

**USANDO FILOGENÉTICA MOLECULAR PARA ELUCIDAR PATRONES Y
PROCESOS DE DIVERSIFICACIÓN EN ANUROS ANDINOS DEL GÉNERO
*PRISTIMANTIS***

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**UNIVERSIDAD INDUSTRIAL DE SANTANDER
FACULTAD DE CIENCIAS
ESCUELA DE BIOLOGÍA
BUCARAMANGA
2016**

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**Trabajo de Grado presentado como requisito para optar al título de
Magíster en Biología**

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BUCARAMANGA

2016

ACKNOWLEDGEMENTS

I would like specially to thank my codirector M. Torres, for his constant guidance and continued support along this work. I thank to my director M.P. Ramírez and to my codirector A.J. Crawford for laboratory space and resources, and comments about this manuscript. I grateful to C. McCain, C. Hutter, J.M. Guayasamín, and E. Ramos-Pallares for methodological advices. I also thank F. Rojas-Runjaic, J.M. Guayasamín, and J.C. Chaparro for confirming elevational records for species from Venezuela, Ecuador, and Peru, respectively. E. Lehr suggested important bibliographical references on Peruvian species. The manuscript was improved by input from J.M. Guayasamín, N.R. Pinto-Sánchez, and two anonymous reviewers of the Ecology and Evolution journal.

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RESUMEN

TÍTULO: USANDO FILOGENÉTICA MOLECULAR PARA ELUCIDAR PATRONES Y PROCESOS DE DIVERSIFICACIÓN EN ANUROS ANDINOS DEL GÉNERO *PRISTIMANTIS*.

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PALABRAS CLAVE: GRADIENTES DE DIVERSIDAD, HIPÓTESIS ESPACIALES, HIPÓTESIS HISTÓRICAS, RIQUEZA DE ESPECIES.

DESCRIPCIÓN

Aunque los gradientes de biodiversidad han sido ampliamente documentados, los factores que gobiernan los patrones de riqueza de especies a gran escala siguen siendo una fuente de intenso debate e interés en ecología, evolución y biología de la conservación. En este estudio se probó si las hipótesis espaciales (relación especie-área, heterogeneidad topográfica, efecto de dominio medio y efecto latitudinal) y las hipótesis históricas (bombeo de especies montañas y museo de especies montañas) explican el patrón de diversidad observado en ranas de lluvia del género *Pristimantis* a lo largo del gradiente altitudinal de los Andes Tropicales. Las ranas de este género presentan un patrón en forma de joroba en la mayoría de los gradientes altitudinales de los Andes Tropicales. Se encontró una gran variabilidad en la relación entre el área y la riqueza de especies a lo largo del área de estudio. La corrección de los efectos de área tuvo poco impacto en la forma del patrón empírico de las curvas de la biodiversidad. Los modelos de dominio medio producen gradientes de riqueza similares a los empíricos, pero el ajuste varió entre cordilleras. El efecto de la heterogeneidad topográfica en la riqueza de especies también varió entre cordilleras. Se encontró una relación negativa significativa entre la latitud y la riqueza de especies. El patrón de riqueza observado también se explica por un mayor tiempo para la especiación (museo de especies) en lugar de altas tasas de especiación en las elevaciones intermedias (bombeo de especies). Estos hallazgos sugieren que los procesos espaciales e históricos explican los patrones de riqueza de ranas *Pristimantis* a lo largo de los Andes Tropicales. Estudios adicionales sobre otros posibles mecanismos (por ejemplo, bióticos y climáticos) son necesarios para elucidar los factores que limitan la distribución de las especies a lo largo de este gradiente de elevación.

* Trabajo de grado

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ABSTRACT

TITLE: USING MOLECULAR PHYLOGENETICS TO ELUCIDATE PATTERNS AND PROCESSES OF DIVERSIFICATION ON ANDEAN ANURANS GENUS *PRISTIMANTIS*.

AUTHOR: FABIO LEONARDO MEZA JOYA* _*

KEYWORDS: DIVERSITY GRADIENT, HISTORICAL HYPOTHESES, SPATIAL HYPOTHESES, SPECIES RICHNESS.

DESCRIPTION

Although biodiversity gradients have been widely documented, the factors governing broad-scale patterns in species richness are still a source of intense debate and interest in ecology, evolution, and conservation biology. Here, we tested whether spatial (species–area effect, topographic heterogeneity, mid-domain null model, and latitudinal effect) and historical (montane species-pump and montane museum) hypotheses explain the pattern of diversity observed along the altitudinal gradient of Andean rain frogs of the genus *Pristimantis*. The genus shows a humpshaped pattern across most of the altitudinal gradients of the Tropical Andes. There was high variability in the relationship between area and species richness along the Tropical Andes. Correcting for area effects had little impact in the shape of the empirical pattern of biodiversity curves. Mid-domain models produced similar gradients in species richness relative to empirical gradients, but the fit varied among mountain ranges. The effect of topographic heterogeneity on species richness varied among mountain ranges. There was a significant negative relationship between latitude and species richness. This pattern is also explained by greater time for speciation (montane museum) rather than faster speciation at mid-elevations (montane species pump). Our findings suggest that spatial and historical processes explain the richness patterns of *Pristimantis* frogs along the Tropical Andes. Explaining the current patterns of biodiversity in this hotspot may require further studies on other possible underlying mechanisms (e.g., biotic and climatic hypotheses) to elucidate the factors that limit the ranges of species along this elevational gradient.

* Research work

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INTRODUCTION

Understanding richness patterns in highly diverse tropical montane regions is a critical issue for ecologists and conservationists (Hutter et al., 2013). Four common types of elevational diversity patterns have been recognized: decreasing with altitude, low plateau, low plateau with a mid-elevational peak, and mid-elevation peak (i.e., hump-shaped or unimodal) patterns (Rahbek 1995, Lomolino 2001, McCain 2009, McCain & Grytnes 2010). Spatial hypotheses (e.g., species-area relationship, mid-domain effect, and spatial environmental heterogeneity) have been regarded as important factors governing species richness gradients (e.g., Rahbek, 1995, 2005; Fu et al., 2006; McCain, 2007a; Chettri et al., 2010; Hu et al., 2011; Stevens et al., 2013; Stein et al., 2014). Abiotic and biotic ecological factors also contribute to explain elevational patterns of biodiversity: Contemporary climate regimen has been recognized as a major predictor of species richness patterns (Rodríguez et al., 2005; McCain, 2010; McCain and Grytnes, 2010) and biotic processes (e.g., ecotone effects, source-sink dynamics, competition, and mutualism) also are a factor that shape diversity gradients (e.g., Terborgh, 1977; Lomolino, 2001; McCain and Grytnes, 2010).

Rain frogs of the genus *Pristimantis* (Caugastoridae *sensu* Padial et al., 2014) are an excellent group for a large-scale study of diversity and distribution. These frogs comprise a major genus of amphibians, with more than 470 species (Padial et al., 2014). They are limited to the Neotropics, from eastern Honduras to Bolivia, including Amazonian Brazil, the Guianas and the Lesser Antilles (Frost, 2013). Most species of the genus occur in moist and forested habitats of the Tropical Andes of Colombia, Ecuador, and Peru (Lynch and Duellman, 1997; Pinto-Sánchez et al., 2012). The elevational range of the genus is broad, from species living at sea level to some occurring above 4500m (Heinicke et al., 2007). There is a number of studies on the taxonomy,

phylogenetics, and biogeography of *Pristimantis* frogs (García-R et al., 2012; Pinto-Sánchez et al., 2012; Padial et al., 2014; among others). However, the large-scale distribution patterns of these frogs are not well understood. Here, we test the spatial and evolutionary origins of elevational richness patterns in the Andes, using *Pristimantis* frogs as a model system.

In Chapter One we describe a hump-shaped pattern of diversity in the Andean rain frogs genus *Pristimantis*, and tested whether this pattern could be explained by spatial hypotheses (species-area relationship, mid-domain effect, topographic heterogeneity, and latitudinal effect). Spatial hypotheses were tested using linear regression models. We examined the fit of the observed diversity to the mid-domain hypothesis using randomizations. The species richness of *Pristimantis* showed a hump-shaped pattern across most of the altitudinal gradients of the Tropical Andes. There was high variability in the relationship between area and species richness along the Tropical Andes. Correcting for area effects had little impact in the shape of the empirical pattern of biodiversity curves. Mid-domain models produced similar gradients in species richness relative to empirical gradients, but the fit varied among mountain ranges. The effect of topographic heterogeneity on species richness varied among mountain ranges. There was a significant negative relationship between latitude and species richness.

In Chapter Two, we use phylogenetic-based methods to identify the evolutionary origins of the hump-shaped patterns of *Pristimantis* frogs in the Andes Mountains. For this, we used elevational distributional data of each species and a time-calibrated phylogeny for the genus. We tested whether the mid-elevation peak of biodiversity observed in rain frogs was explained by the montane species-pump or the montane museum hypotheses. We also estimated the diversification timing to examine it fits the process of Tropical Andes uplift. Finally, we tested for differences in rates of speciation, extinction,

and dispersal among elevational bands dividing the Andean elevational gradient in high, medium, and low elevations. Our results showed that time-for-speciation effect (montane museum model) explained the mid-elevations peaks of diversity in the genus. We also found an early burst of diversification followed by a slowdown in lineage accumulation during the evolutionary history of the genus. Finally, our results strongly support models where diversification rates increase with elevation.

In summary, our findings suggest that spatial factors (i.e., species-area relationship, mid-domain effect, and topographic heterogeneity) are partly linked to the hump-shaped richness patterns in *Pristimantis* frogs, but the relative influence of these processes varied among the different study scales. These observations suggest that spatial effects are not the only mechanism underlying the observed curves of diversity. Latitude also plays an important role shaping the patterns of diversity in this genus. Analyses of Tropical Andes as a whole, showed that the hump-shaped pattern of diversity is explained by a combination of spatial factors (i.e., mid-domain effect) and historical processes (i.e., large tempo for diversification, relatively high diversification rates, and dispersal between elevational bands). Our results increase our current comprehension of the evolutionary mechanisms promoting and maintaining the amphibian fauna in the Tropical Andes.

1 SPATIAL DIVERSITY PATTERNS OF *PRISTIMANTIS* FROGS IN THE TROPICAL ANDES

The unequal distribution of biodiversity on the world is a crucial unresolved issue (Kennedy and Norman, 2005) that has captivated biogeographers and ecologists for centuries (Lomolino, 2001; McCain and Grytnes, 2010; Hu et al., 2011). Although gradients of species diversity have been widely documented, the mechanisms responsible for differences in geographic and taxonomic distribution of biological diversity are still a source of intense debate (Pianka, 1966; Lomolino, 2001; Rahbek, 2005; Stevens et al., 2013; Graham et al., 2014). One of the main gradients of diversity observed in nature is that formed by elevation. The altitudinal patterns of diversity have been studied only recently for many groups of plants and animals, finding four common elevation diversity patterns around the world: decreasing with altitude, low plateau, low plateau with a mid-elevational peak, and mid-elevation peak (i.e., hump-shaped or unimodal) patterns (Rahbek 1995, Lomolino 2001, McCain 2009, McCain & Grytnes 2010). Despite the growing efforts to describe global trends of biodiversity (Jetz & Rahbek 2002, Rahbek 2005, McCain 2009, 2010; Jetz & Fine 2012), there is still a need for the analysis of more altitudinal patterns, especially in the tropical regions where biodiversity is high but poorly sampled. In the case of the megadiverse Andean biota, the diversity patterns of only a handful of taxa have been investigated (Rahbek 1997, Kattan & Franco 2004, McCain 2007a, Hutter et al. 2013, Salazar et al. 2015, among others).

The explanations for observed altitudinal patterns can be classified as climatic, evolutionary, biotic, and spatial (Wiens et al., 2007; McCain and Grytnes, 2010; Acharya et al., 2011). Climate has been evoked as a strong driver of species richness gradients in many taxonomic groups, with temperature, precipitation and productivity as the most commonly studied climatic variables (e.g., Hawkins et al., 2003; Rodríguez et al., 2005; McCain, 2010). Evolutionary history (referring to speciation rates, extinction rates, clade age, and phylogenetic niche conservatism) explains some elevational diversity patterns (e.g., Smith et al.,

2007; Wiens et al., 2007; Hutter et al., 2013). Biotic processes and biological interactions (such as ecotone effects, source-sink dynamics, habitat heterogeneity, habitat complexity, competition, and mutualism) are also related to patterns in species richness (e.g., Terborgh, 1977; Lomolino, 2001; McCain and Grytnes, 2010). Spatial hypotheses, including species-area relationship, mid-domain effect, and spatial environmental heterogeneity, explain some elevation species richness patterns for many taxonomic groups (e.g., Rahbek, 1995, 2005; Fleishman and Mac Nally, 2002; Fu et al., 2006; McCain, 2007a; Chettri et al., 2010; Hu et al., 2011; Stevens et al., 2013; Stein et al., 2014).

Species-area relationships (SAR) predicts a positive relationship between species richness and survey area based on the assumption that more area can bear more species (Rosenzweig, 1995). On mountains, SAR may explain a decreasing richness pattern of diversity when the lower elevations have more land than high elevations (Rahbek, 1997; McCain, 2007a). The same occurs in gradients with more land area at mid-elevations, producing a pattern with a mid-peak of high richness (McCain and Grytnes, 2010). However, the support for this hypothesis is contradictory because the correlation between area and diversity varies from positive to null to even negative (Sanders, 2002; McCain, 2007a, 2009, 2010).

The mid-domain effect (MDE) is a mid-elevation peak of biodiversity based in the stochastic distribution produced by randomly shuffling ranges of distribution within geographic constraints (Colwell and Hurtt, 1994; Colwell and Lees, 2000; Colwell et al., 2004). The constraints may be latitudinal (i.e., latitudes are circumscribed between the poles) or terrestrial (i.e., land is restricted between oceans and elevation of mountain peaks). The conceptual base of MDE has been a hot topic and much controversy has surrounded the assumptions of this model (Koleff and Gaston, 2001; Hawkins and Diniz-Filho, 2002; Zapata et al., 2003, 2005). Despite many studies supporting the mid-domain model predictions, others have found little support, suggesting that this model is not a

general explanation for diversity patterns (Hawkins and Diniz-Filho, 2002; Kerr et al., 2006; Dunn *et al.*, 2007).

Spatial environmental heterogeneity (SEH) may be another determinant of species diversity. Heterogeneous environments can harbor more species, enhance species persistence, and promote adaptive radiations because they can have a rich array of suitable conditions, such as topographic complexity, niche availability, resources, shelter, and refuges (Allouche et al., 2012; Antonelli and Sanmartín, 2011; Fjeldså et al., 2012; Rosenzweig, 1995; Stein et al., 2014; Thuiller et al., 2006). Although environmental heterogeneity has been recognized as a fundamental driver of species richness, evidence supporting this model varies from significant to non-significant or even negative effects (e.g., Fleishman and Mac Nally, 2002; Gazol et al. 2013; Hortal et al. 2009; Laanisto et al. 2013; Tews et al. 2004; Tamme et al. 2010; Stein et al., 2014).

Because the Tropical Andes have a wide latitudinal range, we considered latitude as another key spatial factor for the distribution of diversity. Latitudinal gradients are perhaps the most noticeable and best-studied patterns in ecology (Gaston, 2000; Sanders and Rahbek, 2012; Salazar et al., 2015). With few exceptions (Clarke and Lidgard, 2000), it has been found across taxa that species richness increases with decreasing latitude. However, the causes determining these patterns are still being discussed (Pianka, 1966; Rohde, 1992; Rosenzweig, 1995; Willig et al., 2003; Pyrcz et al., 2013; Salazar et al., 2015).

To investigate the patterns of species richness of *Pristimantis* frogs along elevational and latitudinal gradients of the Tropical Andes we used published data on elevation ranges. First, we described the elevational richness patterns of *Pristimantis* frogs in the Andes Mountains. Then, we assessed how much of the observed elevation patterns of diversity could be explained by area. Third, we tested whether mid-domain effect can explain the empirical patterns along these altitudinal gradients, while accounting for any species-area relationship.

Fourth, we examined the influence of spatial topographic heterogeneity (as a surrogate of spatial environmental heterogeneity) and latitude on the observed diversity patterns. Our results are important to increase our current comprehension of the mechanisms promoting and maintaining the amphibian fauna in the Tropical Andes.

1.1 MATERIALS AND METHODS

1.1.1 Study region

The Tropical Andes extend along the western coast of South America, from Venezuela to northern Chile and Argentina, including extensive areas of Colombia, Ecuador, Peru, and Bolivia (Myers et al., 2000). This region includes many of the Earth's life zones and is considered a biodiversity hotspot due to high species richness and endemism (Myers et al., 2000; Young, 2011). Although the topography of the Tropical Andes is a complex array of mountain ranges, peaks, and basins, the region is commonly divided in two domains, Northern and Central Andes (Gregory-Wodzicki, 2000). The Northern Andes comprise seven mountain ranges north of the Huancabamba depression, whereas the Central Andes includes the largest areas of Andean highlands and comprise six main cordilleras located south of that depression (Figure 1). Because the western cordillera of the Bolivian Andes does not harbor any species of *Pristimantis* frogs, it was excluded from our study. For a detailed description of these mountain ranges see Duellman (1979), Duellman and Pramuk (1999), and Duellman and Lehr (2009). Here we consider 500m a.s.l., a commonly used value (Anderson et al., 2011) as the lower elevation limit of the Tropical Andes.

