were highly variable (average value:  $0.26 \pm 0.05$ , ranging from 0.09 to 0.45). Bryophytes were overall the less precinctive taxon and had an average value of  $0.22 \pm 0.01$  (three studies).

Local studies provided a larger proportion of precinctive taxa than studies at the scale of a whole country. This was observed (1) for amphibians where the three most precinctive studies were supported by local data, (2) for birds (local study: 0.33, study at country level: 0.12), and (3) for pteridophytes, with the only study at local scale providing higher precinctive proportion than any other study at country scale (0.45 versus an average value of 0.22). We observed no clear effect of latitude or country on precinctive scores (one-way ANOVAs on both variables:  $p > 0.05$ ).

### COMMUNITY SIMILARITY BETWEEN ALPINE AREAS: EFFECTS OF DISTANCE (FIG. 4)

The overall similarity between communities from disjointed alpine areas was highest for amphibians, terrestrial plants, and reptiles (mean value of Sørensen's indices:  $0.41 \pm 0.07$ ,  $0.35 \pm 0.03$ , and  $0.34 \pm 0.06$ , respectively); intermediate in wetland plants ( $0.22 \pm 0.03$ ); and lowest in mammals and arthropods ( $0.14 \pm 0.04$  and  $0.16 \pm 0.02$ , respectively). Similarity between communities reduced significantly with spatial distance between alpine areas for each taxonomic group ( $R^2$  ranging from 0.18

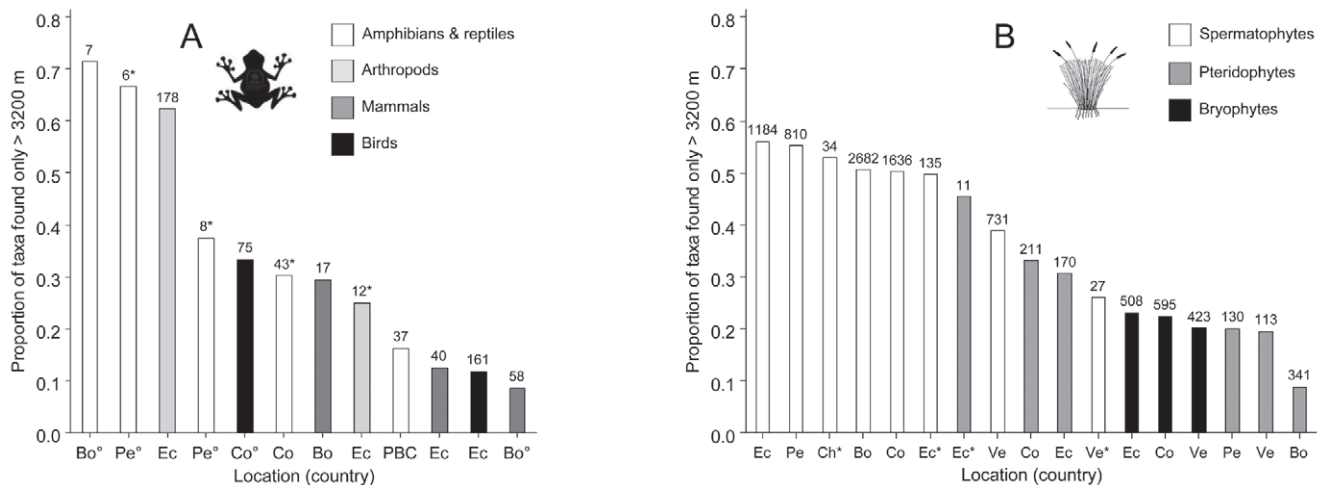
**TABLE 1**  
**Studies incorporated in the database for meta-analyses (See Appendix Tables A1 and A2 for detailed information).**

Study and source	Input to	Elev. Range (m a.s.l.)	Taxonomic group	Country	Latitude	Taxonomic level
Cortez-Fernandez (2006, their Table 2)	Fig. 3	3200–4410	Frogs	Bolivia	16–15°S	Species
Herbario Nacional Bolivia (LPB) and Missouri Botanical Garden (database TROPICOS)	Fig. 3	>3200	Plants (spermatophytes)	Bolivia	Whole country	Species
Jacobsen and Terneus (2001)	Fig. 2	3400–4100	Plants (wetland spermatophytes)	Ecuador	0–1°S	Species
Jacobsen (2000)	Figs. 3, 4	3200–4500	Arthropods (trichopteran)	Ecuador	0–1°S	Genera
Krabbe et al. (2006)	Fig. 3	3200–5200	Birds	Colombia	0–6°N	Species
Luteyn (1999, their checklist)	Fig. 3	3200–5200	Plants (spermatophytes, pteridophytes, bryophytes)	Colombia, Venezuela, Ecuador, Perú	Whole countries	Species
Marquez et al. (2004)	Fig. 3	3200–4200	Plants (spermatophytes: grasses)	Venezuela	9°N	Species
Moret (2005, 2009, unpublished data) (their database)	Figs. 3, 4, 5	3400–5200	Arthropods (carabid beetles)	Ecuador	Whole country	Species
Navas (2003, their figs. 3, 5)	Fig. 3	3200–5000	Reptiles, frogs	Perú, Colombia	Not available	Genera
Novillo and Ojeda (2012, their fig. 2)	Fig. 3	3200–6000	Mammals	Perú, Bolivia, Chile	8–23°S	Species
Ridgely and Greenfield (2006, their maps)	Fig. 3	3200–5000	Birds	Ecuador	Whole country	Species
Ron et al. (2012, their database)	Fig. 3	3200–5000	Frogs	Ecuador	Whole country	Species
Simpson (1975, their table 1)	Fig. 5	>3000	Plants (spermatophytes, pteridophytes)	Colombia	Whole country	Species
Sklenář and Jorgensen (1999)	Figs. 3, 4	3200–5200	Plants (spermatophytes, pteridophytes)	Ecuador	0–3°S	Species
Soria and Kessler (2008); M. Kessler (their unpublished data)	Fig. 3	>3200	Plants (pteridophytes)	Bolivia	Whole country	Species
Tarifa et al. (2007, their fig. 1, table 1)	Fig. 4	3200–4600	Mammals (non-volant), reptiles, amphibians	Bolivia	15–22°S	Species
Tirira (2007, their maps)	Fig. 3	3200–4800	Mammals	Ecuador	Whole country	Species
Villagran et al. (1981)	Fig. 3	3500–4380	Plants (spermatophytes)	Chile	22°S	Species
Vuilleumier (1970, their table 1)	Fig. 5	>3000	Birds	Colombia	Whole country	Species
Wallace et al. (2010, their maps)	Fig. 3	3200–5000	Mammals	Bolivia	Whole country	Species