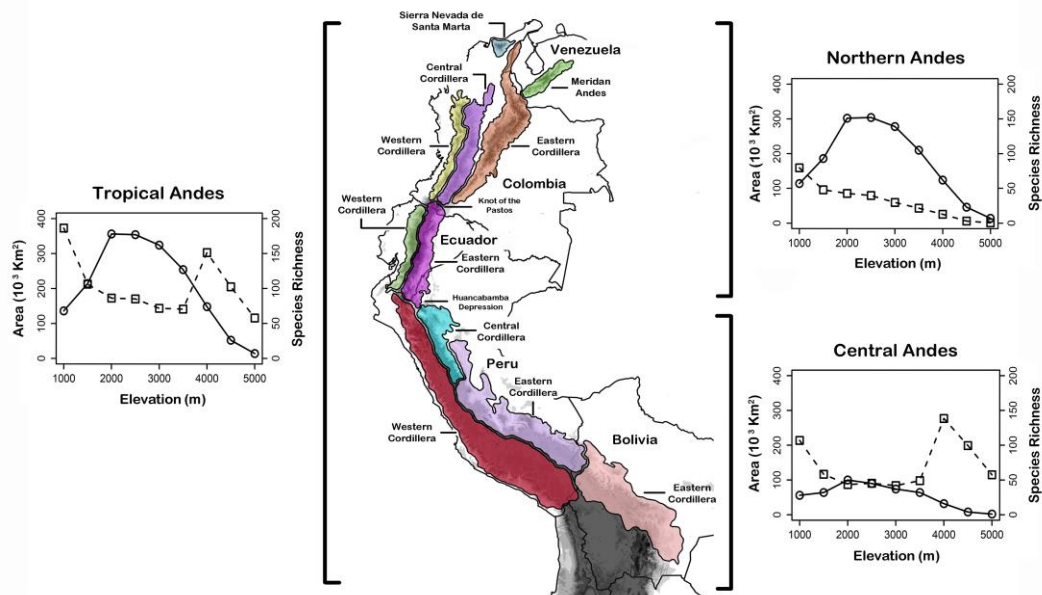


Figure 1. Map of South America indicating the Tropical Andes (dark relief) with the main domains and mountain ranges (or cordilleras) where the genus *Pristimantis* occurs. Lateral figures show the patterns of area (open squares and dotted lines) and species richness (solid circles and solid lines) for the Tropical Andes, Northern Andes, and Central Andes.

1.1.2 Species richness pattern

To estimate altitudinal richness patterns we compiled a gamma-diversity database of the Andean species of *Pristimantis* frogs (see Annex 1). We followed the taxonomic proposal of Padial *et al.* (2014) to define the genus *Pristimantis*. Elevational data were obtained primarily from the Amphibian Species of the World database (Frost, 2013) and the Global Amphibian Assessment initiative (<http://www.iucnredlist.org>). These data were filtered based on original species descriptions, range extension notes, and well-supported observations (e.g., records from online museum catalogues). The occurrence records were verified by experts on the *Pristimantis* of each country (see Acknowledgements). The elevational range of each species was standardized by interpolation; a method that assumes continuous ranges between the minimum and maximum altitudinal records. Species richness was defined as the number of species occurring in each of nine 500m-wide altitudinal bands, following standard practice (e.g., Rahbek, 1997; Smith *et al.*,

2007; Kozak and Wiens, 2010; Hutter *et al.*, 2013). We tested other band-widths that were either wider (1000 m) or narrower (250 m) than 500m. The analyses with these bands are not shown because wider bands were too few for statistical analysis and narrower bands were qualitatively similar than those using 500m-wide bands.

1.1.3 Species-area relationship

Spurious elevational diversity patterns may be due to differences in post-sampling treatment of data (Rahbek, 1995; McCoy, 2002; Nogués-Bravo *et al.*, 2008; McCain and Grytnes, 2010). Rahbek (1995) showed that the pattern where diversity decreases with altitude is in some cases the outcome of non-standardized samples with respect to area. Once samples are standardized a decreasing trend sometimes reveals itself as a hump-shaped pattern. To examine the influence of area on the observed diversity curves, we calculated the area of each 500m elevational band to Tropical Andes, each Andean domain, and each mountain range. The area was calculated using a global digital elevation model (GTOPO30) in Quantum GIS software (QGIS Development Team, 2013). The relationship between the species richness and the size of the area was examined with three regression models (McCain, 2007a): one linear (variables not transformed), another semi-logarithmic (log-transforming area), and another curvilinear (log-transformed both area and species richness). We used the second order Akaike information criterion (AICc) to select the best fitting model. We calculated area-corrected diversity curves using a power function model ($S = cA^z$) with a global taxon-specific z value (slope of linear regressions) for those mountain ranges with significant species-area effects.

1.1.4 Mid-domain effect

We analyzed whether observed gamma diversity patterns fit those expected under mid-domain hypothesis (Colwell and Hurtt, 1994; Colwell *et al.*, 2004)

using the program Mid-Domain Null (McCain, 2004). This program uses a Monte Carlo procedure to simulate species richness curves based on range midpoints or empirical range sizes within the domain limits of the study. The empirical species richness curves were compared with predicted curves based on 50,000 simulations sampled without replacement from empirical species range sizes. The expected results were plotted against the empirical elevation richness to visually examine whether our observed results deviate from the null altitudinal range distribution. We tested the fit between the observed empirical values and the predicted number of species under the mid-domain model using both linear and quadratic regressions. We chose the model with the lowest AICc as the best fitting model. Sampling of simulations with replacement yielded similar results (not shown). The range of species known only from a single locality was increased ± 5 meters to provide a non-zero size range in our analysis, following Hutter *et al.* (2013). Because a species-area relationship is expected to modify the predictions of mid-domain model, we assessed if the fit to this model improved when area effect was accounted (McCain 2007a).

1.1.5 Environmental heterogeneity effect

Some of the most used measures of EH are topographic heterogeneity, diversity of land cover types, and plant species richness (Stein *et al.*, 2014). Here, we use topographic heterogeneity to evaluate the interaction between EH and species richness of *Pristimantis* frogs. Topographic heterogeneity was calculated for each 500m-wide altitudinal bands of Tropical Andes, each Andean domain, and each mountain range, using the topographic ruggedness index (TRI) developed by Riley *et al.* (1999). This index expresses the difference in elevation between neighborhood cells of a digital elevation grid. The TRI was calculated on the GTOPO30 global digital elevation model using the function Ruggedness Index in the Terrain Analysis plugin under QGIS software. Topographic heterogeneity effect was evaluated using three linear regression models: linear (variables not transformed), semi-logarithmic (log-transformed TRI), and curvilinear (log transformed variables). Since area is

often related to SHE (Rosenzweig, 1995), we repeated the topographic heterogeneity analysis accounting for area using as the dependent variable the TRI values divided by the squared root of area. We used AICc to select the best fitting model. Unless otherwise indicated, all statistical analyses were performed using R (R Development Core Team, 2013).

1.1.6 Latitudinal effect

To estimate latitudinal trends, we calculated the mid latitudinal point for each mountain range. Latitudinal effect was evaluated via linear regressions using data from species richness, mid elevational point, mid latitudinal point, and average TRI for each main mountain range. We evaluated four models, with species richness being explained by latitude (model 1), by latitude and altitude (model 2), by latitude and TRI (model 3), and an intercept-only model (model 4). We estimated the parameters' coefficient of these models using averaged modeling (Anderson, 2008), implemented in the R package AICcmodavg (Mazerolle, 2015).

1.2 RESULTS

1.2.1 Species richness pattern

Rain frogs genus *Pristimantis* were distributed over a large altitudinal range in Tropical Andes, with the lowest altitudinal distribution in the lowest elevation limit (500m) and the highest altitudinal distribution up to 4538m. The highest species richness is found in the North Andes (311 spp) and droop markedly in the Central Andes (100 spp), with the lowest diversity in the Bolivian Andes (11 spp). We found a hump-shaped pattern in the tropical Andes and each of its domains and mountain ranges, except in the Bolivian Andes. The elevation of the richness peak varied among domains and mountain ranges (Figure 1, Annex 7). Richness peaked between 2000 and 3500m in the Tropical and

Northern Andes and between 1500 and 3000m in the Central Andes. In the Eastern Cordillera of Bolivia, there was a low plateau pattern, with high species richness at lower elevations (500–2000m a.s.l.).

1.2.2 Species-area relationship

Surface area did not always show a decreasing pattern with ascending elevations. The area of the Tropical and Central Andes (Figure 1) domains decreased with increasing elevation up to 2500-3000m, then increased to reach a peak at an elevation between 3500m and then decreased at higher elevations (Figure 1). In both cases, the peak in area above 3500m of elevation coincided with the existence of high-elevation plateau on the Peruvian and Bolivian Andes. In contrast, the area of the Northern Andes (Figure 1) showed a decreasing pattern, where the area decreased monotonically with an increase of elevation. The area profiles on the main mountain ranges of the Northern Andes domain generally decreased with elevation, whereas the area in the mountain ranges of Central Andes showed a hump at high elevations (see Annex 7).

Surface area did not always show a positive correlation with species richness (Figure 2). The curvilinear effect was the best-fit model to species-area relationships on the Tropical Andes and its domains ($\Delta AICc > 7$). There was no relationship between area and species richness in the Tropical ($r^2 = -0.114$, p-value = 0.681) and Central Andes ($r^2 = -0.036$, p-value = 0.424). In contrast, a significant effect was found in the species-area relationship along the altitudinal gradient in the Northern Andes ($r^2 = 0.777$, p-value < 0.001). Similar results were recorded for all area-species relationships along the main Andean mountain ranges where *Pristimantis* frogs occur. In all cases, the curvilinear effect was always the best-fit model of species-area relationships. Significant curvilinear species-area effects were detected in five mountain ranges on the Northern Andes, with r^2 values ranging from 0.396 to 0.740. Non-significant

relationship between diversity and area (p-value >0.05) were detected along each main mountain range of the Central Andes (see Annex 2).

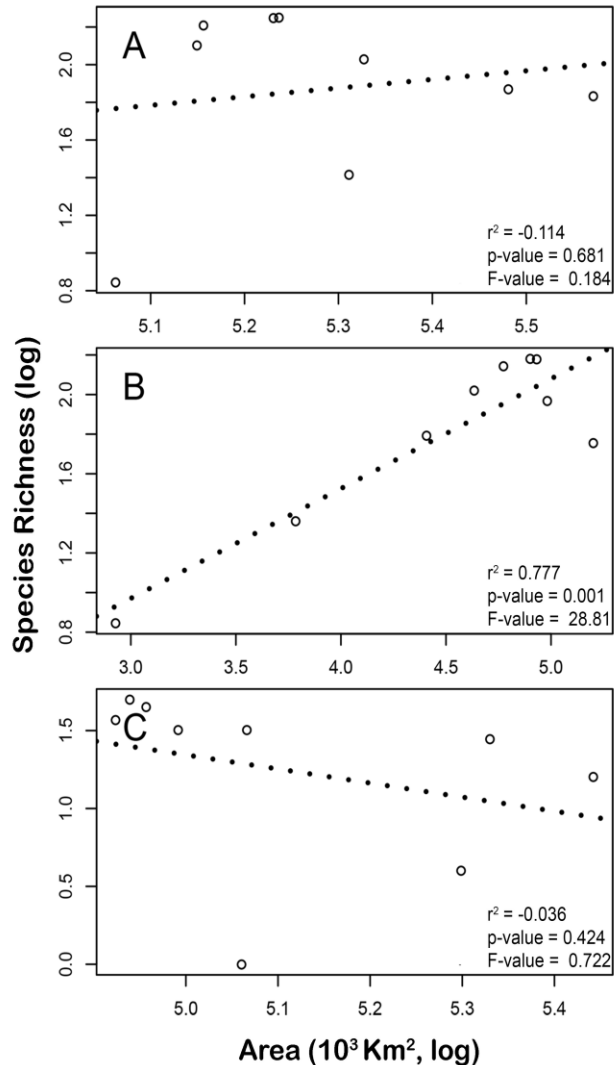


Figure 2. Species-area effects in elevational gradients of the Tropical (A), Northern (B), and Central Andes (C). Values inside each figure are results of simple linear-regressions. All the F-values used $df = 1,7$.

Curvilinear regressions to calculate global taxon-specific z values for correcting area effects give a global z value of 0.36 with 95% confidence limits of 0.18 - 0.54 for *Pristimantis* frogs. Correcting for curvilinear area effects had little impact in the shape of the empirical pattern of biodiversity curves. The shape of the corrected pattern of species richness along the altitudinal gradient in the Northern Andes was very similar to the empirical pattern with the diversity peak

located at high elevations (Figure 2B). Similarly, in each main mountain range where significant curvilinear species-area effects were detected, the diversity patterns showed no change in the location of the diversity peak (see Annex 8).

1.2.3 Mid-domain effect

The MDE analysis produced similar gradients in species richness relative to the empirical gradients, but the fit of the model varied among regions (Figure 3). We identified MDE as a good predictor of species richness in all the Tropical Andes and in the Northern Andes domain, whereas the explanatory power of the model was moderate in the Central Andes domain. The good fit to the null model predictions in the Tropical and Northern Andes was demonstrated by the high r^2 values (0.86 and 0.87, respectively, p -value < 0.001). In contrast, moderate r^2 value was observed in the Central Andes (0.65, p -value 0.005). Quadratic and linear models gave similar results based on r^2 and AICc values (Table 1).

Table 1. Explanatory power of spatial constraint effects (MDE) using linear and quadratic regressions statistics.

Geographic region	Model	F _(1,7)	p-value	r^2	AICc
Tropical Andes	Linear	31.42	0.0008	0.79	73.9
	Quadratic	27.51	0.0001	0.86	70.4
Northern Andes	Linear	55.16	0.0001	0.87	84.1
	Quadratic	24.42	0.0013	0.85	85.4
Central Andes	Linear	15.85	0.0053	0.65	56.6
	Quadratic	8.17	0.0194	0.64	57.5

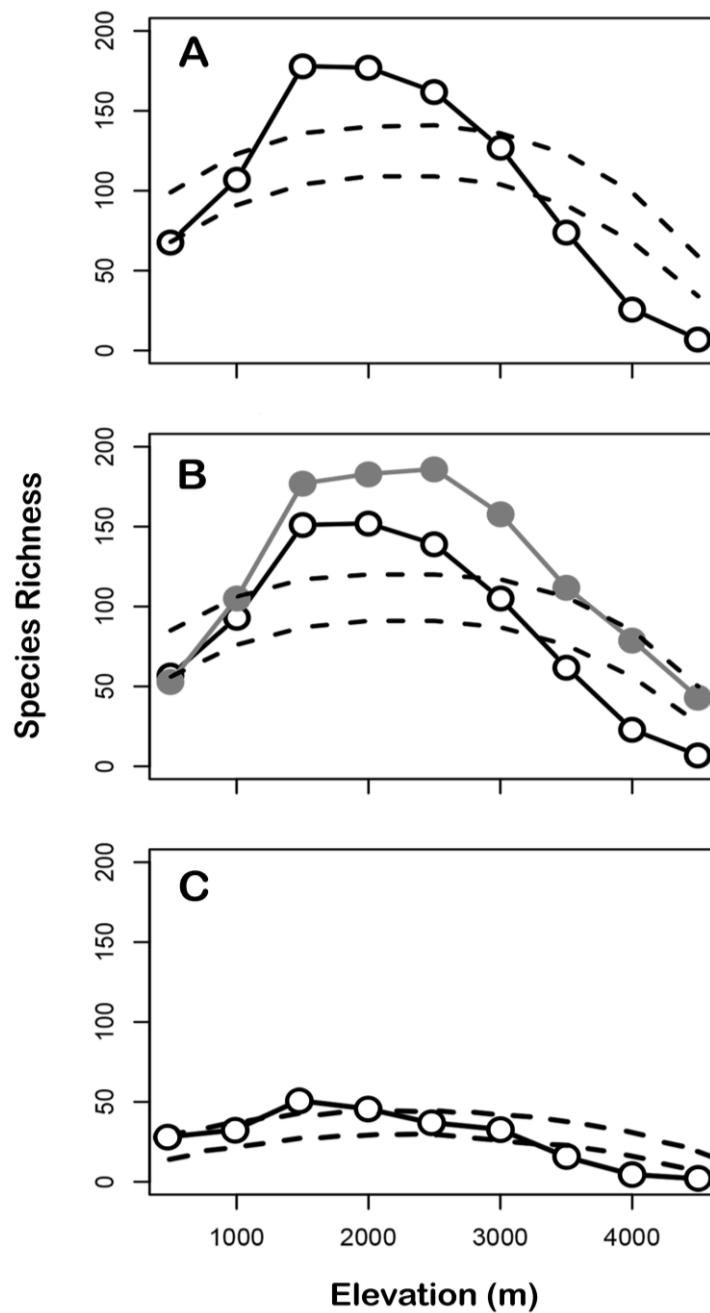


Figure 3. Hump-shaped patterns in species richness for *Pristimantis* frogs along elevational gradients of the Tropical (A), Northern (B), and Central Andes (C). The 95% confidence intervals generated from the mid-domain null model plotted for comparison (dashed lines). Gray line in B indicates the curvilinear area-corrected richness pattern.

Deviations from the null model occurred at mid-elevations and highest elevations for the Tropical Andes and the two domains. The fit to spatial constraints was highly variable in each mountain range studied here. The

quadratic regression was the best model ($\Delta\text{AICc} = 5.5$) for area-corrected diversity curves with MDE predictions for the Northern Andes. This model improved the resulting fit of the model with an r^2 value of 0.9 (p-value <0.001). However, spatial constrain fitting was variable in each mountain range studied here, even when we accounted for species-area effects (see Annex 3).

1.2.4 Environmental heterogeneity effect

Topographic heterogeneity and species richness relationships on Tropical Andes and its domains were best fit by curvilinear models (Annex 4). There was no relationship between TRI and species richness in Tropical ($r^2 = -0.1349$, p-value = 0.831) and Central Andes ($r^2 = 0.018$, p-value = 0.320), but a significant effect was found in the Northern Andes ($r^2 = 0.366$, p-value = 0.049). Similarly, a curvilinear effect was the best-fit model in the main Andean mountain ranges studied here. Significant effects were detected in three mountain ranges on the Northern Andes, with r^2 values ranging from 0.767 to 0.847. In contrast, in the Central Andes only the Eastern Cordillera of Peru showed a significant effect ($r^2 = 0.445$; p-value = 0.030).

1.2.5 Latitudinal effects

We found a negative relationship between species richness and latitude in the three models (model 1, 2, and 3). The models with the best fit were model 1 (species richness explained by latitude) and model 3 (species richness explained by latitude plus spatial topographic heterogeneity), which differ by a ΔAICc of 0.94. Based on average modeling values of the three proposal models, latitude was the most important parameter explaining species richness of *Pristimantis* frogs (model-averaged estimate = -4.55) in comparison with topography heterogeneity (model-averaged estimate = -0.07) and elevation (model-averaged estimate = 0.01).

1.3 DISCUSSION

The Tropical Andes harbor an extraordinary number of species, but a detailed picture of the spatial distribution of this biodiversity along altitudinal and latitudinal gradients is still incipient (Mutke et al., 2014). Many studies have documented that species richness along elevational gradients in Tropical Andes generally follows a hump-shaped pattern with the highest richness at some mid-elevational point. Recent evidence suggests that historical and ecological processes are the major drivers of this pattern in Andean frogs (Hutter et al., 2013; Castroviejo-Fisher et al., 2014). Here we found that in *Pristimantis* rain frogs, the hump-shaped richness pattern is consistent across multiple mountain ranges, even when accounting for area. We also found that in some Andean elevational gradients, MDE seem to be a good predictor of species richness patterns, but the fit to the model varied among mountain ranges. Our findings suggest that spatial factors are partly linked to biodiversity patterns.

1.3.1 Species richness pattern

The richness of several Tropical Andes clades reaches its diversity peak at intermediate elevations (e.g., birds: Rahbek, 1997; Kattan and Franco, 2004; McCain, 2009; mammals: McCain, 2007a,b; glassfrogs: Hutter et al., 2013; ferns: Karger et al., 2011; Salazar et al., 2015). This spatial pattern has also been observed in several clades from many other mountain regions around the world (e.g., treefrogs of Middle America: Smith et al., 2007; salamanders of Middle America: Wiens et al., 2007; fishes of Tibetan Plateau: Li et al., 2009; salamanders of North America: Kozak and Wiens, 2010; birds of Himalaya: Acharya et al., 2011; among others). *Pristimantis* frogs generally showed a hump-shaped pattern with the highest richness at mid-elevations in the Tropical Andes. This pattern was consistent along each Andean mountain range studied here except for the Bolivian Andes, where we observed a low plateau pattern, with the high species richness at lower elevations.

The only other elevation gradient of diversity for the Bolivian Andes, regarding dung beetles (Herzog et al., 2013), shows a distribution pattern with a peak of highest richness between 250 and 499m a.s.l., similar to what we observed in *Pristimantis*. The low plateau pattern in Bolivia could be associated with contemporary climatic factors (e.g., temperature, productivity and water availability), which have been proposed to influence elevational biodiversity patterns (see below). Alternatively, due the arid and semi-arid climatic conditions in most highlands of the Bolivian Andes (Garreaud et al., 2003), we hypothesize a higher rate of extinction and lower rate of speciation on this area relative to humid Andean lowlands adjacent to the Amazonia. Furthermore, the retention of ancestral climatic tolerances (niche conservatism hypothesis) could have constrained the current geographic distribution of most lowland species, as suggested by Herzog et al. (2013). Additional analyses of elevational diversity in the Bolivian Andes will help to the understanding of the mechanism driving this pattern of biodiversity.

1.3.2 Species-area relationship

Area is an important factor to explain species richness patterns along elevational gradients because different altitudinal bands have different areas (Körner, 2000; Sanders, 2002; McCain and Grytnes, 2010). On mountains, area usually declines with increasing elevation and, as a result, gamma diversity tends to follow the same pattern (Rosenzweig, 1995; Rahbek, 1997; Lomolino, 2001; McCain, 2007a). However, in large and complex mountain systems, such as the Tropical Andes, relief variation influences elevational belt areas, resulting in area profiles that do not follow a uniform pattern.

Our results show that area influences richness patterns of *Pristimantis* frogs in the Tropical Andes. In 45% of the mountain ranges studied here area was related to the elevational pattern in species richness (see Annex 2). Interestingly, the area effect was more pronounced in the Northern Andes,

where 71% of the elevational gradients of species richness showed strong responses to area. This effect could be associated with the fact that in the Northern Andes, area generally decreases with elevation, which leads to strong species-area relationships (see McCain, 2007a). In contrast, in the Central Andes, area showed a peak at high elevations coinciding with the extensive areas of altiplano in highlands, resulting in negative or non-significant relationships between diversity and area.

The high variability in the response of elevational diversity to area indicates that it influences species richness patterns of *Pristimantis* frogs, but it is not the main driver of the observed curves of diversity. Similar responses have also been reported in previous analyses of several mountain systems (McCain, 2007a; Karger et al., 2011). Such results suggest that area could represent a source of error if is not properly accounted for in the analyses, but it is not the sole explanatory mechanism of the observed curves of biodiversity (McCain, 2007a).

1.3.3 Mid-domain effect

Despite the shape of the empirical biodiversity curves deviating from the MDE prediction, regressions analysis (linear and quadratic) showed that this model explains an important proportion of the altitudinal patterns of *Pristimantis* diversity in the Tropical and Northern Andes. Spatial constraints around main mountain ranges studied here were also highly variable (see Annex 3). In fact, only 45% of the elevational gradients were consistent with MDE predictions. Previous analyses suggested that the species-area relationship influencing the MDE fit in several degrees (McCain, 2005, 2007a). Some studies have found significant increases in MDE fit (Sanders, 2002; Bachman et al., 2004) when area effect was accounted for, whereas others found no large improvements or even decreases (McCain, 2005, 2007a, 2009). We found that the fits to MDE vary when area effect was included in the model, being improved in some cases, but worsened in others. After the area effect in the model was included, only one gradient fits with MDE (see Annex 3), supporting the idea that area is

an important factor that should be taken into consideration in the spatial analysis of diversity (see McCain, 2007a).

1.3.4 Environmental heterogeneity effect

Our analysis indicates that topographic heterogeneity effects on species richness of *Pristimantis* frogs differs spatially. We did not find any significant relationship between topographic heterogeneity and species richness in Tropical Andes (as a whole) or in the Central Andes domain. Remarkably, topographic effects were more pronounced in the Northern Andes domain, where topographic heterogeneity explains partially the observed pattern of species richness in this domain and three of its mountain ranges (Annex 4). This positive relationship has been related to the fact that highly heterogeneous regions provide more long-term stable niches to support more species than regions of lower heterogeneity (Rosenzweig, 1995; Thuiller et al., 2006; Allouche et al., 2012; Stein et al., 2014). The absence of topographic heterogeneity effects in southern latitudes (i.e., Central Andes domain and most of its mountain ranges) may be due to the strong influence of climatic seasonality of the Andes south of the Equator, a recognized factor limiting the occurrence of tropical species (see below). Although our results shown that topographic heterogeneity is in some cases a good predictor of species richness patterns of *Pristimantis* frogs, the high level of variation found in our analysis suggests that other factors are also important driving for species diversity. Further studies may help to understand whether other components of spatial environmental heterogeneity (e.g., land cover types, vegetation diversity, and soil type, among others) also explain the species richness patterns in montane anurans.

1.3.5 Latitudinal effect

The highest diversity of the genus *Pristimantis* was found in latitudes slightly north of the equatorial line and decreased in northern (Sierra Nevada de Santa

Marta in Colombia and Meridian Andes in Venezuela) and southern (Bolivian Andes) latitudes. In one of the few studies on the latitudinal gradient of biodiversity in the Tropical Andes, a similar latitudinal pattern was found in eastern Andean Lepidoptera species. However, in these butterflies and moths the peak of highest richness is reached at southern latitudes between the Huancabamba depression and central Peru (Pyrzcz et al., 2013). In Lepidoptera species, the latitudinal gradient has been explained as a result of greater area, age of the southern tropical Andes, and seasonal temperatures of the Andes south of the Equator (Pyrzcz et al., 2013). However, since the highest richness of *Pristimantis* frogs was found in the northern tropical Andes, we consider that area and geological age may not represent the main factors shaping the latitudinal diversity of the genus. The dramatic decrease in species richness in the Bolivian Andes has been observed in other taxa (birds: Rahbek and Graves, 2001; insects: Pyrcz et al., 2013). This phenomenon has been related to increased seasonality in southern Bolivia, which has been recognized as a crucial limiting factor for tropical species (Pyrzcz and Gareca, 2009; Pyrcz et al., 2013). Our data also suggest that in the western Andes there is higher species richness in northern rather than in southern latitudes among *Pristimantis* frogs; further analyses on other taxa may reveal if this is a common pattern and which mechanisms are shaping latitudinal patterns of species richness in Andean organisms.

1.3.6 Climatic drivers

Several ongoing climatic factors (such as temperature, productivity, and precipitation) have been proposed to influence elevational biodiversity patterns in a wide range of organisms along Andean elevational gradients (birds: Terborgh, 1977; McCain, 2009; bats: McCain, 2007b; epiphytes: Krömer et al., 2005). However, few studies have investigated the role of these variables explaining elevational patterns of species richness among Andean amphibians. Recent evidence from the Antioquia department in the Central Cordillera of Colombia shows a high correlation between amphibian species richness and

temperature and precipitation (Ortiz-Yusty et al., 2013). An analysis of this kind, extended to the Andes Mountains, might indicate if climatic factors are also critical to explaining the diversity of *Pristimantis*. The fact that *Pristimantis* frogs are restricted principally to moist forest habitats (Lynch and Duellman, 1997; Pinto-Sánchez et al., 2012), suggests that a combination of climatic optimal conditions and local environmental features play an important role in shaping the species richness patterns. Further studies to examine the relationship between species richness and climatic variables should compile climatic data estimates per altitudinal band in Tropical Andes, a piece of information currently unavailable. Such data could be analyzed using regression analysis models (e.g., ordinary least squares, generalized least squares, among others) and have the potential to shed more light on how climate variables are important in shaping diversity curves in rain frogs and other taxa.

2 HISTORICAL DIVERSIFICATION PROCESSES EXPLAINING THE ELEVATIONAL RICHNESS PATTERN OF *PRISTIMANTIS* FROGS IN THE ANDES

The first depiction of the spatial patterns of Neotropical biodiversity along latitudinal gradients was made von Humboldt and Bonpland (1807) in their seminal *Essai sur la géographie des plantes*. They revealed that altitude was another crucial dimension of spatial distribution of species and made the first description of elevational changes in plant communities along Andean mountains. Nowadays, elevational gradients are recognized as one of the most fundamental patterns of life on Earth and have become bulwarks in studies of biogeography, ecology, evolution, and conservation biology (Lomolino, 2001; McCain and Grytnes, 2010; Sanders and Rahbek, 2012). For the Andes, we now know the elevational diversity patterns of groups of birds (Rahbek, 1995, 1997; Kattan and Franco, 2004), mammals (McCain, 2007a; Mena et al., 2011), frogs (Hutter et al., 2013; Meza-Joya and Torres, 2016), fishes (Jaramillo-Villa et al., 2010), and ferns (Salazar et al., 2015). Most of these studies have recovered a hump-shaped or unimodal pattern of biodiversity, with the high richness concentrated at intermediate Andean elevations (e.g., Rahbek, 1995, 1997; Kattan et al. 2004; McCain, 2007a; Mena et al., 2011; Hutter et al., 2013; Meza-Joya and Torres, 2016), a pattern observed in several clades from many other montane regions worldwide (e.g., Middle American treefrogs: Smith et al., 2007; Middle America salamanders: Wiens et al., 2007; Tibetan fishes: Li et al., 2009; North American salamanders: Kozak and Wiens, 2010; Himalayan birds: Acharya et al., 2011; among others).

The accumulation of elevational data for many montane biotas calls for the question: what are the processes that produce such recurrent hump-shaped pattern? The potential explanations for the mid-elevation peak of biodiversity frequently observed on montane biotas have been traditionally explained based on climate, space, and biotic processes; and more recently on evolutionary history (Pianka, 1966; Gaston, 2000; McCain, 2007b). Elucidating the

evolutionary origins of elevational biodiversity patterns requires a phylogenetic framework to incorporate the processes of speciation, extinction, and dispersal, all of which are responsible for the accumulation of species within a community or region (Ricklefs 1987; Smith et al., 2007; Wiens et al., 2007). Two evolutionary hypotheses have been proposed to explain the mid-elevation pattern of biodiversity frequently observed on montane biotas. The montane museum hypothesis (Smith et al., 2007; Wiens et al., 2007) predicts that more species occur at mid-elevations because the habitats presently at these elevations were occupied first in the evolutionary history of a given group, leaving more time for speciation and species accumulation (i.e., the time-for-speciation effect; Stephens and Wiens, 2003). The montane species-pump hypothesis (Smith et al., 2007) instead predicts that more species occurs at mid-elevations due to higher net diversification rates resulted from faster speciation events.

Support for the montane museum hypothesis have been found in elevational patterns of Middle (Wiens et al., 2007) and North American salamanders (Kozak and Wiens, 2010), Middle American treefrogs (Smith et al., 2007), Asian Tibetan fishes (Li et al., 2009), and Andean glassfrogs (Hutter et al., 2013). The montane species-pump hypothesis fits only the altitudinal pattern of the Middle American treefrogs (Smith et al., 2007). Several authors have proposed that high diversity of Andean taxa is due to faster speciation related to orogenic events and historical climatic change (e.g., Lynch and Duellman, 1997; Kattan et al., 2004; Rosser et al., 2012), a scenario similar to the montane species-pump. Moreover, results of phylogenetic studies in several taxa inhabiting the Andes Mountains show patterns and rates of speciation also consistent with the montane species-pump (e.g., plants: Hughes and Eastwood, 2006; butterflies: Hall, 2005; Rosser et al., 2012; birds: Ribas et al., 2007; Sedano and Burns, 2010; frogs: Graham et al., 2004; Santos et al., 2009). To summarize, the high richness at intermediate elevations frequently fits the montane museum hypothesis rather than montane species-pump hypothesis. However, this result is far from conclusive because the evidence is just a handful of studies.

Furthermore, even though the two hypotheses are not mutually exclusive, few studies test them explicitly and jointly to determine the relative strength of the evolutionary process that conform these hypotheses. Here we perform such analysis using *Pristimantis*, one of the most diverse genera of vertebrates (Padial et al., 2014).

Among Neotropical regions, Andes Mountains harbor extremely high species-rich assemblages of many animal and plant taxa, being recognized as a biodiversity hotspot (Ceballos and Ehrlich, 2006; Kier et al., 2009; Myers et al., 2000). One of the animal taxa most representative of the high Andean biodiversity and endemism are the anurans (Duellman, 1999). Tropical Andes harbor the greatest frog diversity worldwide with a high number of restricted-range species that are increasingly threatened by habitat modification and climate change (e.g., Grenyer et al., 2006; La Sorte and Jetz, 2010; Myers et al., 2000). Anuran communities in the Andes Mountains are often dominated by direct-developing *Pristimantis* frogs into the family Craugastoridae (Lynch and Duellman, 1997; Mendoza et al., 2015; Padial et al., 2014; Pinto-Sánchez et al., 2014), the richest genus of vertebrates in the world with more than 470 species (Padial et al., 2014).

Rain frogs (species of the genus *Pristimantis*) are an excellent group for an evolutionary analysis of the patterns of diversification along the altitudinal gradient in Tropical Andes for several reasons. The geographic distribution and evolutionary history suggests a South American origin for the genus (Hedges et al., 2008; Heinicke et al., 2007; Mendoza et al., 2015; Pinto-Sánchez et al., 2012), currently with most of its species occurring in the Andes of Colombia, Ecuador, and Peru (Lynch and Duellman, 1997; Pinto-Sánchez et al., 2012). *Pristimantis* frogs reach their diversity peak at intermediate elevations (Meza-Joya and Torres, 2016). Although the unimodal pattern of biodiversity observed in *Pristimantis* frogs is partly linked to spatial factors (i.e., mid-domain effect, species-area relationship, and environmental heterogeneity), the evolutionary processes underlying this pattern of distribution remain poorly understood

(Meza-Joya and Torres, 2016). Previous indirect sources of evidence indicate that the altitudinal pattern of *Pristimantis* can be explained by the montane species-pump hypothesis. The high diversity of the genus has been related to faster speciation linked to orogenic events and historical climatic regimens (Lynch and Duellman, 1997), a similar situation than that proposed by the montane species-pump hypothesis. However, contrary to the montane museum hypothesis, a phylogenetic analysis of Terrarana frogs (which includes the genus *Pristimantis*) showed that younger clades have more species than older ones (Gonzalez-Voyer et al., 2011). Similarly, middle elevational bands on northwestern Andes has been identified as main areas for the radiation of the genus, with some instances of speciation occurring in the low elevational bands (Mendoza et al., 2015). None of these analyses is a direct test of the evolutionary hypotheses at the genus *Pristimantis* level.

Fortunately, the growing molecular data available for the species of *Pristimantis* and recently developed computational methods to study macroevolution allow a direct test of the two evolutionary hypotheses using a phylogenetic framework. In this chapter, we seek to identify the evolutionary origins of elevational richness patterns of *Pristimantis* frogs in the Andes Mountains. To do this, we combined elevational distributional data of each species and a time-calibrated phylogeny for the genus. We further tested if the mid-elevation peak of biodiversity observed in this genus was explained by the montane species-pump or the montane museum hypotheses. We also tested if diversification occurred simultaneously with or after the most recent uplift phases of Tropical Andes. Our results increased our current comprehension of the evolutionary mechanisms promoting and maintaining the amphibian fauna in the Tropical Andes.

2.1 MATERIAL AND METHODS

2.1.1 Elevational richness data

We followed the taxonomic proposal of Padial et al. (2014) to define *Pristimantis*, but recognizing *Tachiramantis* as a new genus (Heinicke et al., 2015). Elevational data for Andean species of *Pristimantis* frogs were obtained from Meza-Joya and Torres (2016), excluding all former *Tachiramantis* species (Heinicke et al., 2015). This database includes data for 367 species of *Pristimantis* frogs inhabiting the Andes Mountains, having for each species the minimum, maximum, midpoint, and range size of elevation (meters above sea level). For a more detailed description of these data see Annex 1. Posterior data analysis was performed using 500-m-wide altitudinal bands following standard practice (e.g., Rahbek, 1997; Smith et al., 2007; Wiens et al., 2007; Kozak and Wiens, 2010; Hutter et al., 2013).

2.1.2 Phylogeny

We used the molecular time-calibrated maximum clade credibility (MCC) tree of the genus *Pristimantis* published by Pinto-Sánchez et al. (2012). This tree comprises 136 nominal species, including 24 non-Andean and 112 Andean taxa, the latter accounting for one third of the *Pristimantis* diversity in Tropical Andes. Non-Andean taxa were excluded from our analyses. For montane species-pump and montane museum analyses, we created a ‘clade tree’, leaving only one sample for each species (i.e., one terminal for each species) pruning from the MCC tree non-specific taxa (i.e., terminals without identification to the species level, *affinis*, or *confer*). For these analyses, we identified 10 monophyletic clades in the pruned MCC tree (Annex 9). For diversification analyses, outgroup species were pruned from the MCC tree. These analyses were implemented to a regional scale including Tropical Andes as a whole. All analyses were performed using R packages (R Development Core Team 2015).