to 0.53;  $p \leq 0.05$ ), except for amphibians ( $R^2 = 0.05$ ;  $p > 0.05$ ). Among plants, average similarity between terrestrial plants exceeded similarity between wetland plants ( $0.35 \pm 0.03$  vs.  $0.22 \pm 0.03$ ), but pairwise distance correlated better with similarity for terrestrial plants than for wetland plants ( $R^2 = 0.53$  and  $R^2 = 0.28$ , respectively). Among animals, the best relationship between distance and community similarity was obtained with reptiles and carabids ( $R^2 = 0.47$  and  $R^2 = 0.38$ , respectively;  $p \leq 0.001$ ), whereas distance explained 18% of variation in the similarity observed in mammal communities ( $p \leq 0.05$ ).

#### DRIVERS OF STRICT ENDEMISM IN ISOLATED ALPINE AREAS (FIG. 5)

The average proportion of strict endemics in selected alpine areas was  $0.32 \pm 0.09$  for carabid beetles (terrestrial arthropods) in Ecuador,  $0.21 \pm 0.05$  for plants in Colombia, and  $0.13 \pm 0.05$  for birds in Colombia (see Appendix Table A2). In each group, the maximum proportion of strict endemism was observed (1) in the smallest alpine areas, and (2) at the most remote sites from nearest large alpine areas. Both variables explained 33% of the



**FIGURE 3. Proportion of taxa precinctive to tropical alpine areas in the Andes among the total number of taxa present in these areas. (A) animals (mammals, birds, reptiles/amphibians, arthropods: carabid beetles and aquatic trichopteran) and (B) plants (terrestrial and wetland spermatophytes, pteridophytes, bryophytes). All data at species level except of \*genus level. Numbers on top of histograms refer to taxonomic richness. Co: Colombia; Ve: Venezuela; Ec: Ecuador; Pe: Peru; Bo: Bolivia; Ch: Chile; PBC: Peru + Bolivia + Chile. °Study conducted at a local level (e.g. elevation transect).**

strict endemism in plants (stepwise regression;  $R^2$  adjusted = 0.33,  $p \leq 0.05$ ). However, only the “distance to nearest large alpine area” term, and not “area,” had a significant effect on the observed number of strict endemics in carabids and birds (stepwise regressions; arthropods:  $R^2 = 0.61$ ,  $p \leq 0.001$ ; birds:  $R^2 = 0.47$ ,  $p \leq 0.01$ ). In each group, a secondary peak of strict endemism was observed in small alpine areas with short distance to the nearest large alpine area. In plants and birds, this peak referred to data from the Sierra Nevada de Santa Marta (Colombia), while in carabids it was sustained by data from the páramo ‘Llanganates’ (Ecuador).