2.1.3 Montane species-pump hypothesis

We tested for a relationship between elevational range and diversification rates. For each clade, we calculated the mean elevational midpoint from all sampled species within the clade and determined a diversification rate with the method-of-moments estimator (Magallón and Sanderson, 2001) using Geiger v. 2.0.6 (Harmon et al., 2015). A positive relationship between these variables supports this hypothesis. Although stem-group ages incorporate incomplete sampling in the phylogeny better than crown group ages (see Hutter et al., 2013), we used both ages independently. Because the uncertainty on estimating relative extinction rate (see Rabosky, 2010), we repeated the analysis using the extinction rate derived from diversification analyses ($\mu = 0.02$; see below), and alternatively low, middle and high relative extinction values ($\varepsilon = 0, 0.45$, and 0.90 , respectively). The relationship between diversification rate and elevation was assessed using a phylogenetic generalized least squares regression (PGLS; Martins and Hansen, 1997) with Caper version 0.5.2 (Orme et al., 2013). We also conducted an independent analysis using the ancestral elevation midpoint instead of the mean elevational midpoint. For this, we assessed four evolutionary models (Brownian motion, white noise, lambda model, and Ornstein-Uhlenbeck) following Hutter et al. (2013). Then, the branches MCC tree was transformed according to the best-fitting model of character evolution based on the AICc values. Model testing and tree transformation were performed using Geiger. Ancestral elevational midpoints were estimated using PGLS ancestral reconstruction in Ape version 3.4 (Paradis et al., 2015).

2.1.4 Montane museum hypothesis

Montane museum hypothesis was tested by assessing the relationship between the colonization time of each elevational band and the species richness occurring at that band. Support of this hypothesis is observed as a positive relationship between these variables. Species richness was calculated as the

number of species occurring in each altitudinal band. Colonization times were estimated from ancestral midpoint of elevational range reconstruction (see above), recording the age of the oldest node with an ancestral midpoint occurring in each band. The relationship between species richness and the first time of colonization was examined with linear regressions using both raw values and log-transformed richness values (following Rabosky, 2012). To address possible artefacts related to reconstructions, we simulated species' elevational ranges and tested whether the observed time-richness relationship was stronger than expected under stochastic sampling (following Kozak and Wiens, 2010) and performed additional reconstructions including the MCC tree outgroup taxa to address uncertainty at the root (following Hutter et al., 2013).

2.1.5 Diversification Analyses

To examine the tempo and mode of diversification of *Pristimantis* frogs, we calculated the number of lineages through time (LTT) using the functions implemented in Ape version 3.4 (Paradis et al., 2015), Laser version 2.4-1 (Rabosky and Schliep, 2013), Phytools version 0.5-20 (Revell, 2016), TreePar version 3.3 (Stadler, 2015a), and TreeSim version 2.2 (Stadler, 2015b). To visualize the pattern of diversification for the MCC tree we constructed a LTT plot and simulated 1000 trees under a pure birth model (PB) using Phytools. To correct for incomplete sampling in the phylogeny we used the CorSim approach (Cusimano et al., 2012) to simulate missing species under a constant rate birth-death model (BD) assuming random sampling, using TreePar and TreeSim. To assess for constant rates of diversification we implemented the γ statistic using the constant rates (CR) and the Monte Carlo constant rates (MCCR), for the empirical and the 1000 BD simulated trees, respectively.

Because LTT-based methods fail to account for extinction (Quental and Marshall, 2010; Etienne et al., 2012; McGuire et al., 2014), we used alternatively the Bayesian Analysis of Macroevolutionary Mixtures (BAMM) approach to estimate the diversification pattern of *Pristimantis* through time. We

performed BAMM runs using the speciation/extinction model on the MCC phylogeny, each with 1 million generations of Markov Chain Monte Carlo (MCMC) sampling parameters every 1000 generations. To correct for incomplete taxon sampling, we assumed random missing data and fixed the global sampling fraction to 0.33 because the studied MCC tree contain 33% of Andean *Pristimantis* species. We computed tree appropriate speciation and extinction prior values for the phylogeny using the function set BAMM priors. Convergence of runs was assessed using Coda version 0.18-1 (Plummer et al., 2015), and the output was analyzed in BAMMtools version 2.5.0 (Rabosky et al., 2014).

To test for differences in rates of speciation, extinction, and dispersal between elevational bands we used the MuSSE (Multi-State Speciation and Extinction) model (FitzJohn, 2012) implemented in the R package Diversitree version 0.9-8 (Fitzjohn, 2015). For this, we coded the elevational midpoint of each species of *Pristimantis* frogs in Tropical Andes based on our diversity curve as follows: low elevations ($x < 1500$ m) as 1, intermediate elevations ($1501 \text{ m} < x < 2500$ m) as 2, and high elevations ($2501 \text{ m} < x$) as 3. Alternative elevational gradient coding gave similar results. Furthermore, we included a sampling proportion parameter, which account for incomplete taxon sampling, which we calculated from the data (low elevations = 0.4, mid-elevations = 0.3, and high elevations = 0.2). We tested a set of distinct models using the MCC tree described above as follows: First, we established a “null model” in which all parameters were fit to be equals between elevational bands. Then, we compared this model with a set of submodels in which one or more parameters were constrained between elevational bands, as follows: (1) speciation equal, dispersal varying, no extinctions; (2) speciation and dispersal varying, no extinctions; (3) speciation and dispersal varying, extinctions equal; (4) speciation, extinction, and dispersal varying. In addition, in all models we constrained transitions between states to only occur with adjacent states, as recommended by FitzJohn (2012). Log-likelihoods were compared using the AIC to discriminate between models.

2.2 RESULTS

2.2.1 Montane species-pump hypothesis

We found no relationship between the elevational distribution of clades and their diversification rates. Results were consistent using both average elevation ($r^2 = 0.02$, p-value = 0.91; Figure 4A) and reconstructed elevational midpoint values ($r^2 = 0.04$, p-value = 0.49; Figure 4B). We obtained qualitatively similar results using estimates of diversification rates based on crown ages, as well as using our estimated extinction rate and assuming low, medium, and high relative extinction rates (Annex 5). We also found a negative relationship between clade species richness and clade diversification rate ($r^2 = 0.31$, p-value = 0.06), suggesting that diversification rates variation is decoupled from clade richness. Overall, our results suggested that diversification rates did not explain elevational richness patterns in *Pristimantis* frogs, rejecting the montane species-pump hypothesis.

2.2.2 Montane museum hypothesis

We found a positive relationship between the species richness of elevational bands and their first colonization time (raw richness: $r^2 = 0.65$, p-value = 0.01; log-transformed richness: $r^2 = 0.45$, p-value = 0.04; Figure 4C, D, respectively). Ancestral reconstructions suggested that *Pristimantis* frogs were present in mid-elevation habitats ancestrally (1500-2500m, between ~40-33 mya), and then colonized lower and higher elevation multiple times (Figure 5), supporting time-for-speciation effect as a strongly predictor of species richness inhabiting currently intermediate elevational bands. In summary, our results supported the montane museum hypothesis. It is unlikely that the observed relationships were an artifact of the ancestral reconstruction method used here because observed relationship between time and species richness is much stronger than expected under stochastic simulations and because including outgroups in our analyses gave similar results (raw richness: $r^2 = 0.57$, p-value = 0.02; log-transformed richness: $r^2 = 0.43$, p-value = 0.04).

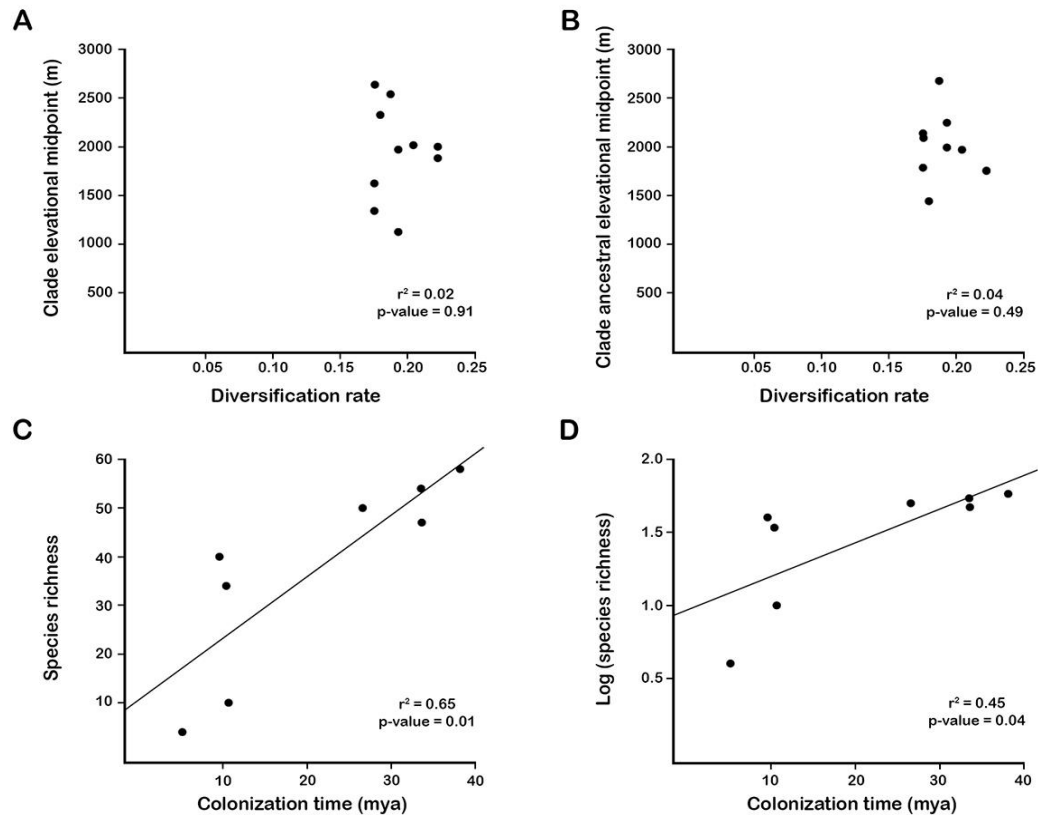


Figure 4. PGLS regressions between diversification rates (based on stem ages) of elevational bands versus clade elevational midpoint (A) and clade ancestral elevational midpoint (B). Linear regression between the species richness (raw and logarithmized) versus relative first colonization time of 500-m elevational bands (C, D).

2.2.3 Diversification analyses

The LTT analysis showed a heterogeneous diversification rate in the evolutionary history of rain frogs, with a gamma statistic (γ) of -5.69, $p\text{-value} < 0.001$, indicating a rapid early burst of diversification (between ~ 40 and 27 mya), followed by a slowdown in diversification rates close to the present (Figure 6). The CorSiM method implemented to account for incomplete sampling in the MCC tree also reject a constant-rate model, corroborating a bursts of lineage accumulation early in the history of *Pristimatis* (mean γ value of -2.43, $p\text{-value} < 0.01$).

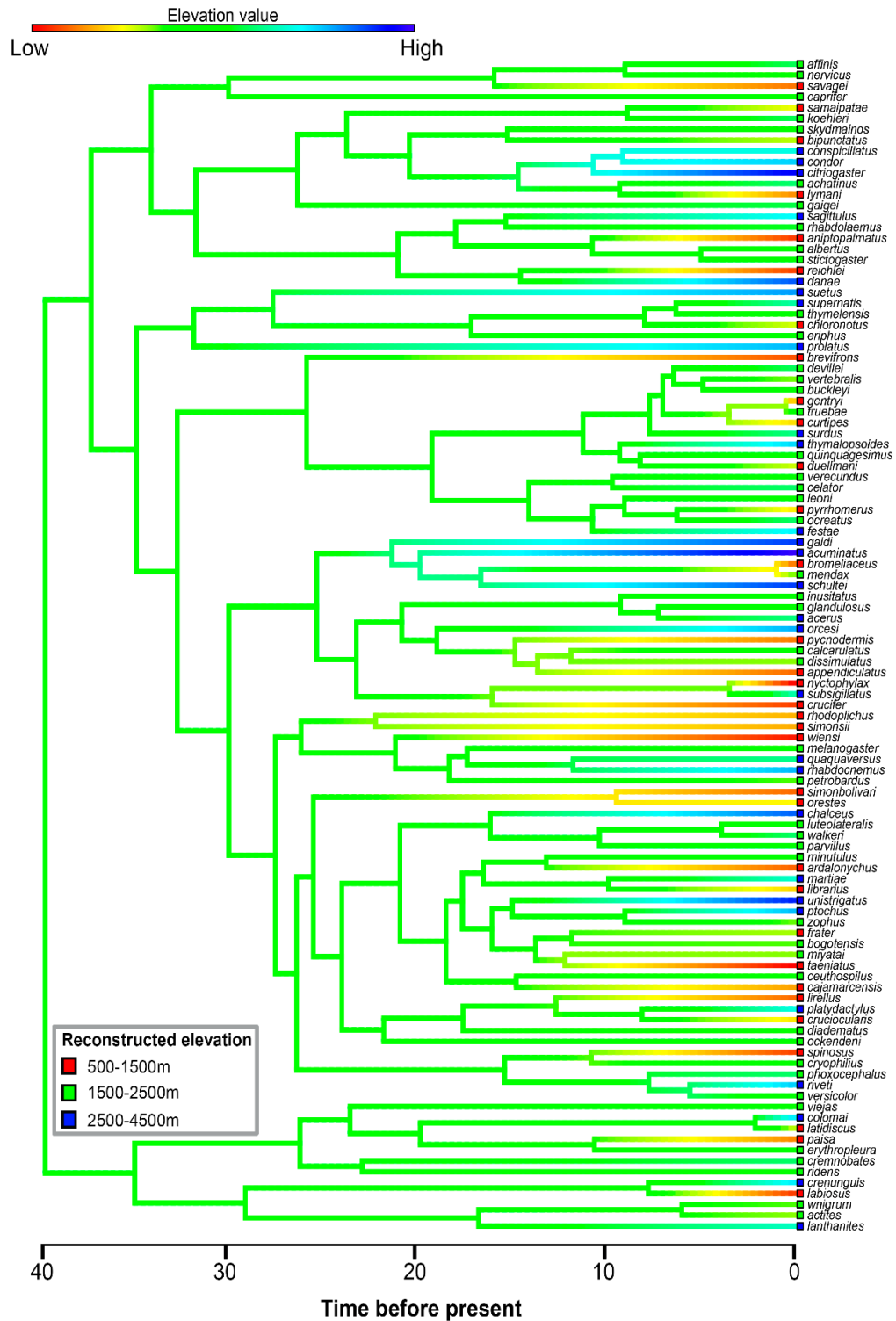


Figure 5. Phylogeny of *Pristimantis* frogs showing estimated divergence times and ancestral character estimation of elevation (as continuous trait) along the branches and nodes of the tree. Colored squared at the tips represent the general elevational categories for each species' current elevational midpoint. Phylogeny is taken from Pinto-Sánchez et al. (2012).

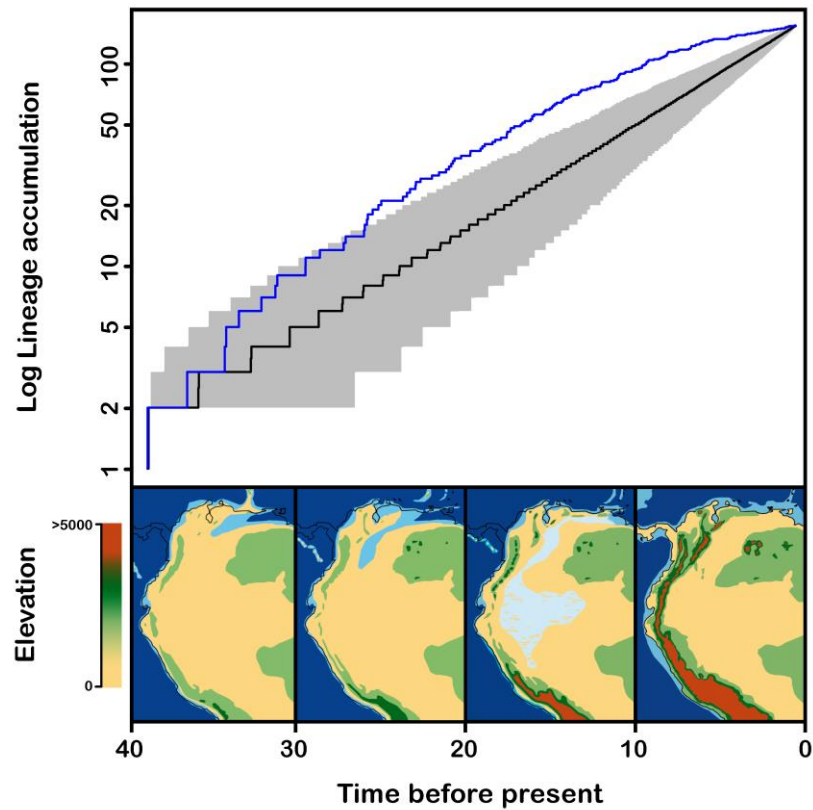


Figure 6. Lineages-through-time (LTT) plots for *Pristimantis* frogs (blue line), showing the mean LTT from PB 1000 simulations (black line) and its 95% confidence intervals (shaded area). Below is a schematic summary of major tectonic events on Tropical Andes of Andes in the last 40 my (adapted from Hoorn et al., 2010).

BAMM analyses also support for heterogeneous diversification rates (posterior probability, PP = 0.91), indicating again an early burst of diversification follows for a go-slow to the present time, with a diversification rate from 0.30 on the root to 0.078 on the tip of the MCC tree (Figure 7). These observations are congruent with the results obtained from LTT analyses, which support the same pattern of diversification. Despite that overall diversification rate is shown to vary along the phylogeny, there was no evidence for rate shifts between clades of *Pristimantis*. The PP for the model accounting for no evolutionary shifts between lineages was 0.91, while the PP for shift configurations were < 0.009 (Annex 10).