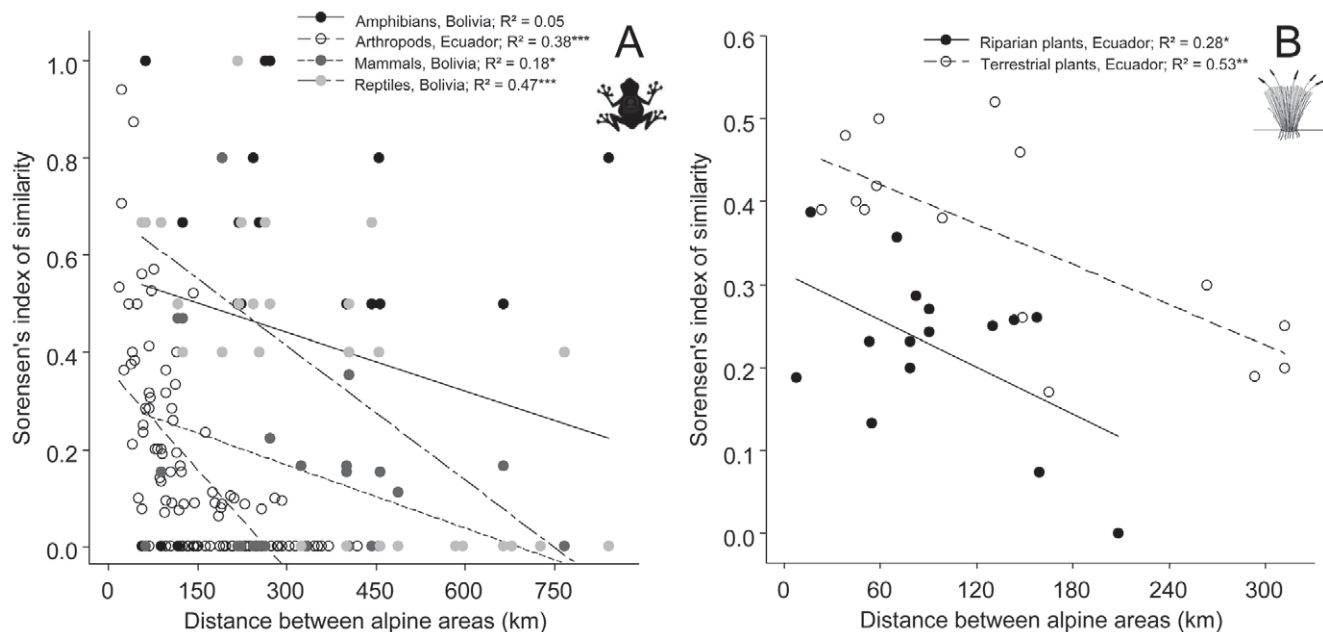
## Discussion

### CONTINENTAL INSULARITY AT VARIOUS SCALES EXPLAINS BIODIVERSITY PATTERNS

In contrast with patterns of plant species richness, which are poorly related to current degree of isolation and extent of tropical alpine areas of the Andes (see review in Smith and Young, 1987), our data demonstrate that beta-diversity and endemism in the tropical alpine islands of the Andes are certainly dependent on the current degree of continental insularity, at various spatial scales.

At local/country scale, elevation shifts from the Andean forests to alpine areas (3000–3500 m) resulted in the existence of alpine communities with more than one-third of precinctive taxa (Fig. 3), thus revealing a strong environmental barrier between these two types of ecosystems. Contrastingly to other alpine environments, TAEs experience unusual abiotic constraints such as high frequency of freeze-thaw cycles, edaphic and atmospheric aridity overall stronger than in other alpine regions due to the absence of protective snow cover, and/or the inversion of precipitation gradients (see review in Anthelme and Dangles, 2012). In some taxonomic groups (e.g., spermatophytes), these constraints are easily noticeable in the development of peculiar

growth forms, such as giant rosettes of giant cushion-like species (Fig. 1, parts A and C), which are well adapted to these specific constraints (Monasterio and Sarmiento, 1991; Kleier and Rundel, 2009; Anthelme et al., 2012), and by physiological traits particularly resistant to low temperature and water stress (e.g., Rundel et al., 2003; Macek et al., 2009; Sklenář et al., 2010; Almeida et al., 2013). Lower precinctive scores in pteridophytes and bryophytes may be indebted to the higher dispersal capacities of these taxa combined with an overall high tolerance and/or resistance to desiccation (Sakai and Larcher, 1987; Muñoz et al., 2004; Anthelme et al., 2011), which may permit species to occupy wider vertical distribution ranges. However, higher endemism in bryophytes observed in the northern Andes than in the central Andes (Churchill, 2009) suggests that continental insularity also affects the diversity of this group. Concerning animals, while taxon richness generally decreases with elevation (Jacobsen, 2008b; Herzog et al., 2011, and reference therein), the highland fauna, however, is not simply an attenuated version of the adjacent lowland fauna and many taxa are specific to high-elevation sites (e.g., the frogs of the genera *Atelopus* [Navas, 2003], the rodent *Thomasomys vulcani* [Tirira, 2007], the bird *Theristicus melanopsis* [Ridgely and Greenfield, 2006]; Fig. 1, part B). Moreover, the lower proportion of precinctive taxa in birds and mammals in comparison with amphibians, reptiles, and arthropods is likely due to group-specific differences in (1) mobility (Brown and Lomolino, 1998) and (2) a tolerance to greater climatic constraints at higher elevation, both in favor of endotherm mammals and amphibians (Laurance et al., 2011). From this viewpoint, carabids considered in our study are not fully representative of terrestrial arthropods, which may be expected to display overall lower proportions of precinctive taxa (Gonzalez and Engel, 2004). However, morphological adaptations such as wing atrophy or smaller body size are known from a number of tropical alpine insects, increasing their possibility to adapt to local conditions by finding sheltered microhabitats, but limiting their dispersion to adjacent lowlands (Sømme, 1989). Specialization to high elevation habitats can also occur in highly



**FIGURE 4.** Relationships between community similarity and spatial distance between pairs of alpine areas for (A) animals; (B) plants.  $R^2$  extracted from linear regressions for each taxonomic group. Similarity expressed with Sørensen's index.

mobile organisms such as birds, for which ca. 15–20 species are limited to *Polylepis* woodlands above 3500 m a.s.l. in the Peruvian and Bolivian puna (e.g., *Oreomanes fraseri*, which feed exclusively on branches and trunks of *Polylepis*; Fjeldsa, 1993). However, from a methodological viewpoint, we must keep in mind that variation in the area sampled has a substantial influence on the proportion of precinctive taxa. The reduction of this proportion at country scale might be the result of a “compensation effect” with taxa precinctive on a single elevation gradient becoming ubiquitous at country scale.

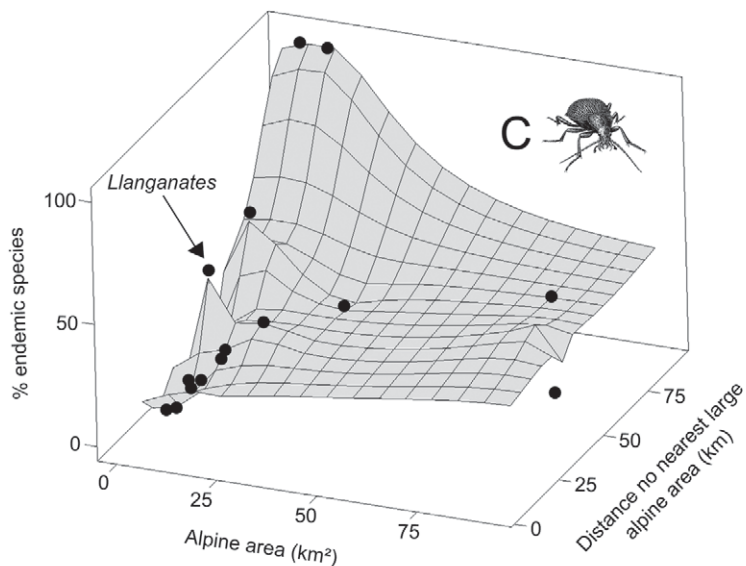
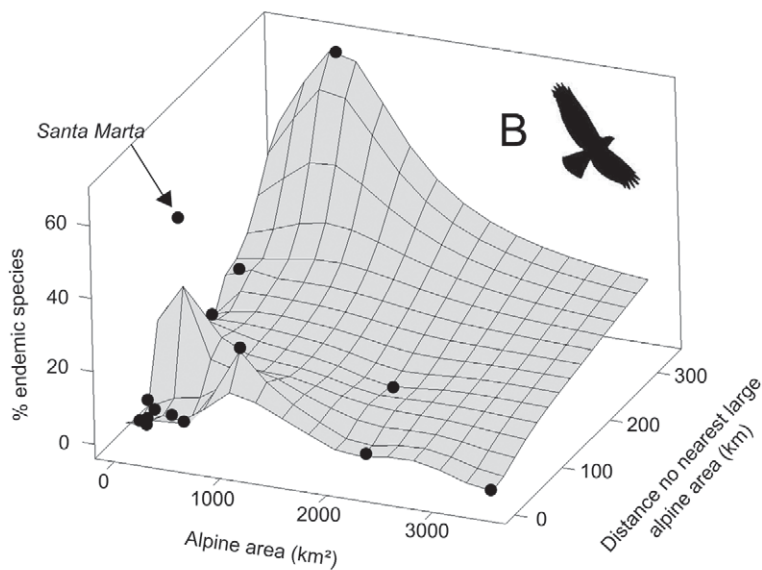
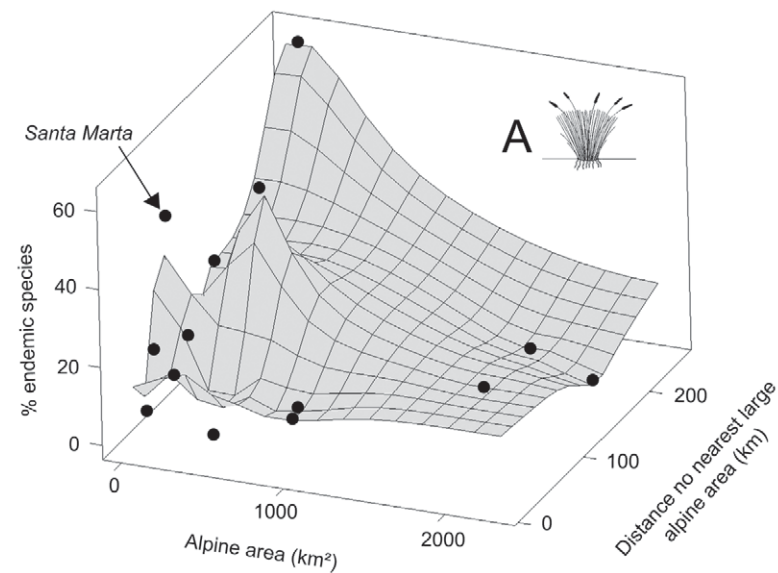
At regional scale, isolation between pairs of islands has frequently been cited to increase beta-diversity in the tropical High Andes (Smith and Young, 1987; Luteyn, 1999; Hughes and Eastwood, 2006). Our data corroborate this opinion for a large pool of taxonomic groups, with distance among tropical alpine islands being negatively correlated with the similarity between alpine communities (except for amphibians). In plants, terrestrial communities are without surprise more similar than communities restricted to humid ecosystems (wetland plants), which are much highly scattered in the High Andes. But the reduced influence of distance on the community similarity of the high Andean wetlands is an original result, which may deserve further investigation (existence of a relatively homogeneous wetland plant community at the scale of the tropical Andes?). Interestingly, when considering only the Poaceae family among terrestrial plants (which is one of the families with the most efficient propagule dispersion capacities across wind dispersal), similarity is much higher than in other studies on spermatophytes. Similarly, wind pollination capacities have been shown to reduce the effects of isolation by distance in the High Andes (Schmidt-Lebuhn et al., 2007). Accordingly, seed dispersal and pollination capacity (by wind) are certainly major drivers of plant beta-diversity in isolated alpine islands of the Andes, as initially suggested by Hedberg (1969). Among others, it ex-

plains why one of the most isolated alpine areas in the tropical Andes, the Sumaco Volcano in Ecuadorian Amazonia, is largely dominated by Poaceae and more generally speaking by plants with high seed dispersal capacities (Løjtant and Molau, 1983).