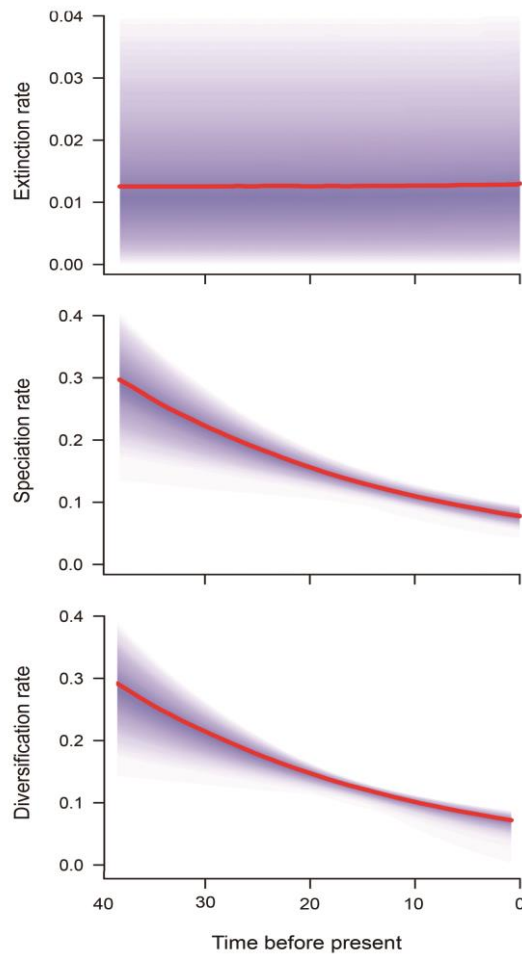


Figure 7. Bamm plots showing overall patterns of extinction (A), speciation (B) and net diversification (C) rates for *Pristimantis* frogs with 95% confidence intervals.

Bamm analyses also suggested an overall speciation rate higher (mean $0.12 \pm \text{SD } 0.01$) than extinction rate (mean $0.02 \pm \text{SD } 0.02$) for the phylogeny. The estimates of temporal variation in speciation, extinction, and diversification rates suggested that extinction was lower, and slightly constant through time, than speciation. In contrast, speciation rates, as well as the net diversification rates, were higher early (~ 40 mya) and then decreased towards present (Figure 7).

The 8-parameter MuSSE model ($\lambda_1 \neq \lambda_2 \neq \lambda_3$, $q_{12} \neq q_{21} \neq q_{23} \neq q_{32}$, $\mu = 0$) was strongly supported over alternative submodels (Annex S6). This model does not support modal patterns in speciation rates (i.e., highest diversification at mid-elevations) and instead strongly support models where diversification rates increase with elevation (Figure 8). These results agree with those from montane

pump analyses which shown that the hump-shaped elevational pattern in *Pristimantis* frogs is not explained by diversification rates (see above). Furthermore, MuSSE analyses also suggest that dispersal vary between elevational bands, with higher dispersal from high to low elevations, rather than from mid-elevation to adjacent elevational bands (Figure 8; Annex 6).

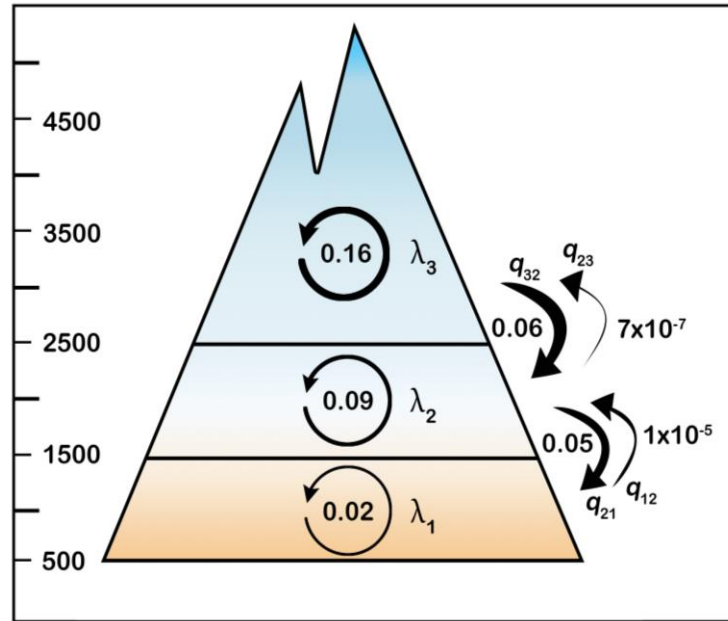


Figure 8. Results summary of the MuSSE best-fit model for the elevational distributions of Andean *Pristimantis* frogs. Speciation rates and dispersal rates are denoted by λ and q , respectively. Wider lines indicate high values of the measured parameter.

2.3 DISCUSSION

Rain frogs genus *Pristimantis* originated in South America 40 mya, and subsequently began an explosive diversification invading Central America, the Amazonian, and the Caribbean (Heinicke et al., 2007; Pinto-Sánchez et al., 2012; Padial et al., 2014; Mendoza et al., 2015). Although currently the genus is recognized as the most diverse amphibian group, no studies have investigated how the processes of speciation, extinction, and dispersal drive elevational richness patterns in the Tropical Andes. Previous studies have suggested that

recent Andean uplift during the Pliocene is a major event promoting the high species richness in *Pristimantis* frogs, as predicted by the montane species-pump hypothesis (e.g., Lynch and Duellman, 1997; Mendoza et al., 2015). However, these studies did not test directly how the historical processes responsible for species' accumulation (i.e., speciation, extinction and dispersal) drive the mid-elevation peak in species richness found in *Pristimantis* frogs.

Here we shown that long time-for-speciation in current intermediate elevations are responsible for the high species richness of rain frogs in this zone, supporting the montane museum hypothesis. Indeed, species into this genus have been accumulating richness for ~37-33 my in today mid-elevation habitats. Recent evidence also suggests that the mid-elevation diversity peaks in Andean glassfrogs (Centrolenidae) are explained by montane museum model (Hutter et al., 2013). Similar results have been found in other Neotropical anuran taxa (e.g., glassfrogs: Hutter et al., 2013; Castroviejo-Fisher et al., 2014; dart-poison frogs: Santos et al., 2009), where most diversification events occurs before the Pliocene, supporting greater time-for-speciation as the main factor promoting the evolutionary radiations of these taxa. Additional support for this hypothesis from other montane regions around the world includes Middle American treefrogs (Smith et al., 2007), plethodontid salamanders (Wiens et al., 2007), Tibetan fishes (Li et al., 2009), and Appalachian plethodontid salamanders (Kozak and Wiens, 2010).

Our analyses using both the MCC tree and the incomplete sampling corrected trees, detected an early burst of diversification followed by a lineage slowdown to the present time, as denoted by the γ values (-5.69 and -2.43, respectively; p-value < 0.001). BAMM analyses of rates-through-time using both strategies (i.e., empirical and complete simulated trees) also support this finding, highlighting no shifts in diversification through time during the genus radiation. The early burst of diversification agree with the results from Heinicke et al. (2007), who suggested that the taxa began an explosive diversification early in the evolutionary history of *Pristimantis* frogs. Overall, our diversification analysis

suggests that lineage accumulation in rain frogs appears to be uncoupled from recent events of Andean uplift, but coincident with ancient orogenic events. Thus, greater time-for-speciation effect, rather than species-pump underlying recent speciation, could represent the most important factor explaining the current diversity of the genus.

Slowdown of net diversification rates, usually associated to go-slows in speciation rates, has been identified as an emergent pattern in evolutionary biology (see Morlon et al., 2010; Moen and Morlon, 2014). Indeed, several studies have shown this pattern from other Neotropical (e.g., birds: McGuire et al., 2014; frogs: Santos et al., 2009; mammals: Parada et al., 2015) and Andean radiations (e.g., frogs: Hutter et al., 2013; butterflies: Da-Silva et al., 2016). Biological explanations for this pattern have stressed the role of niche differentiation as a consequence of filling of niche space (see Rabosky, 2009). However, the extent to which lineage accumulation patterns is linked to a major role for adaptive radiation remains unclear (Rabosky and Alfaro, 2010). Recent evidence suggests that other factors (e.g., methodological artifacts, protracted speciation, environment-driven bursts of speciation) than niche differentiation could alternatively explain the observed diversification slowdowns in several clades (see Pennell et al., 2012; Moen and Morlon, 2014). More studies examining patterns of lineage diversification are needed to a better understanding of tempo and mode of evolutionary radiations on Tropical Andes.

We also found an increased diversification pattern from low to highlands, with highest diversification rates in highland rain frogs lineages (Figure 8; Annex 6). Increased diversification rates of Andean anurans in highlands have been related to ecological opportunity in new available habitats and/or speciation driven by recent glaciations (see Hutter et al., 2013). In other Andean highland lineages (e.g., plants: Hughes and Eastwood, 2006; hummingbirds: Weir, 2006; Butterflies: Da-Silva et al., 2016) this pattern has been related to vicariance and rapid speciation drives for extensive glaciation during the past ~2 my. This hypothesis is supported by recent diversification in highland lineages of

Pristimantis frogs (see Mendoza et al., 2015), but our results shown that major diversification events were not that recent. Similarly, Andean glassfrogs exhibits the same increased diversification pattern with major diversification pre-dating Andean glaciations (Hutter et al., 2013). In contrast, results from historical biogeography of rain frogs suggest most diversification inside the 1000-3000m elevational range (Mendoza et al., 2015). Nevertheless, this study did not estimate diversification rates along the elevational gradient of Tropical Andes, so this conclusion lacks of empirical support.

Interestingly, increased diversification rates in rain frogs lineages at high elevations do not resulted in greater diversity, probably due to highland were colonized later in the evolutionary history of the genus (in average near ~18 mya), leading to few tempo for species accumulation; and in a minor intensity due to decreased diversity due to dispersal from high to intermediate lands ($q = 0.06$). Surprisingly, we also found dispersal from low to highlands to be very limited (Figure 8; Annex 6). These results suggest that a proportion of lowland species, especially those below 1000m, resulted from relatively early dispersal events (~9.6 mya) from mid to low-elevations. Similar dispersal events from Andes Mountains into lowland adjacent areas have been observed by biogeographical analyses of *Pristimantis* frogs (Mendoza et al., 2015). In addition, dendrobatid frogs diversity in lowland areas is thought to be result of repeated dispersal events of Andean lineages (Santos et al., 2009). In contrast, limited dispersal of montane clades into lowlands has been observed in Andean glassfrogs, suggesting an instance of climatic-niche conservatism (Hutter et al., 2013).

Several studies have suggested extensive speciation via niche divergence in Andean amphibians (e.g., Lynch and Duellman, 1997; Graham et al., 2004; Kozak and Wiens, 2010). The dispersal abilities and high diversification rates of species living in highland habitats suggests a scenario of niche divergence, whereas infrequent dispersal in species inhabiting lowlands supports a scenario of niche conservatism (for the latter see Wiens et al., 2010). Other potential

explanation comes from studies of thermal tolerances in amphibians. Frogs from lowland humid forests have narrower thermal ranges than those inhabiting montane highlands (Navas et al., 2013), which may explain at least in part the observed dispersal pattern. However, the available data and our analyses are not sufficient enough to explain the observed dispersal pattern in terms of thermal tolerances, climate-niche evolution, or any other way.

The estimated extinction and speciation rates (Figure 7), shown that despite net diversification has experience a slowdown over time, probably as the saturation of ecological niches and habitat is reached, the speciation-extinction equilibrium has not been reached. Thus, the decline in speciation rate has not actually led to lower diversification or lower richness, and we expect a species accumulation processes leading to further higher diversity than those that occur today. If niche differentiation is linked to evolutionary radiation of rain frogs, the unbalanced speciation-extinction dynamics in the genus suggests that Tropical Andes harbor a high niche space available to further genus diversification. These results highpoint that the range of ecological diversity that has evolved in Andean rain frogs, and other biota in Andes Mountains, should be incorporated in policy and management for conservation of biodiversity.

CONCLUSION

Rain frogs genus *Pristimantis* generally shown a hump-shaped pattern with the highest richness at intermediate elevations. This pattern is explained by a combination of spatial factors (i.e., species-area relationships and mid-domain effect) and topographic heterogeneity effects. However, the relative influence of these processes on species richness varied among the different study locations, suggesting that spatial effects are not the only mechanism underlying the observed curves of diversity. Species richness of *Pristimantis* genus is distributed unequally across the latitudinal gradient of Tropical Andes, suggesting that latitude also play an important role shaping the patterns of diversity. Our results also suggest that elevational variation in species richness may be explained by time-for-speciation effect and increasing diversification pattern from low to highlands. We also showed a rapid early burst of diversification coincident with ancient orogenic events of Tropical Andes. Overall, historical analyses suggest that high species richness at intermediate elevations can be explained by: relatively high diversification rates, dispersal events especially from highlands, and large tempo for diversification. Further studies of other factors (e.g., climatic effects, ecological interactions, climatic-niche evolution, source-sink factors, or even human activities) may explain more the altitudinal and latitudinal patterns of diversity in this genus.

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ANNEXES

Annex 1. For each species, we provide the minimum, maximum, midpoint, and range size of elevation (meters above sea level). If a species occurs in the Andes and adjacent lowlands we assumed its potential elevational range from the minimum non-Andean elevation to the maximum Andean elevation. Species with distributional range out of Andes were excluded from our analyses.

Species	Minimum	Maximum	Midpoint	Range Size	Reference
<i>P. acatallelus</i>	1410	2600	2005	1190	Ruiz-Carranza <i>et al.</i> (1997); Frost (2013); IUCN (2013)
<i>P. acerus</i>	2660	2750	2705	90	Lynch and Duellman (1980); Frost (2013); IUCN (2013)
<i>P. achatinus</i>	0	2600	1300	2600	Frost (2013); IUCN (2013); Rojas <i>et al.</i> (2013)
<i>P. actinolaimus</i>	1800	2000	1900	200	Galvis-Peñuela and Rueda-Almonacid (2004)
<i>P. actites</i>	760	2486	1623	1726	Frost (2013); IUCN (2013)
<i>P. acuminatus</i>	100	900	500	800	Frost (2013); IUCN (2013)
<i>P. acutirostris</i>	1740	2400	2070	660	Frost (2013); IUCN (2013)
<i>P. adiasolus</i>	1200	1200	1200	0	Duellman and Hedges (2007); IUCN (2013)
<i>P. aemulatus</i>	1410	1430	1420	20	Ruiz-Carranza <i>et al.</i> (1997); Frost (2013)
<i>P. affinis</i>	2600	3300	2950	700	Frost (2013); IUCN (2013)
<i>P. alalocophus</i>	2650	3100	2875	450	Frost (2013); IUCN (2013)
<i>P. albericoi</i>	950	950	950	0	Ruiz-Carranza <i>et al.</i> (1997); Frost (2013); IUCN (2013)
<i>P. albertus</i>	1970	1970	1970	0	Duellman and Lehr (2009); Frost (2013); IUCN (2013)
<i>P. altamnis</i>	400	1000	700	600	Elmer and Cannatella (2008); Frost (2013); IUCN (2013)
<i>P. ameliae</i>	2500	2500	2500	0	Barrio-Amorós (2011); Frost (2013)
<i>P. amydrotus</i>	1500	1500	1500	0	Duellman and Lehr (2007, 2009); Frost (2013); IUCN (2013)
<i>P. andinognomus</i>	2400	2800	2600	400	Lehr and Coloma (2008)
<i>P. anemerus</i>	2770	2770	2770	0	Duellman and Pramuk (1999); Frost (2013)
<i>P. angustilineatus</i>	1880	2500	2190	620	Frost (2013); IUCN (2013)
<i>P. aniptopalmatus</i>	2300	2600	2450	300	Duellman and Lehr (2009); Frost (2013); IUCN (2013)

<i>P. anolirex</i>	1900	3550	2725	1650	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. apiculatus</i>	1750	2120	1935	370	Frost (2013); IUCN (2013)
<i>P. appendiculatus</i>	1460	2800	2130	1340	Frost (2013); IUCN (2013)
<i>P. aquilonaris</i>	2000	2500	2250	500	Lehr <i>et al.</i> (2007); Duellman and Lehr (2009); IUCN (2013)
<i>P. ardalonychus</i>	680	1200	940	520	Lehr <i>et al.</i> (2007); Duellman and Lehr (2009); IUCN (2013)
<i>P. atrabracus</i>	2963	3330	3147	367	Duellman and Pramuk (1999); Lehr <i>et al.</i> (2007); Frost (2013)
<i>P. atratus</i>	2195	2850	2523	655	Lynch (1979); Frost (2013); IUCN (2013)
<i>P. aurantiguttatus</i>	1000	1900	1450	900	Frost (2013); IUCN (2013)
<i>P. avicuporum</i>	1700	2030	1865	330	Frost (2013); IUCN (2013)
<i>P. bacchus</i>	1314	2300	1807	986	Frost (2013); IUCN (2013); MHUA (2013)
<i>P. baiotis</i>	1780	2000	1890	220	Lynch (1998); Frost (2013); IUCN (2013)
<i>P. balionotus</i>	2800	2800	2800	0	Lynch (1979); Frost (2013); IUCN (2013)
<i>P. bambu</i>	2876	2989	2933	113	Arteaga-Navarro and Guayasamín (2011); Frost (2013)
<i>P. baryecus</i>	2195	2988	2592	793	Lynch (1979); Frost (2013); IUCN (2013)
<i>P. batrachites</i>	2180	2250	2215	70	Lynch (2003a); Frost (2013); IUCN (2013)
<i>P. bearsei</i>	500	730	615	230	Dulleman (1992); Duellman and Lehr (2009); Frost (2013)
<i>P. bellae</i>	1800	2300	2050	500	Reyes-Puig and Yáñez-Muñoz (2012)
<i>P. bellator</i>	1900	3100	2500	1200	Lehr <i>et al.</i> (2007); Duellman and Lehr (2009); Frost (2013)
<i>P. bellona</i>	1100	2000	1550	900	Frost (2013); IUCN (2013)
<i>P. bernali</i>	2350	2350	2350	0	Lynch (1986); Frost (2013); IUCN (2013)
<i>P. bicantus</i>	2100	2300	2200	200	Guayasamín and Funk (2009)
<i>P. bicolor</i>	1750	2400	2075	650	Rueda-Almonacid and Lynch (1983); Frost (2013); IUCN (2013)
<i>P. bipunctatus</i>	230	2320	1275	2090	Lehr <i>et al.</i> (2006); Duellman and Lehr (2009); Frost (2013)
<i>P. boconoensis</i>	2700	3150	2925	450	Stuart <i>et al.</i> (2008); Frost (2013)
<i>P. bogotensis</i>	2600	3400	3000	800	Frost (2013)
<i>P. Boulengeri</i>	2520	2920	2720	400	Lynch (1981); Frost (2013)
<i>P. brevifrons</i>	1140	2610	1875	1470	Lynch (1981, 1998); IUCN (2013)
<i>P. briceni</i>	1600	3300	2450	1700	Stuart <i>et al.</i> (2008); Frost (2013)
<i>P. bromeliaceus</i>	1500	2622	2061	1122	Duellman and Lehr (2009); Frost (2013); IUCN (2013)
<i>P. buckleyi</i>	2400	3700	3050	1300	Mueses-Cisneros (2005); Frost (2013); IUCN (2013)
<i>P. bustamante</i>	2745	3016	2881	271	Chaparro <i>et al.</i> (2012); Frost (2013)
<i>P. cabrerai</i>	1140	1940	1540	800	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. cacao</i>	2190	2600	2395	410	Lynch (1998); Frost (2013); IUCN (2013)