Among animals, the overall pattern of similarity between pairs of communities in the Bolivian puna may appear counter-intuitive as (non-volant) mammals display a stronger similarity among alpine islands than amphibians and reptiles, which generally have lower dispersal capacities. As proposed by Tarifa et al. (2007), such pattern can be explained by (1) a reduced species pool of amphibians and reptiles in the dry puna, (2) the occurrence of a few cosmopolitan species, and (3) a better adaptation of mammals to specific niches in alpine areas. However, distance-similarity relationships may differ in more humid, high-elevation locations of the tropical Andes, such as in the Colombian and Ecuadorian páramos, which are known to shelter site-specific amphibian communities (Navas, 2003; Ron et al., 2012). Also, species of the frog genera *Telmatobius* (see Fig. 1, part D) are known to be highly endemic from specific locations, with species turnover taking place within a few tens or, at most, hundreds of kilometers (De La Riva et al., 2005). Overall, our knowledge of the factors influencing community similarity among alpine areas is likely to be influenced by the size of the species pool considered and also strongly limited by the patchiness of available information in the tropical Andes.

In addition to variation in elevation at local scale and distance between pairs of alpine islands, two other variables—“distance to nearest large alpine area” and to a lesser extent “alpine area”—were positively correlated with strict endemism for the three studied groups (arthropods, plants, birds). This finding supports our argumentation that the current degree of isolation of continental insularity in the tropical Andes is a strong driver of the organization of beta-diversity (Vuilleumier, 1970; Simpson, 1975).





**FIGURE 5.** Proportion of strict endemism found in three taxonomic groups in each alpine area, in relation to the extent of the alpine area and the distance to the nearest large alpine area. (A) Plants in Colombia (>3200 m); (B) birds in Colombia (>3200 m); (C) arthropods (carabid beetles) in Ecuador (>4000 m). Black points represent the data used for extrapolation in the 3D surface plots.

The existence of secondary peaks of strict endemism in relatively small areas such as the Sierra Nevada de Santa Marta, which is separated from the main Cordillera by a very low lowland matrix (Fig. 5, parts A and B), suggests that lowland matrices likely have a key influence on beta-diversity patterns. This is supported by various observations on TAE plant communities in East Africa (Hedberg, 1969), Ecuador (Løjtnant and Molau, 1983), and Colombia (Sklenář and Balslev, 2005), and on arthropod communities in Ecuador (Moret, 2005). In contrast to oceanic islands where the quality of the matrix is homogenous, continental insularity implies different degrees of matrix resistances among isolated alpine areas. As shown above, the resistance may primarily be dependent on elevation, with lowlands being barriers, but also opportunities for colonization, especially under the effects of large-scale climatic fluctuations (Smith and Young, 1987; Sklenář et al., 2011). Nevertheless, other factors may influence the resistance of the continental matrix, among which are human activities such as the rapidly advancing agricultural frontier at higher elevations (Hedberg, 1969; Sklenář and Ramsay, 2001; Morales and Sarmiento, 2002). Furthermore, this resistance differs among groups, as for plants it is usually lethal landing outside of TAE during dispersal event, while for animals it does not have to be.

#### MULTIPLE DRIVERS OF CONTINENTAL INSULARITY

The purpose of this study was to examine the effects of contemporary isolation by distance, area, and variation in elevation on the organization of biodiversity in the tropical Andes. However, apart from biogeographical and historical drivers, whose role on biodiversity organization in the High Andes has been amply documented (e.g., Fjeldsa, 1993; Richter et al., 2009; Sklenář et al., 2011), other factors would certainly deserve more attention when trying to provide a synthetic explanation of observed diversity patterns in the tropical Andes. For example, local climatic variations, especially those observed between western and eastern sides of large Andean summits, are potential drivers of isolation (e.g., see dry and isolated “Arenal Grande” on the western side of Chimborazo, Ecuador; Moret, 2009; Sklenář and Ramsay, 2001; Kessler et al., 2011). Also, the presence of large lakes (Lake Titicaca; ancient lake Minchin) was cited as a potential factor of isolation in the altiplano (Simpson, 1975). As said before, human activities are expected to modify the degree of isolation of alpine areas by making the surrounding matrix more resistant to migration of natural species, but also by promoting the transport and introduction of species adapted to such disturbances (e.g., invasive species; Pauchard et al., 2009).

From this viewpoint, the secondary peaks of strict endemism that have been observed in several small alpine areas, despite their short distance to the nearest large alpine area (Fig. 5), deserve a special attention. For example, the Llanganates area in central Ecuador displays an outstanding 50% of strict endemic Carabid beetles above 4000 m (Moret, unpublished data), which cannot be explained by the existence of a topographical barrier. In this case, future studies should consider a combination of other factors, such as wet microclimate, absence of anthropogenic perturbation, specific soil properties, and most of all absence of Pleistocene and Holocene volcanic activity.

Finally, because of their high elevation, tropical alpine regions of the Andes are probably one of the terrestrial ecosystems that will face the highest warming up to 2100 (Bradley et al., 2006). In this context,

species that occur in alpine areas may be especially prone to extinction under the effects of climate change because (1) they inhabit environments with a relatively low total colonizable area and have nowhere to migrate upward (Gosling et al., 2009), and (2) the rapid shift of the upper limits of alpine areas to higher elevation increases the isolation of contiguous viable populations (Jørgensen et al., 2011; Larsen et al., 2011; Laurance et al., 2011; Velásquez-Tibatá et al., 2013). It must be taken into account, however, that species at higher elevations may be able to reduce their extinction risk by having possibly larger vertical distribution ranges (e.g., Herzog et al., 2013). Further research in the line of that presented in this paper is urgently needed to better predict the response of the biodiversity of high mountains to rapid anthropogenic changes in the tropical Andes.

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## APPENDIX

TABLE A1

Raw data for analyses of Sorensen's similarity between communities, at regional scale (see also Table 1 for data source).

Taxon and country	Number of alpine sites taken into consideration	Source
Riparian plants, Ecuador	6	Jacobsen and Terneus (2001)
Terrestrial plants, Ecuador	6	Sklenar and Jorgensen (1999)
Mammals, Bolivia	8	Tarifa et al. (2007)
Amphibians, Bolivia	8	Tarifa et al. (2007)
Reptiles, Bolivia	8	Tarifa et al. (2007)
Arthropods, Ecuador	15	Moret (2005, 2009, unpub. data)
Taxon and country	Distance (km)	Similarity (Sorensen)
Riparian plants, Ecuador	208	0.00
Riparian plants, Ecuador	82	0.29
Riparian plants, Ecuador	157	0.26
Riparian plants, Ecuador	159	0.07
Riparian plants, Ecuador	70	0.36
Riparian plants, Ecuador	130	0.25
Riparian plants, Ecuador	53	0.23
Riparian plants, Ecuador	54	0.13
Riparian plants, Ecuador	143	0.26
Riparian plants, Ecuador	78	0.23
Riparian plants, Ecuador	78	0.20
Riparian plants, Ecuador	16	0.39
Riparian plants, Ecuador	7	0.19
Riparian plants, Ecuador	90	0.24
Riparian plants, Ecuador	90	0.27
Terrestrial plants, Ecuador	147	0.46
Terrestrial plants, Ecuador	312	0.20
Terrestrial plants, Ecuador	45	0.40
Terrestrial plants, Ecuador	59	0.50
Terrestrial plants, Ecuador	57	0.42
Terrestrial plants, Ecuador	165	0.17
Terrestrial plants, Ecuador	148	0.26
Terrestrial plants, Ecuador	131	0.52
Terrestrial plants, Ecuador	98	0.38
Terrestrial plants, Ecuador	312	0.25
Terrestrial plants, Ecuador	293	0.19
Terrestrial plants, Ecuador	263	0.30
Terrestrial plants, Ecuador	23	0.39
Terrestrial plants, Ecuador	50	0.39
Terrestrial plants, Ecuador	38	0.48
Mammals, Bolivia	88	0.15
Mammals, Bolivia	487	0.11
Mammals, Bolivia	400	0.15
Mammals, Bolivia	457	0.15

**TABLE A1**  
**Continued**

Taxon and country	Distance (km)	Similarity (Sorensen)
Mammals, Bolivia	663	0.17
Mammals, Bolivia	677	0.00
Mammals, Bolivia	842	0.00
Mammals, Bolivia	403	0.35
Mammals, Bolivia	323	0.17
Mammals, Bolivia	400	0.17
Mammals, Bolivia	595	0.00
Mammals, Bolivia	583	0.00
Mammals, Bolivia	767	0.00
Mammals, Bolivia	123	0.47
Mammals, Bolivia	115	0.47
Mammals, Bolivia	218	0.00
Mammals, Bolivia	253	0.00
Mammals, Bolivia	442	0.00
Mammals, Bolivia	55	0.67
Mammals, Bolivia	262	0.00
Mammals, Bolivia	270	0.22
Mammals, Bolivia	332	0.00
Mammals, Bolivia	453	0.00
Mammals, Bolivia	217	0.00
Mammals, Bolivia	223	0.00
Mammals, Bolivia	403	0.00
Mammals, Bolivia	62	0.00
Mammals, Bolivia	242	0.00
Mammals, Bolivia	190	0.80
Amphibians, Bolivia	88	0.00
Amphibians, Bolivia	487	0.00
Amphibians, Bolivia	400	0.50
Amphibians, Bolivia	457	0.50
Amphibians, Bolivia	663	0.50
Amphibians, Bolivia	677	0.00
Amphibians, Bolivia	842	0.80
Amphibians, Bolivia	403	0.00
Amphibians, Bolivia	323	0.00
Amphibians, Bolivia	400	0.00
Amphibians, Bolivia	595	0.00
Amphibians, Bolivia	583	0.00
Amphibians, Bolivia	767	0.00
Amphibians, Bolivia	123	0.67
Amphibians, Bolivia	115	0.00
Amphibians, Bolivia	218	0.67
Amphibians, Bolivia	253	0.67
Amphibians, Bolivia	442	0.50