<i>P. caeruleonotus</i>	2500	2900	2700	400	Lehr <i>et al.</i> (2007); Duellman and Lehr (2009); Frost (2013)
<i>P. cajamarcensis</i>	1800	3100	2450	1300	Duellman and Lehr (2009); IUCN (2013)
<i>P. calcaratus</i>	1400	2700	2050	1300	Frost (2013); IUCN (2013)
<i>P. calcarulatus</i>	1140	2700	1920	1560	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. capitonis</i>	2440	2800	2620	360	Lynch (1998); Frost (2013); IUCN (2013)
<i>P. caprifer</i>	50	950	500	900	Frost (2013); IUCN (2013)
<i>P. carlossanchezi</i>	2400	2550	2475	150	Arroyo (2007); Frost (2013); IUCN (2013)
<i>P. carmelitae</i>	1520	2200	1860	680	Frost (2013); IUCN (2013)
<i>P. carrangerorum</i>	1350	2060	1705	710	Lynch (1994a); Frost (2013); IUCN (2013)
<i>P. caryophyllaceus</i>	0	1500	750	1500	IUCN (2013)
<i>P. celator</i>	1780	2600	2190	820	Lynch (1998); Frost (2013); IUCN (2013)
<i>P. ceuthospilus</i>	1500	1840	1670	340	Duellman and Lehr (2009); Frost (2013); IUCN (2013)
<i>P. chalceus</i>	50	1970	1010	1920	Lynch and Duellman (1997); Frost (2013); IUCN (2013)
<i>P. chimu</i>	3000	3100	3050	100	Lehr (2007), Duellman and Lehr (2009); Frost (2013); IUCN (2013)
<i>P. chloronotus</i>	2285	3350	2818	1065	Lynch and Duellman (1980); Frost (2013); IUCN (2013)
<i>P. chrysops</i>	900	2200	1550	1300	Frost (2013); IUCN (2013)
<i>P. citriogaster</i>	600	1094	847	494	Camacho-Badani <i>et al.</i> (2012); Frost (2013)
<i>P. colodactylus</i>	2195	3140	2668	945	Duellman and Lehr (2009); Frost (2013); IUCN (2013)
<i>P. colomai</i>	830	1200	1015	370	Lynch and Duellman (1997); Stuart <i>et al.</i> (2008); IUCN (2013)
<i>P. colonensis</i>	2200	2750	2475	550	Mueses-Cisneros (2007); Yáñez-Muñoz <i>et al.</i> (2012)
<i>P. colostichos</i>	3000	3600	3300	600	La Marca and Smith (1982); Stuart <i>et al.</i> (2008); IUCN (2013)
<i>P. condor</i>	1500	1975	1738	475	Duellman and Lehr (2009); Frost (2013)
<i>P. conservatio</i>	1640	1640	1640	0	Barrio-Amorós <i>et al.</i> (2013)
<i>P. conspicillatus</i>	0	600	300	600	Duellman and Lehr (2009); Frost (2013); IUCN (2013)
<i>P. cordovae</i>	3400	3642	3521	242	Duellman and Lehr (2007, 2009); Frost (2013); IUCN (2013)
<i>P. corniger</i>	1500	2600	2050	1100	Lynch and Suárez-Mayorga (2003); IUCN (2013)
<i>P. coronatus</i>	2850	2850	2850	0	Duellman and Lehr (2009); Frost (2013); IUCN (2013)
<i>P. corrugatus</i>	3000	3300	3150	300	Duellman and Lehr (2009); Frost (2013); IUCN (2013)
<i>P. cosnipatae</i>	1570	1800	1685	230	Duellman and Lehr (2009); Frost (2013); IUCN (2013)
<i>P. cremnobates</i>	1410	1700	1555	290	Lynch and Duellman (1980); Frost (2013); IUCN (2013)
<i>P. crenunguis</i>	760	2486	1623	1726	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. cristinae</i>	1530	3500	2515	1970	Rueda-Solano and Vargas-Salinas (2010); Frost (2013)
<i>P. crucifer</i>	1200	1800	1500	600	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)

<i>P. cruciocularis</i>	1330	1850	1590	520	Lehr <i>et al.</i> (2006); Duellman and Lehr (2009); IUCN (2013)
<i>P. cruentus</i>	200	805	503	605	Frost (2013)
<i>P. cryophilus</i>	2835	3384	3110	549	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. cryptomelas</i>	2470	3100	2785	630	Duellman and Lehr (2009); Frost (2013); IUCN (2013)
<i>P. cuentasi</i>	2800	2800	2800	0	Lynch (2003b); Frost (2013); IUCN (2013)
<i>P. culatensis</i>	2870	2900	2885	30	La Marca (2007); IUCN (2013)
<i>P. cuneirostris</i>	1700	1700	1700	0	Duellman and Lehr (2009); Frost (2013); IUCN (2013)
<i>P. curtipes</i>	2750	4400	3575	1650	Frost (2013); IUCN (2013)
<i>P. danae</i>	500	1850	1750	1350	Duellman and Lehr (2009); Frost (2013); Chaparro, J.C. (pers.
<i>P. degener</i>	830	1200	1015	370	Lynch and Duellman (1997); Frost (2013); IUCN (2013)
<i>P. deinops</i>	1750	2600	2175	850	Lynch (1998); Frost (2013); IUCN (2013)
<i>P. devillei</i>	2350	3150	2750	800	Frost (2013); IUCN (2013)
<i>P. diadematus</i>	0	1150	575	1150	Duellman and Lehr (2009); IUCN (2013)
<i>P. diaphonus</i>	1180	1250	1215	70	Lynch (1998); Frost (2013); IUCN (2013)
<i>P. diogenes</i>	1470	1600	1535	130	Lynch (1998); Frost (2013); IUCN (2013)
<i>P. dissimulatus</i>	1920	2020	1970	100	Lynch and Duellman (1997); Stuart <i>et al.</i> (2008); IUCN (2013)
<i>P. dorsopictus</i>	2400	3000	2700	600	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. douglasi</i>	1800	2550	2175	750	Stuart <i>et al.</i> (2008); Frost (2013)
<i>P. duellmani</i>	1780	2700	2240	920	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. duende</i>	3450	3450	3450	0	Lynch (2001); Frost (2013); IUCN (2013)
<i>P. elegans</i>	2600	3300	2950	700	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. epacrus</i>	740	1660	1200	920	Lynch and Suárez-Mayorga (2000); IUCN (2013)
<i>P. eremitus</i>	1540	2100	1820	560	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. eriphus</i>	2160	2750	2455	590	Guayasamín and Funk (2009); Frost (2013); IUCN (2013)
<i>P. ernesti</i>	3900	3900	3900	0	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. erythropleura</i>	980	2600	1790	1620	Ruiz-Carranza <i>et al.</i> (1997); Frost (2013); IUCN (2013)
<i>P. eugeniae</i>	1700	2010	1855	310	Lynch and Duellman (1997); Frost (2013); IUCN (2013)
<i>P. exoristus</i>	665	1830	1248	1165	Duellman and Lehr (2009); Frost (2013); IUCN (2013)
<i>P. factiosus</i>	1800	2200	2000	400	Lynch and Rueda-Almonacid (1998a); IUCN (2013)
<i>P. fallax</i>	1100	1850	1475	750	Lynch and Rueda-Almonacid (1999); IUCN (2013)
<i>P. fasciatus</i>	800	1200	1000	400	Barrio-Amorós <i>et al.</i> (2007); IUCN (2013)
<i>P. fenestratus</i>	100	1800	950	1700	Duellman and Lehr (2009); Frost (2013)
<i>P. festae</i>	2360	4400	3380	2040	Frost (2013); IUCN (2013)

<i>P. fetusus</i>	1800	2650	2225	850	Lynch and Rueda-Almonacid (1998a); Frost (2013)
<i>P. flabellidiscus</i>	2860	2920	2890	60	La Marca (2007)
<i>P. flavobracatus</i>	1770	1770	1770	0	Lehr <i>et al.</i> (2006); Duellman and Lehr (2009); IUCN (2013)
<i>P. floridus</i>	700	2000	1350	1300	Lynch and Duellman (1997); Duellman and Lehr (2009)
<i>P. frater</i>	1000	1600	1300	600	Frost (2013); IUCN (2013)
<i>P. gagliardoi</i>	2876	2989	2933	113	Bustamante and Mendelson (2008); Frost (2013)
<i>P. gagei</i>	150	1200	675	1050	Ruiz-Carranza <i>et al.</i> (1996); IUCN (2013)
<i>P. galdi</i>	1000	2250	1625	1250	Duellman and Lehr (2009); IUCN (2013)
<i>P. ganonotus</i>	1700	2000	1850	300	Duellman and Lynch (1988); Frenkel <i>et al.</i> (2011)
<i>P. ginesi</i>	2900	4000	3450	1100	IUCN (2013); La Marca (2007)
<i>P. gentryi</i>	2850	3380	3115	530	Lynch and Duellman (1997); Frost (2013); IUCN (2013)
<i>P. gladiator</i>	2270	2910	2590	640	Mueses-Cisneros (2005); Guayasamín and Funk (2009)
<i>P. glandulosus</i>	2105	2980	2543	875	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. gracilis</i>	1430	2740	2085	1310	Lynch (1986); Lynch (1998)
<i>P. grandiceps</i>	2200	2400	2300	200	Ruiz-Carranza <i>et al.</i> (1996); Frost (2013); IUCN (2013)
<i>P. gryllus</i>	900	2020	1460	1120	Barrio-Amorós <i>et al.</i> (2012)
<i>P. hamiotae</i>	2140	2140	2140	0	Lynch and Duellman (1997); Frost (2013); IUCN (2013)
<i>P. hectus</i>	1200	2020	1610	820	Lynch and Duellman (1997); Frost (2013); IUCN (2013)
<i>P. helvolus</i>	1800	2000	1900	200	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. hernandezi</i>	2300	2600	2450	300	Frost (2013)
<i>P. huicundo</i>	3229	3700	3465	471	Guayasamin <i>et al.</i> (2004); Frost (2013); IUCN (2013)
<i>P. hybotragus</i>	300	920	610	620	Lynch (1998); IUCN (2013)
<i>P. ignicolor</i>	2160	2750	2455	590	Lynch and Duellman (1980); Frost (2013); IUCN (2013)
<i>P. illotus</i>	1380	2560	1970	1180	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. incanus</i>	1700	2200	1950	500	Stuart <i>et al.</i> (2008); IUCN (2013)
<i>P. incomptus</i>	1370	1910	1640	540	Stuart <i>et al.</i> (2008); Duellman and Lehr (2009); IUCN (2013)
<i>P. infraguttatus</i>	2000	2180	2090	180	Duellman and Pramuk (1999); Duellman and Lehr (2009)
<i>P. insignitus</i>	1530	2134	1832	604	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. inusitatus</i>	1300	2160	1730	860	Guayasamín and Funk (2009); Frost (2013); IUCN (2013)
<i>P. ixalus</i>	1300	1700	1500	400	Lynch (2003a); Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. jabonensis</i>	3100	3200	3150	100	La Marca (2007)
<i>P. jaimiei</i>	800	1580	1190	780	Lynch (1992, 1998); IUCN (2013)
<i>P. johannesdei</i>	1410	1800	1605	390	Lynch (1998); Ruiz-Carranza <i>et al.</i> (1996); IUCN (2013)

<i>P. jorgevelosai</i>	1900	2200	2050	300	Lynch (1994b); Acosta-Galvis (2000)
<i>P. juanchoi</i>	1500	2090	1795	590	Stuart <i>et al.</i> (2008); IUCN (2013)
<i>P. jubatus</i>	2550	2750	2650	200	García and Lynch (2006); Frost (2013); IUCN (2013)
<i>P. kareliae</i>	2500	3400	2950	900	La Marca (2005); Frost (2013); IUCN (2013)
<i>P. katoptroides</i>	1000	2700	1850	1700	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. kelephus</i>	1900	2250	2075	350	Lynch (1998); Frost (2013); IUCN (2013)
<i>P. kirklandi</i>	2200	2200	2200	0	Frost (2013)
<i>P. koehleri</i>	437	735	586	298	Padial and De la Riva (2009)
<i>P. labiosus</i>	30	1600	815	1570	Lynch (1998); Acosta-Galvis (2000); Frost (2013)
<i>P. lacrimosus</i>	100	1100	600	1000	Duellman and Lehr (2009); IUCN (2013)
<i>P. lancinii</i>	2500	3430	2965	930	Donoso-Barros (1965); La Marca (2007); IUCN (2013)
<i>P. lanthanites</i>	200	1650	925	1450	Duellman and Lehr (2009); IUCN (2013)
<i>P. lasalleorum</i>	3700	3850	3775	150	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. lassoalcalai</i>	1827	1950	1889	123	Barrio-Amorós <i>et al.</i> (2010); Frost (2013)
<i>P. laticlavus</i>	1200	2565	1883	1365	Frost (2013); IUCN (2013)
<i>P. latidiscus</i>	2	950	476	948	Lynch (1998); Frost (2013); IUCN (2013)
<i>P. lemur</i>	1800	2650	2225	850	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. lentiginosus</i>	1700	1800	1750	100	Rivero (1982b)
<i>P. leptolophus</i>	2800	3300	3050	500	Lynch (1980); Acosta-Galvis (2000); IUCN (2013)
<i>P. leucopus</i>	2300	2900	2600	600	Acosta-Galvis (2000); Guayasamín and Funk (2009); IUCN (2013)
<i>P. leucorrhinus</i>	2500	2500	2500	0	Duellman and Lehr (2009); Frost (2013)
<i>P. librarius</i>	220	560	390	340	Frost (2013); IUCN (2013)
<i>P. lichenoides</i>	2000	2450	2225	450	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. lindae</i>	1700	1700	1700	0	Duellman and Lehr (2009); Frost (2013); IUCN (2013)
<i>P. lirellus</i>	470	1200	835	730	Duellman and Lehr (2009); Frost (2013); IUCN (2013)
<i>P. lividus</i>	2135	2750	2443	615	Almendáriz and Orcés (2004); Duellman and Lehr (2009)
<i>P. llojsintuta</i>	2000	2200	2100	200	Frost (2013); IUCN (2013)
<i>P. loujosti</i>	2800	2800	2800	0	Frost (2013)
<i>P. loustes</i>	1200	1410	1305	210	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. lucasi</i>	2790	3000	2895	210	Duellman and Chaparro (2008); Frost (2013); IUCN (2013)
<i>P. lucidosignatus</i>	2115	2115	2115	0	Rödder and Schmitz (2009); Frost (2013)
<i>P. luteolateralis</i>	1140	1960	1550	820	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. lutitus</i>	1750	2400	2075	650	Jerez <i>et al.</i> (2001); IUCN (2013)

<i>P. lymani</i>	450	3200	1825	2750	Venegas (2005); Duellman and Lehr (2009); IUCN (2013)
<i>P. lynchi</i>	2460	3340	2900	880	IUCN (2013)
<i>P. maculosus</i>	2560	2900	2730	340	Acosta-Galvis (2000); Frost (2013); IUCN (2013)
<i>P. mariaelenae</i>	3596	3596	3596	0	Venegas and Duellman (2012); Frost (2013); IUCN (2013)
<i>P. mars</i>	1760	1790	1775	30	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. martiae</i>	300	1300	800	1000	Ruiz-Carranza <i>et al.</i> (1996); Duellman and Lehr (2009); Frost (2013)
<i>P. mazar</i>	2895	3415	3155	520	Guayasamin and Arteaga (2013)
<i>P. medemi</i>	450	1800	1125	1350	Malambo and Marin (2006); Frost (2013); IUCN (2013)
<i>P. megalops</i>	1300	2450	1875	1150	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. melanogaster</i>	2800	3470	3135	670	Duellman and Lehr (2009); Frost (2013); IUCN (2013)
<i>P. melanoproctus</i>	1800	1800	1800	0	Frost (2013); IUCN (2013)
<i>P. mendax</i>	1700	3325	2513	1625	Duellman and Lehr (2009); Frost (2013)
<i>P. meridionalis</i>	2290	2290	2290	0	Duellman and Lehr (2009); Frost (2013); IUCN (2013)
<i>P. merostictus</i>	2400	2400	2400	0	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. minimus</i>	1250	1685	1468	435	Terán-Valdez and Guayasamin (2010); Frost (2013)
<i>P. minutulus</i>	1970	1970	1970	0	Duellman and Hedges (2007); Duellman and Lehr (2009)
<i>P. miyatai</i>	1740	2400	2070	660	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. mnionaetes</i>	3060	3800	3430	740	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. modipeplus</i>	2560	3700	3130	1140	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. molybrignus</i>	1110	2350	1730	1240	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. mondolfii</i>	1120	1120	1120	0	Frost (2013); IUCN (2013)
<i>P. muricatus</i>	800	1380	1090	580	Ortega-Andrade <i>et al.</i> (2010); Frost (2013); IUCN (2013)
<i>P. muscosus</i>	1800	2500	2150	700	Duellman and Lehr (2009); Yáñez-Muñoz <i>et al.</i> (2012)
<i>P. myersi</i>	2900	3275	3088	375	Acosta-Galvis (2000); Frost (2013); IUCN (2013)
<i>P. myops</i>	1500	2250	1875	750	Lynch (1998)
<i>P. caliginosus</i>	1650	1650	1650	0	Frost (2013); IUCN (2013)
<i>P. nephophilus</i>	1080	2500	1790	1420	Duellman and Lehr (2009); Frost (2013); IUCN (2013)
<i>P. nervicus</i>	3100	3870	3485	770	Acosta-Galvis (2000); Frost (2013); IUCN (2013)
<i>P. nicefori</i>	2500	4100	3300	1600	Frost (2013); IUCN (2013)
<i>P. nigrogriseus</i>	1150	2835	1993	1685	Stuart <i>et al.</i> (2008); IUCN (2013)
<i>P. nyctophylax</i>	1140	2100	1620	960	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. obmutescens</i>	3200	3500	3350	300	Lynch (1980); Lynch <i>et al.</i> (1996); Frost (2013); IUCN (2013)
<i>P. ocellatus</i>	1050	2600	1825	1550	Lynch and Burrowes (1990); Lynch (1998); IUCN (2013)