**TABLE A1**  
**Continued**

Taxon and country	Distance (km)	Similarity (Sorensen)
Amphibians, Bolivia	55	0.00
Amphibians, Bolivia	262	1.00
Amphibians, Bolivia	270	1.00
Amphibians, Bolivia	453	0.80
Amphibians, Bolivia	217	0.50
Amphibians, Bolivia	223	0.50
Amphibians, Bolivia	403	0.40
Amphibians, Bolivia	62	1.00
Amphibians, Bolivia	242	0.80
Amphibians, Bolivia	190	0.80
Reptiles, Bolivia	88	0.67
Reptiles, Bolivia	487	0.00
Reptiles, Bolivia	400	0.00
Reptiles, Bolivia	457	0.00
Reptiles, Bolivia	663	0.00
Reptiles, Bolivia	677	0.00
Reptiles, Bolivia	725	0.00
Reptiles, Bolivia	842	0.00
Reptiles, Bolivia	403	0.40
Reptiles, Bolivia	323	0.00
Reptiles, Bolivia	400	0.00
Reptiles, Bolivia	595	0.00
Reptiles, Bolivia	583	0.00
Reptiles, Bolivia	767	0.40
Reptiles, Bolivia	123	0.40
Reptiles, Bolivia	115	0.50
Reptiles, Bolivia	218	0.50
Reptiles, Bolivia	253	0.40
Reptiles, Bolivia	442	0.67
Reptiles, Bolivia	55	0.67
Reptiles, Bolivia	262	0.67
Reptiles, Bolivia	270	0.50
Reptiles, Bolivia	453	0.40
Reptiles, Bolivia	217	1.00
Reptiles, Bolivia	223	0.67
Reptiles, Bolivia	403	0.50
Reptiles, Bolivia	62	0.67
Reptiles, Bolivia	242	0.50
Reptiles, Bolivia	190	0.40
Arthropods, Ecuador	67	0.00
Arthropods, Ecuador	133	0.00
Arthropods, Ecuador	150	0.00
Arthropods, Ecuador	170	0.00

**TABLE A1**  
**Continued**

Taxon and country	Distance (km)	Similarity (Sorensen)
Arthropods, Ecuador	186	0.00
Arthropods, Ecuador	272	0.00
Arthropods, Ecuador	67	0.00
Arthropods, Ecuador	88	0.00
Arthropods, Ecuador	162	0.00
Arthropods, Ecuador	228	0.00
Arthropods, Ecuador	284	0.00
Arthropods, Ecuador	345	0.00
Arthropods, Ecuador	370	0.00
Arthropods, Ecuador	418	0.00
Arthropods, Ecuador	68	0.29
Arthropods, Ecuador	87	0.13
Arthropods, Ecuador	106	0.29
Arthropods, Ecuador	122	0.15
Arthropods, Ecuador	211	0.10
Arthropods, Ecuador	25	0.36
Arthropods, Ecuador	57	0.24
Arthropods, Ecuador	108	0.26
Arthropods, Ecuador	174	0.11
Arthropods, Ecuador	230	0.00
Arthropods, Ecuador	291	0.10
Arthropods, Ecuador	312	0.00
Arthropods, Ecuador	358	0.00
Arthropods, Ecuador	20	0.71
Arthropods, Ecuador	40	0.88
Arthropods, Ecuador	55	0.67
Arthropods, Ecuador	144	0.09
Arthropods, Ecuador	69	0.31
Arthropods, Ecuador	71	0.53
Arthropods, Ecuador	56	0.56
Arthropods, Ecuador	114	0.40
Arthropods, Ecuador	169	0.00
Arthropods, Ecuador	229	0.09
Arthropods, Ecuador	246	0.00
Arthropods, Ecuador	291	0.00
Arthropods, Ecuador	20	0.94
Arthropods, Ecuador	36	0.38
Arthropods, Ecuador	126	0.09
Arthropods, Ecuador	85	0.14
Arthropods, Ecuador	81	0.20
Arthropods, Ecuador	44	0.38
Arthropods, Ecuador	95	0.10
Arthropods, Ecuador	149	0.00



**TABLE A1**  
**Continued**

Taxon and country	Distance (km)	Similarity (Sorensen)
Arthropods, Ecuador	209	0.00
Arthropods, Ecuador	228	0.00
Arthropods, Ecuador	272	0.00
Arthropods, Ecuador	16	0.53
Arthropods, Ecuador	105	0.09
Arthropods, Ecuador	103	0.15
Arthropods, Ecuador	96	0.32
Arthropods, Ecuador	39	0.40
Arthropods, Ecuador	77	0.20
Arthropods, Ecuador	131	0.00
Arthropods, Ecuador	190	0.09
Arthropods, Ecuador	206	0.00
Arthropods, Ecuador	251	0.00
Arthropods, Ecuador	90	0.19
Arthropods, Ecuador	119	0.17
Arthropods, Ecuador	111	0.33
Arthropods, Ecuador	47	0.50
Arthropods, Ecuador	68	0.32
Arthropods, Ecuador	119	0.00
Arthropods, Ecuador	177	0.09
Arthropods, Ecuador	192	0.00
Arthropods, Ecuador	237	0.00
Arthropods, Ecuador	205	0.11
Arthropods, Ecuador	189	0.08
Arthropods, Ecuador	113	0.19
Arthropods, Ecuador	56	0.08
Arthropods, Ecuador	50	0.10
Arthropods, Ecuador	93	0.07
Arthropods, Ecuador	104	0.00
Arthropods, Ecuador	147	0.00
Arthropods, Ecuador	33	0.50
Arthropods, Ecuador	96	0.36
Arthropods, Ecuador	162	0.24
Arthropods, Ecuador	219	0.00
Arthropods, Ecuador	279	0.10
Arthropods, Ecuador	302	0.00
Arthropods, Ecuador	351	0.00
Arthropods, Ecuador	76	0.57
Arthropods, Ecuador	142	0.52
Arthropods, Ecuador	196	0.00
Arthropods, Ecuador	257	0.08
Arthropods, Ecuador	282	0.00
Arthropods, Ecuador	334	0.00