<i>P. ockendeni</i>	300	1200	750	900	Duellman and Lehr (2009); IUCN (2013)
<i>P. ocreatus</i>	3500	4150	3825	650	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. olivaceus</i>	350	1650	1000	1300	Duellman and Lehr (2009); Frost (2013); IUCN (2013)
<i>P. onorei</i>	705	2115	1410	1410	Rödger and Schmitz (2009); Frost (2013)
<i>P. orcesi</i>	3160	3800	3480	640	Almendáriz and Orcés (2004); Frost (2013); IUCN (2013)
<i>P. orestes</i>	2720	3120	2920	400	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. ornatissimus</i>	400	1800	1100	1400	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. ornatus</i>	2400	3000	2700	600	Duellman and Lehr (2009); Frost (2013); IUCN (2013)
<i>P. orpacobates</i>	700	2000	1350	1300	Lynch (1998); Acosta-Galvis (2000); IUCN (2013)
<i>P. ortizi</i>	3264	3420	3342	156	Guayasamin <i>et al.</i> (2004); Frost (2013); IUCN (2013)
<i>P. padrecarlosi</i>	1750	1950	1850	200	Mueses-Cisneros (2006); Frost (2013); IUCN (2013)
<i>P. paisa</i>	1800	3100	2450	1300	Lynch and Ardila-Robayo (1999); Frost (2013); IUCN (2013)
<i>P. palmeri</i>	900	2400	1650	1500	Bolívar-García <i>et al.</i> (2011); Frost (2013); IUCN (2013)
<i>P. paramerus</i>	2900	3330	3115	430	Rivero (1982a)
<i>P. pardalinus</i>	2640	2640	2640	0	Duellman and Lehr (2009); Frost (2013); IUCN (2013)
<i>P. parectatus</i>	1800	2850	2325	1050	Lynch and Rueda-Almonacid (1998b); IUCN (2013)
<i>P. parvillus</i>	220	2000	1110	1780	Ruíz-Carranza <i>et al.</i> (1996); Acosta-Galvis (2000); IUCN (2013)
<i>P. pastazensis</i>	1800	1840	1820	40	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. pataikos</i>	1800	3470	2635	1670	Stuart <i>et al.</i> (2008); Duellman and Lehr (2009); Frost (2013)
<i>P. pecki</i>	1138	1700	1419	562	Duellman and Lehr (2009); IUCN (2013)
<i>P. pedimontanus</i>	980	1700	1340	720	Frost (2013); IUCN (2013)
<i>P. penelopus</i>	1180	1500	1340	320	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. peraticus</i>	2850	3460	3155	610	Lynch (1980); Acosta-Galvis (2000); IUCN (2013)
<i>P. percnopterus</i>	1380	2400	1890	1020	Duellman and Lehr (2009); Frost (2013); IUCN (2013)
<i>P. percultus</i>	2850	2850	2850	0	Lynch (1979); Stuart <i>et al.</i> (2008); Frost (2013)
<i>P. permixtus</i>	1900	3700	2800	1800	Méndez-Narváez <i>et al.</i> (2010); Frost (2013); IUCN (2013)
<i>P. peruvianus</i>	200	2050	1125	1850	Duellman and Lehr (2009); Frost (2013); IUCN (2013)
<i>P. petersi</i>	1410	2750	2080	1340	Mueses-Cisneros (2005); Frost (2013); IUCN (2013)
<i>P. petrobardus</i>	1500	2500	2000	1000	Duellman (1991); Duellman and Lehr (2009); Frost (2013)
<i>P. phalaroinguinis</i>	1800	2600	2200	800	Duellman and Lehr (2007, 2009); Frost (2013); IUCN (2013)
<i>P. phalarus</i>	2160	2400	2280	240	Lynch (1998); Acosta-Galvis (2000); Frost (2013); IUCN (2013)
<i>P. pharangobates</i>	1180	2759	1970	1579	Duellman and Lehr (2009); Frost (2013); IUCN (2013)
<i>P. philipi</i>	3580	3820	3700	240	Lynch and Duellman (1995); Frost (2013); IUCN (2013)

<i>P. phoxocephalus</i>	1800	3100	2450	1300	Duellman and Lehr (2007, 2009); Frost (2013); IUCN (2013)
<i>P. phragmipleuron</i>	1800	1800	1800	0	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. piceus</i>	2400	3400	2900	1000	Ruíz-Carranza <i>et al.</i> (1996); Frost (2013); IUCN (2013)
<i>P. pinguis</i>	3000	3916	3458	916	Duellman and Pramuk (1999); Duellman and Lehr (2009)
<i>P. platytilus</i>	1580	2600	2090	1020	Lynch (1996); Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. platydactylus</i>	930	3470	2200	2540	Lehr <i>et al.</i> (2006); Duellman and Lehr (2009); IUCN (2013)
<i>P. pleurostriatus</i>	2316	2316	2316	0	Frost (2013); IUCN (2013)
<i>P. polemistes</i>	2300	2320	2310	20	Lynch and Ardila-Robayo (2004); Frost (2013); IUCN (2013)
<i>P. polychrus</i>	1140	1540	1340	400	Ruiz-Carranza <i>et al.</i> (1997); Frost (2013); IUCN (2013)
<i>P. prolatus</i>	1140	1700	1420	560	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. prolixodiscus</i>	1600	2700	2150	1100	Lynch (1978); Barrio-Amorós (2004); IUCN (2013)
<i>P. proserpens</i>	1707	2622	2165	915	Lynch (1979); Duellman and Lehr (2009); Frost (2013)
<i>P. pteridophilus</i>	1500	2710	2105	1210	Lynch and Duellman (1997); Frost (2013); IUCN (2013)
<i>P. ptochus</i>	2100	2250	2175	150	Lynch (1998); Frost (2013); IUCN (2013)
<i>P. pugnax</i>	1660	3300	2480	1640	Mueses-Cisneros (2005); IUCN (2013)
<i>P. pycnodermis</i>	2652	3384	3018	732	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. pyrrhomerus</i>	2075	3000	2538	925	Lynch and Duellman (1997); Frost (2013); IUCN (2013)
<i>P. quantus</i>	2100	2250	2175	150	Lynch (1998); Stuart <i>et al.</i> (2008); Frost (2013)
<i>P. quaquaversus</i>	200	1900	1050	1700	Duellman and Pramuk (1999); Duellman and Lehr (2009)
<i>P. quicato</i>	2600	2900	2750	300	Ospina-Sarria <i>et al.</i> (2011); Frost (2013)
<i>P. quinquagesimus</i>	1410	2710	2060	1300	Lynch and Duellman (1997); Frost (2013); IUCN (2013)
<i>P. racemus</i>	3030	3570	3300	540	Lynch <i>et al.</i> (1996); Frost (2013); IUCN (2013)
<i>P. reclusas</i>	2800	2800	2800	0	Lynch (2003b); Frost (2013); IUCN (2013)
<i>P. reichlei</i>	0	1500	750	1500	Duellman and Lehr (2009); Frost (2013); IUCN (2013)
<i>P. renjiformis</i>	2000	2800	2400	800	Lynch (2000); Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. repens</i>	3150	3720	3435	570	Rojas and Gutiérrez (2008); Frost (2013); IUCN (2013)
<i>P. restrepoi</i>	1790	2250	2020	460	Lynch (1998); Acosta-Galvis (2000); IUCN (2013)
<i>P. rhabdocnemus</i>	230	2900	1565	2670	Duellman and Lehr (2009)
<i>P. rhabdolaemus</i>	300	2650	1475	2350	Duellman and Lehr (2009)
<i>P. rhigophilus</i>	2360	3100	2730	740	La Marca (2007); Frost (2013)
<i>P. rhodoplichus</i>	1800	3050	2425	1250	Duellman and Lehr (2009); Frost (2013); IUCN (2013)
<i>P. rhodostichus</i>	1080	1800	1440	720	Duellman and Lehr (2009); Yáñez-Muñoz <i>et al.</i> (2012); IUCN (2013)
<i>P. ridens</i>	10	1060	535	1050	Lynch (1998); Acosta-Galvis (2000); IUCN (2013)

<i>P. rivasi</i>	1389	1945	1667	556	Barrio-Amorós <i>et al.</i> (2010); Frost (2013); IUCN (2013)
<i>P. riveti</i>	2620	3600	3110	980	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. romanorum</i>	2600	2900	2750	300	Yáñez-Muñoz <i>et al.</i> (2010); Frost (2013)
<i>P. roseus</i>	0	900	450	900	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. rubicundus</i>	1080	1300	1190	220	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. ruedai</i>	1000	1900	1450	900	Lynch (1998); Stuart <i>et al.</i> (2008); Frost (2013)
<i>P. rufiocularis</i>	1138	2870	2004	1732	Duellman and Lehr (2009)
<i>P. rufoviridis</i>	1800	2237	2019	437	Valencia <i>et al.</i> (2010, 2011)
<i>P. ruidus</i>	2317	2317	2317	0	Lynch (1979); Frost (2013); IUCN (2013)
<i>P. ruthveni</i>	1800	3500	2650	1700	Rueda-Solano and Vargas-Salinas (2010); Frost (2013)
<i>P. sagittulus</i>	1970	2479	2225	509	Duellman and Lehr (2009)
<i>P. salaputium</i>	1500	2400	1950	900	Duellman and Lehr (2009); Frost (2013)
<i>P. samaipatae</i>	800	2000	1400	1200	Frost (2013)
<i>P. sanctaemartae</i>	1100	2600	1850	1500	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. sanguineus</i>	50	1500	775	1450	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. satagius</i>	3300	3800	3550	500	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. savagei</i>	1000	2400	1700	1400	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. schultei</i>	2400	2850	2625	450	Duellman and Lehr (2009); Frost (2013); IUCN (2013)
<i>P. scitulus</i>	2620	2620	2620	0	Duellman and Lehr (2009); Frost (2013); IUCN (2013)
<i>P. scoloblepharus</i>	2620	2800	2710	180	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. scolodiscus</i>	1200	1780	1490	580	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. scopaeus</i>	3580	3600	3590	20	Ruíz-Carranza <i>et al.</i> (1996)
<i>P. seorsus</i>	3350	3350	3350	0	Duellman and Lehr (2009); IUCN (2013)
<i>P. serendipitus</i>	1700	1850	1775	150	Duellman and Lehr (2009); IUCN (2013)
<i>P. signifer</i>	1850	1860	1855	10	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. silverstonei</i>	1700	2250	1975	550	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. simonbolivari</i>	3200	3200	3200	0	Wiens and Coloma (1992); Frost (2013); IUCN (2013)
<i>P. simonsii</i>	3050	3760	3405	710	Duellman and Lehr (2009); Frost (2013)
<i>P. simoteriscus</i>	3580	3680	3630	100	Lynch <i>et al.</i> (1996); Stuart <i>et al.</i> (2008); IUCN (2013)
<i>P. simoterus</i>	2700	4350	3525	1650	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. siopelus</i>	1700	2020	1860	320	Lynch and Burrowes (1990); IUCN (2013)
<i>P. sirnigeli</i>	2800	3050	2925	250	Yáñez-Muñoz <i>et al.</i> (2010); Frost (2013)
<i>P. skydmainos</i>	0	950	475	950	Duellman and Lehr (2009); Cisneros-Heredia <i>et al.</i> (2009)

<i>P. sobetes</i>	1700	2050	1875	350	Stuart <i>et al.</i> (2008); IUCN (2013)
<i>P. spectabilis</i>	3300	3300	3300	0	Duellman and Lehr (2009); Frost (2013)
<i>P. spilogaster</i>	2200	2400	2300	200	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. spinosus</i>	1707	2835	2271	1128	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. sternothylax</i>	1500	4538	3019	3038	Duellman and Lehr (2009); Yáñez-Muñoz <i>et al.</i> (2012)
<i>P. stictoboubonus</i>	3000	3130	3065	130	Duellman and Lehr (2009); IUCN (2013)
<i>P. stictogaster</i>	1470	2790	2130	1320	Duellman and Lehr (2009); Frost (2013)
<i>P. stipa</i>	3596	3596	3596	0	Venegas and Duellman (2012); Frost (2013); IUCN (2013)
<i>P. subsigillatus</i>	100	930	515	830	Lynch and Duellman (1997)
<i>P. suetus</i>	1800	2800	2300	1000	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. sulculus</i>	1700	2020	1860	320	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. supernatis</i>	2280	3500	2890	1220	Lynch (1979); Frost (2013); IUCN (2013)
<i>P. surdus</i>	1550	3190	2370	1640	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. susaguae</i>	2530	2900	2715	370	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. taciturnus</i>	2400	2670	2535	270	Lynch and Suárez-Mayorga (2003); IUCN (2013)
<i>P. taeniatus</i>	0	1400	700	1400	IUCN (2013)
<i>P. tamsitti</i>	1350	2040	1695	690	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. tanyrhynchus</i>	2050	2050	2050	0	Lehr (2007); Duellman and Lehr (2009); IUCN (2013)
<i>P. tayrona</i>	1300	2700	2000	1400	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. telefericus</i>	3400	3500	3450	100	La Marca (2005); IUCN (2013)
<i>P. tenebrionis</i>	220	830	525	610	Lynch and Duellman (1997); Frost (2013); IUCN (2013)
<i>P. thectopternus</i>	1580	2520	2050	940	Lynch (1998)
<i>P. thyellus</i>	2900	3800	3350	900	La Marca (2007); Frost (2013)
<i>P. thymalopsoides</i>	2460	2480	2470	20	Lynch and Duellman (1997); Frost (2013); IUCN (2013)
<i>P. thymelensis</i>	3220	4150	3685	930	Mueses-Cisneros (2005); IUCN (2013)
<i>P. torrenticola</i>	1800	2400	2100	600	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. trachyblepharis</i>	320	1250	785	930	Frost (2013); IUCN (2013)
<i>P. tribulosus</i>	1900	2400	2150	500	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. truebae</i>	2870	3190	3030	320	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. tubernasus</i>	1000	2300	1650	1300	Ruíz-Carranza <i>et al.</i> (1996); Frost (2013); IUCN (2013)
<i>P. tungurahua</i>	2500	2750	2625	250	Reyes-Puig <i>et al.</i> (2011); Frost (2013)
<i>P. turik</i>	1700	1700	1700	0	Barrio-Amorós <i>et al.</i> (2007); Frost (2013)
<i>P. uisae</i>	2700	2700	2700	0	Frost (2013); IUCN (2013)

<i>P. unistrigatus</i>	2200	3400	2800	1200	Lynch and Duellman (1997); Mueses-Cisneros (2005); IUCN (2013)
<i>P. uranobates</i>	2800	3480	3140	680	Lynch (1991); Ruíz-Carranza <i>et al.</i> (1996)
<i>P. vanadise</i>	1800	2600	2200	800	Frost (2013); IUCN (2013)
<i>P. variabilis</i>	100	600	350	500	Duellman and Lehr (2009); Frost (2013)
<i>P. veletis</i>	1800	2450	2125	650	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. ventriguttatus</i>	1700	1800	1750	100	Lehr and Köhler (2007); IUCN (2013)
<i>P. ventrimarmoratus</i>	0	1740	870	1740	Padial <i>et al.</i> (2004); Duellman and Lehr (2009); IUCN (2013)
<i>P. verecundus</i>	900	2020	1460	1120	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. versicolor</i>	665	3100	1883	2435	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. vertebralis</i>	1800	3000	2400	1200	Lynch and Duellman (1997); Frost (2013); IUCN (2013)
<i>P. vicarius</i>	2900	3275	3088	375	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. vidua</i>	2710	3100	2905	390	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. viejas</i>	800	1880	1340	1080	Frost (2013); IUCN (2013)
<i>P. vilcabambae</i>	2050	2050	2050	0	Lehr (2007); Frost (2013); IUCN (2013)
<i>P. viridicans</i>	1700	2680	2190	980	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. viridis</i>	1480	1940	1710	460	Stuart <i>et al.</i> (2008); Frost (2013); IUCN (2013)
<i>P. w-nigrum</i>	800	3300	2050	2500	Duellman and Lehr (2009); Frost (2013); IUCN (2013)
<i>P. wagteri</i>	2800	3000	2900	200	Venegas (2007); Duellman and Lehr (2009); IUCN (2013)
<i>P. walkeri</i>	100	1270	685	1170	Frost (2013); IUCN (2013)
<i>P. wiensi</i>	1600	1735	1668	135	Duellman and Lehr (2009); Frost (2013); IUCN (2013)
<i>P. xeniolum</i>	3300	3600	3450	300	Lynch (2001); Frost (2013); IUCN (2013)
<i>P. xestus</i>	4050	4050	4050	0	Lynch (1995); Frost (2013); IUCN (2013)
<i>P. xylochobates</i>	2100	2250	2175	150	Lynch and Ruiz-Carranza (1996); IUCN (2013)
<i>P. yukpa</i>	600	1200	900	600	Barrio-Amorós <i>et al.</i> (2007); Frost (2013)
<i>P. yumbo</i>	2400	2900	2650	500	Yáñez-Muñoz <i>et al.</i> (2010); Frost (2013)
<i>P. yustizi</i>	600	1600	1100	1000	Frost (2013); IUCN (2013)
<i>P. zoilae</i>	2060	2550	2305	490	Mueses-Cisneros (2007); Frost (2013); IUCN (2013)
<i>P. zophus</i>	2030	2800	2415	770	Lynch and Ardila-Robayo (1999); IUCN (2013)

Annex 2. Species-area effect using non-transformed variables (linear effect), log-transformed variables (curvilinear effect), and log-transformed area (semi-log effect). Significant area effects are marked with asterisks (*). The models with the lowest AICc are shown in boldface type. Mountain ranges are sorted by domain and latitude from north to south.

Geographic region	Linear effect		Curvilinear effect		Semi-log effect	
	r^2	p -value	r^2	p -value	r^2	p -value
Northern Andes domain						
Merida Andes, Venezuela	-0.140	0.903	0.396	0.041*	0.081	0.233
Sierra Nevada de Santa Marta, Colombia	-0.131	0.796	-0.068	0.505	-0.067	0.503
Eastern Cordillera, Colombia	-0.108	0.654	0.590	0.009*	0.279	0.083
Central Cordillera, Colombia	-0.050	0.457	0.624	0.007*	0.312	0.069
Western Cordillera, Colombia	0.412	0.037*	0.904	0.052	0.654	0.010*
Eastern Cordillera, Ecuador	0.063	0.255	0.719	0.002*	0.391	0.042*
Western Cordillera, Ecuador	0.251	0.097	0.740	0.002*	0.433	0.032*
Central Andes domain						
Eastern Cordillera, Peru	-0.105	0.638	-0.141	0.914	-0.136	0.841
Central Cordillera, Peru	0.064	0.253	0.360	0.052	0.313	0.068
Western Cordillera, Peru	0.160	0.156	0.121	0.190	0.175	0.145
Eastern Cordillera, Bolivia	0.476	0.024*	0.296	0.075	0.324	0.064

Annex 3. Fitting of the spatial constraint effects model (MDE) for empirical and corrected biodiversity curves using linear and quadratic regressions statistics for each main mountain ranges studied here. Significant MDE are marked with asterisks (*). The models with the lowest AICc are shown in boldface type. Mountain ranges are sorted by domain and latitude from north to south.