**TABLE A1**  
**Continued**

Taxon and country	Distance (km)	Similarity (Sorensen)
Arthropods, Ecuador	68	0.41
Arthropods, Ecuador	123	0.00
Arthropods, Ecuador	184	0.06
Arthropods, Ecuador	208	0.00
Arthropods, Ecuador	257	0.00
Arthropods, Ecuador	56	0.00
Arthropods, Ecuador	117	0.07
Arthropods, Ecuador	142	0.00
Arthropods, Ecuador	193	0.00
Arthropods, Ecuador	61	0.29
Arthropods, Ecuador	88	0.20
Arthropods, Ecuador	144	0.00
Arthropods, Ecuador	39	0.21
Arthropods, Ecuador	95	0.00
Arthropods, Ecuador	57	0.25

**TABLE A2**  
**Raw data used for analyses on strict endemism (see also Table 1 for data source).**

Taxon	Country	Páramo	Species richness	Endemic taxa	% Endemic taxa	Alpine area (km <sup>2</sup> )	Elevation (m a.s.l.)	Distance from large alpine area (km)	Source
Plants	Colombia	Chiles	14	0	0.00	412	1260	36	Simpson75
Plants	Colombia	Pasto	19	1	0.05	56	770	25	Simpson75
Plants	Colombia	Puracé	38	3	0.08	911	1170	25	Simpson75
Plants	Colombia	Farallones	16	2	0.13	45	1050	100	Simpson75
Plants	Colombia	Sumapaz	42	4	0.10	1856	1060	166	Simpson75
Plants	Colombia	Quindio	34	4	0.12	956	1900	22	Simpson75
Plants	Colombia	Frontino	4	1	0.25	22	580	142	Simpson75
Plants	Colombia	paramillo	2	1	0.50	45	460	51	Simpson75
Plants	Colombia	Cocuy	37	2	0.05	2295	1995	156	Simpson75
Plants	Colombia	Santurban	26	5	0.19	303	600	10	Simpson75
Plants	Colombia	Tama	16	3	0.19	67	613	38	Simpson75
Plants	Colombia	Mérida	21	3	0.14	1901	1502	81	Simpson75
Plants	Colombia	Perija	8	5	0.63	112	700	249	Simpson75
Plants	Colombia	Santa Marta	26	14	0.54	472	2300	91	Simpson75
Birds	Colombia	Ecuador	65	1	0.02	3487	2397	1	Vuilleumier70
Birds	Colombia	Chiles	36	1	0.03	326	1264	36	Vuilleumier70
Birds	Colombia	Las papas-Coconuco	30	1	0.03	501	1170	26	Vuilleumier70
Birds	Colombia	Sumapaz	37	3	0.08	2031	1060	116	Vuilleumier70
Birds	Colombia	Tolima-Quindio	35	9	0.26	989	1900	25	Vuilleumier70
Birds	Colombia	Paramillo	11	1	0.09	25	460	186	Vuilleumier70

TABLE A2

Continued

Taxon	Country	Páramo	Species richness	Endemic taxa	% Endemic taxa	Alpine area (km <sup>2</sup> )	Elevation (m a.s.l.)	Distance from large alpine area (km)	Source
Birds	Colombia	Cocuy	21	1	0.05	2168	1998	14	Vuilleumier70
Birds	Colombia	Pamplona	11	1	0.09	217	700	14	Vuilleumier70
Birds	Colombia	Cachira	13	0	0.00	143	735	19	Vuilleumier70
Birds	Colombia	tama	17	0	0.00	46	613	29	Vuilleumier70
Birds	Colombia	Batallon	13	0	0.00	66	662	55	Vuilleumier70
Birds	Colombia	Mérida	29	6	0.21	198	1502	204	Vuilleumier70
Birds	Colombia	Perija	4	2	0.50	167	750	75	Vuilleumier70
Birds	Colombia	Santa Marta	18	12	0.67	606	2275	330	Vuilleumier70
Birds	Colombia	Cendé	15	0	0.00	70	552	35	Vuilleumier70
Arthropods	Ecuador	Chiles	6	6	1.00	5.44	638	92.9	Moret
Arthropods	Ecuador	Cotacachi	6	0	0.00	2.81	789	50.9	Moret
Arthropods	Ecuador	Pichincha	8	0	0.00	3.69	644	37	Moret
Arthropods	Ecuador	Atacazo	9	2	0.22	14.2	313	28	Moret
Arthropods	Ecuador	Corazon	8	0	0.00	3.02	638	20.1	Moret
Arthropods	Ecuador	Illinizas	7	0	0.00	4.65	1113	21.2	Moret
Arthropods	Ecuador	Chimborazo	14	8	0.57	91.1	2260	39.2	Moret
Arthropods	Ecuador	Imbabura	5	0	0.00	0.73	459	35.6	Moret
Arthropods	Ecuador	Cayambe	11	2	0.18	11.9	1640	11.6	Moret
Arthropods	Ecuador	Antisana-Cotopaxi	17	3	0.18	93	1747	39.2	Moret
Arthropods	Ecuador	Llanganates	12	6	0.50	8.2	421	35.3	Moret
Arthropods	Ecuador	El Altar	6	2	0.33	21.9	1169	32.2	Moret
Arthropods	Ecuador	Ayapungu-Cerro Sorochi	15	9	0.60	8.5	580	55.6	Moret
Arthropods	Ecuador	Nudo de Azuay	4	1	0.25	31.7	325	57.2	Moret
Arthropods	Ecuador	Nudo de Cajas	4	4	1.00	12.6	320	91.7	Moret

Notes: Species richness is the total number of species observed in each páramo. Simpson75 refers to Simpson, 1975; Vuilleumier70 refers to Vuilleumier, 1970; Moret refers to Moret et al., 2005, Moret, 2009, and Moret, unpublished data (see reference list for full reference).