Geographic region	Empirical curves				Corrected curves			
	Linear		Quadratic		Linear		Quadratic	
	r^2	p -value	r^2	p -value	r^2	p -value	r^2	p -value
Northern Andes domain								
Merida Andes, Venezuela	0.631	0.020	0.728	0.033	0.326	0.105	0.606	0.069
Sierra Nevada de Santa Marta, Colombia	0.862	0.004*	0.818	0.036	-	-	-	-
Eastern Cordillera, Colombia	0.822	0.001*	0.970	<0.001*	0.643	0.010	0.589	0.047
Central Cordillera, Colombia	0.851	<0.001*	0.881	0.002*	0.865	<0.001*	0.901	0.001*
Western Cordillera, Colombia	0.168	0.172	0.002	0.429	-	-	-	-
Eastern Cordillera, Ecuador	0.702	0.006	0.647	0.032	0.793	0.002*	0.830	0.006
Western Cordillera, Ecuador	0.219	0.115	0.104	0.303	0.182	0.140	0.046	0.366
Central Andes domain								
Eastern Cordillera, Peru	-0.051	0.434	-0.398	0.768	-	-	-	-
Central Cordillera, Peru	0.935	0.001*	0.964	0.003*	-	-	-	-
Western Cordillera, Peru	0.813	<0.001*	0.922	<0.001*	-	-	-	-
Eastern Cordillera, Bolivia	-0.231	0.816	0.648	0.097	-	-	-	-

Annex 4. Effect of spatial topographic heterogeneity effect on species richness using non-transformed variables (linear effect), log-transformed variables (curvilinear effect), and log-transformed area (semi-log effect). Significant topographic heterogeneity effects are indicated with asterisk (*). The models with the lowest AICc are shown in boldface type. Mountain ranges are sorted by domain and latitude from north to south.

Geographic region	Linear effect		Curvilinear effect		Semi-log effect	
	r^2	p -value	r^2	p -value	r^2	p -value
Northern Andes domain						
Merida Andes, Venezuela	0.616	0.007*	0.769	0.001*	0.664	0.005*
Sierra Nevada de Santa Marta, Colombia	0.133	0.191	0.295	0.075	0.198	0.128
Eastern Cordillera, Colombia	0.892	<0.001*	0.847	<0.001*	0.833	<0.001*
Central Cordillera, Colombia	0.502	0.020*	0.354	0.053	0.439	0.031*
Western Cordillera, Colombia	0.569	0.011*	0.767	0.001*	0.492	0.021*
Eastern Cordillera, Ecuador	-0.008	0.366	-0.103	0.632	-0.047	0.450
Western Cordillera, Ecuador	-0.107	0.649	-0.103	0.630	-0.112	0.674
Central Andes domain						
Eastern Cordillera, Peru	0.647	0.005*	0.445	0.030*	0.483	0.023*
Central Cordillera, Peru	-0.134	0.824	-0.14	0.899	-0.142	0.952
Western Cordillera, Peru	-0.108	0.652	-0.079	0.541	-0.045	0.445
Eastern Cordillera, Bolivia	0.573	0.011*	0.299	0.074	0.570	0.011*

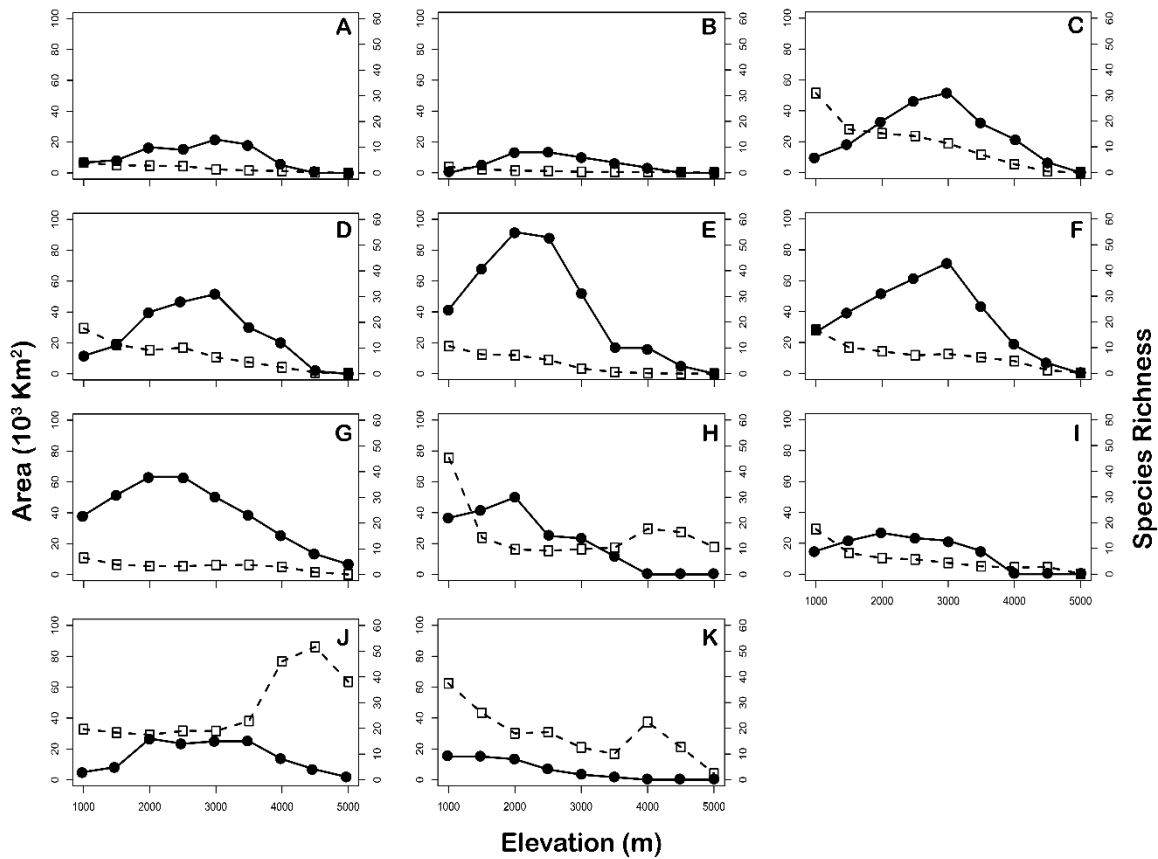
Annex 5. PGLS regressions between diversification rates estimates for stem-group and crown-group ages and clade elevation (midpoint and ancestral reconstructed midpoint). Diversification rates estimates include our BAMM calculated extinction rate (0.02) and three different relative extinction rates (ε): low (0), middle (0.45), and high value (0.90). All regressions were not significant (range of PGLS results: $r^2 = 0.02$ -0.18; p-values = 0.19-0.91).

Method	Clade elevation	Extinction value	Slope	Intercept
Stem age	Midpoint	0	-526.56	1568.93
Stem age	Midpoint	0.02	-526.56	1568.15
Stem age	Midpoint	0.45	-526.56	1544.61
Stem age	Midpoint	0.90	-526.56	1454.13
Crown age	Midpoint	0	-1232.61	-1579.74
Crown age	Midpoint	0.02	-1232.61	-1579.74
Crown age	Midpoint	0.45	-1232.61	-1633.99
Crown age	Midpoint	0.90	-1232.61	-2044.53
Stem age	Ancestral midpoint	0	-2165.44	423.87
Stem age	Ancestral midpoint	0.02	-2165.44	420.66
Stem age	Ancestral midpoint	0.45	-2165.44	323.84
Stem age	Ancestral midpoint	0.90	-2165.44	-48.226
Crown age	Ancestral midpoint	0	1337.97	4132.23
Crown age	Ancestral midpoint	0.02	1337.97	4132.33
Crown age	Ancestral midpoint	0.45	1337.97	4191.13
Crown age	Ancestral midpoint	0.90	1337.97	4636.75

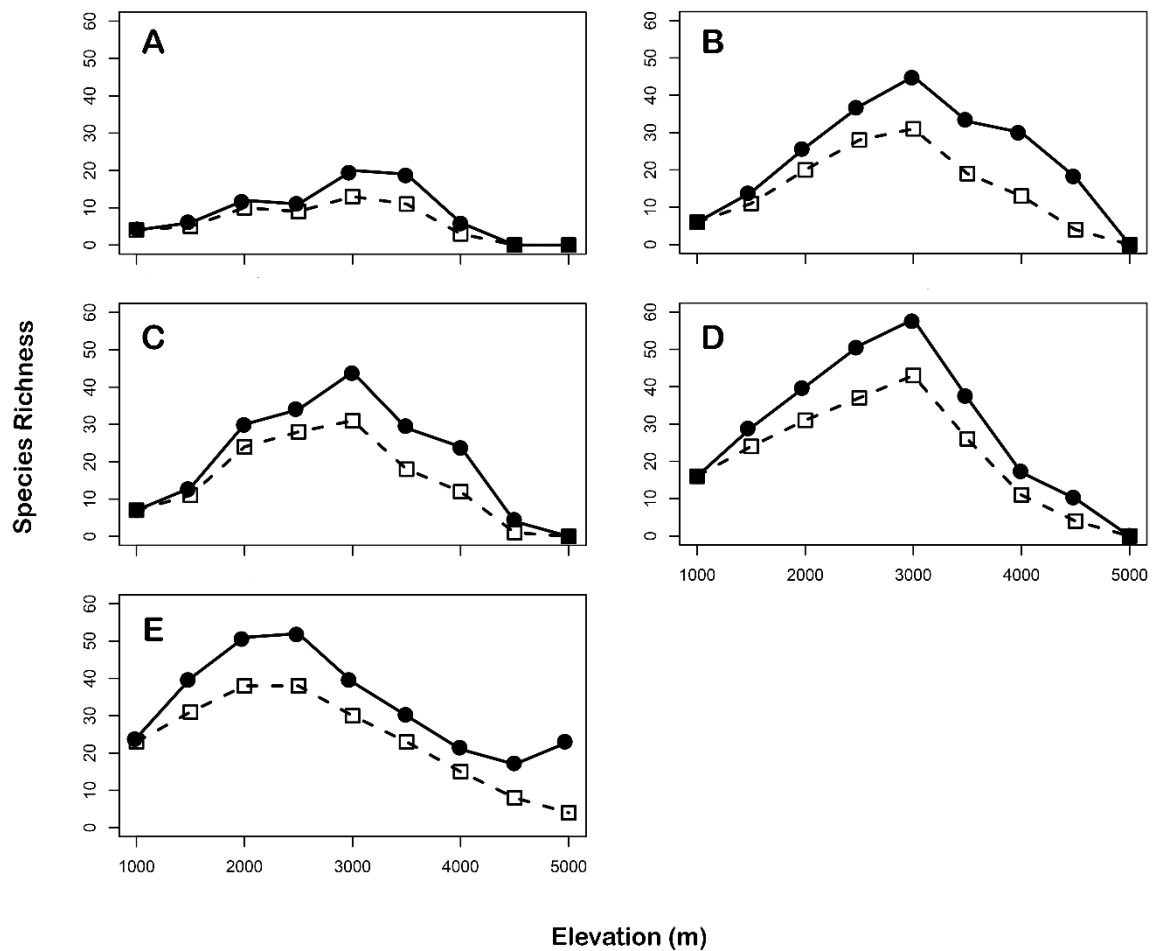
Annex 6. Summary of results from the Multiple State Speciation and Extinction (MuSSE) analyses for the elevational distributions of Andean *Pristimantis* frogs. Null model is indicated with asterisk (*). The model with the lowest AICc are shown in boldface type. Speciation rates (λ), extinction rates (μ), and dispersal rates (q).

Model	λ_1	λ_2	λ_3	μ_1	μ_2	μ_3	q_{12}	q_{21}	q_{23}	q_{32}	df	AIC
$\lambda_1 = \lambda_2 = \lambda_3, q_{12} = q_{21} = q_{23} = q_{32}, \mu_1 = \mu_2 = \mu_3^*$	0.14	0.14	0.14	8.17^{-07}	8.17^{-07}	8.17^{-07}	0.04	0.04	0.04	0.04	3	994.07
$\lambda_1 = \lambda_2 = \lambda_3, q_{12} \neq q_{21} \neq q_{23} \neq q_{32}, \mu = 0$	0.11	0.11	0.11	0.0	0.0	0.0	0.05	0.04	0.01	0.05	5	992.76
$\lambda_1 \neq \lambda_2 \neq \lambda_3, q_{12} \neq q_{21} \neq q_{23} \neq q_{32}, \mu = 0$	0.03	0.09	0.16	0.0	0.0	0.0	1.21^{-05}	0.05	6.56^{-07}	0.06	7	973.24
$\lambda_1 \neq \lambda_2 \neq \lambda_3, q_{12} \neq q_{21} \neq q_{23} \neq q_{32}, \mu_1 = \mu_2 = \mu_3$	0.02	0.09	0.16	7.18^{-06}	7.18^{-06}	7.18^{-06}	2.68^{-07}	0.05	2.33^{-07}	0.06	10	979.24
$\lambda_1 \neq \lambda_2 \neq \lambda_3, q_{12} \neq q_{21} \neq q_{23} \neq q_{32}, \mu_1 \neq \mu_2 \neq \mu_3$	0.02	0.09	0.16	6.50^{-07}	2.72^{-06}	2.14^{-07}	2.76^{-06}	0.05	2.10^{-09}	0.06	8	975.25

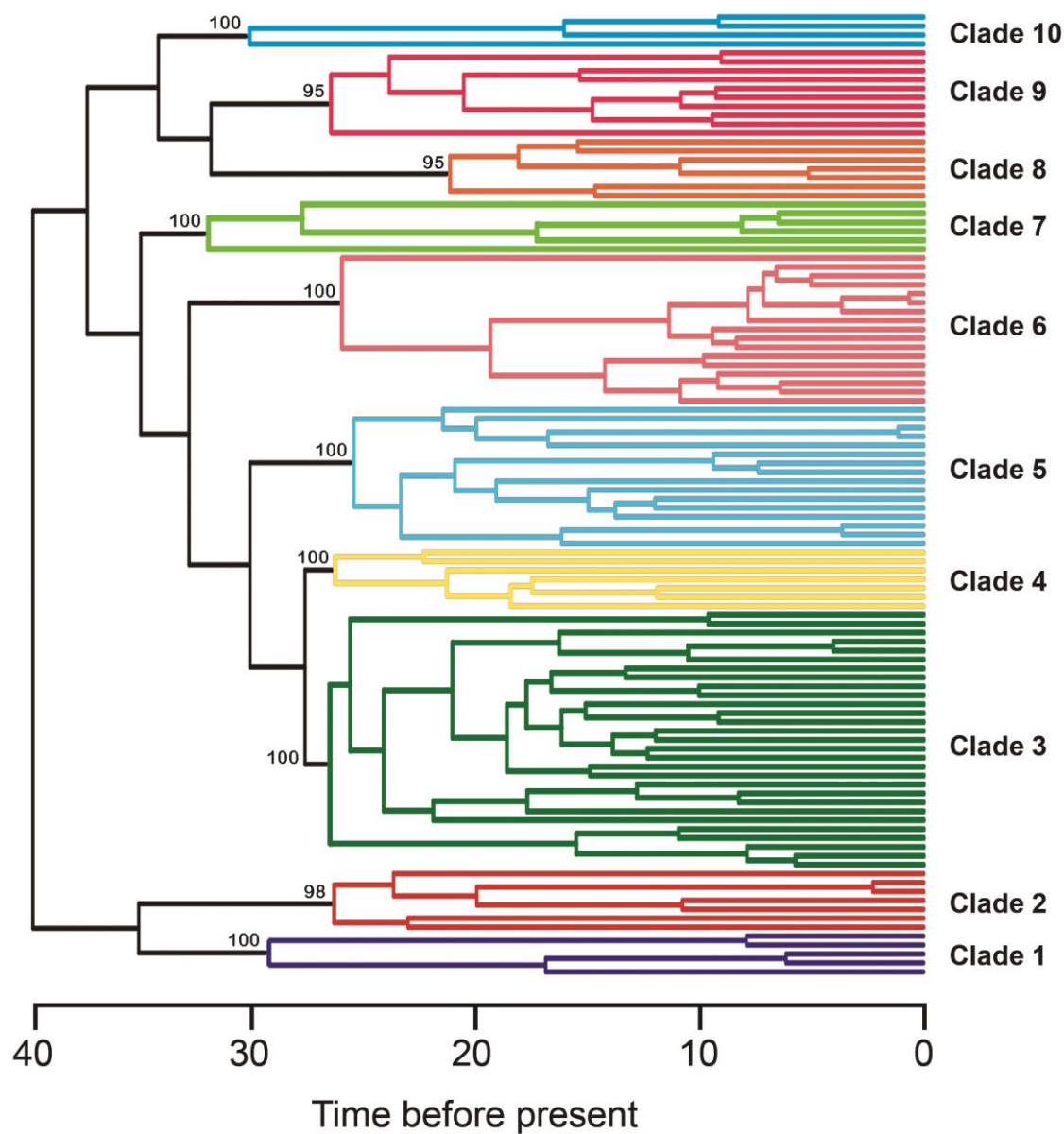
Annex 7. Area profiles (open squares and dotted lines) and diversity pattern (solid circles and solid lines) along elevational gradients on main mountain ranges of Tropical Andes. (A) Merida Andes, Venezuela. (B) Sierra Nevada de Santa Marta, Colombia. (C) Eastern Cordillera, Colombia. (D) Central Cordillera, Colombia. (E) Western Cordillera, Colombia. (F) Eastern Cordillera, Ecuador. (G) Western Cordillera, Ecuador. (H) Eastern Cordillera, Peru. (I) Central Cordillera, Peru. (J) Western Cordillera, Peru. (K) Eastern Cordillera, Bolivia.



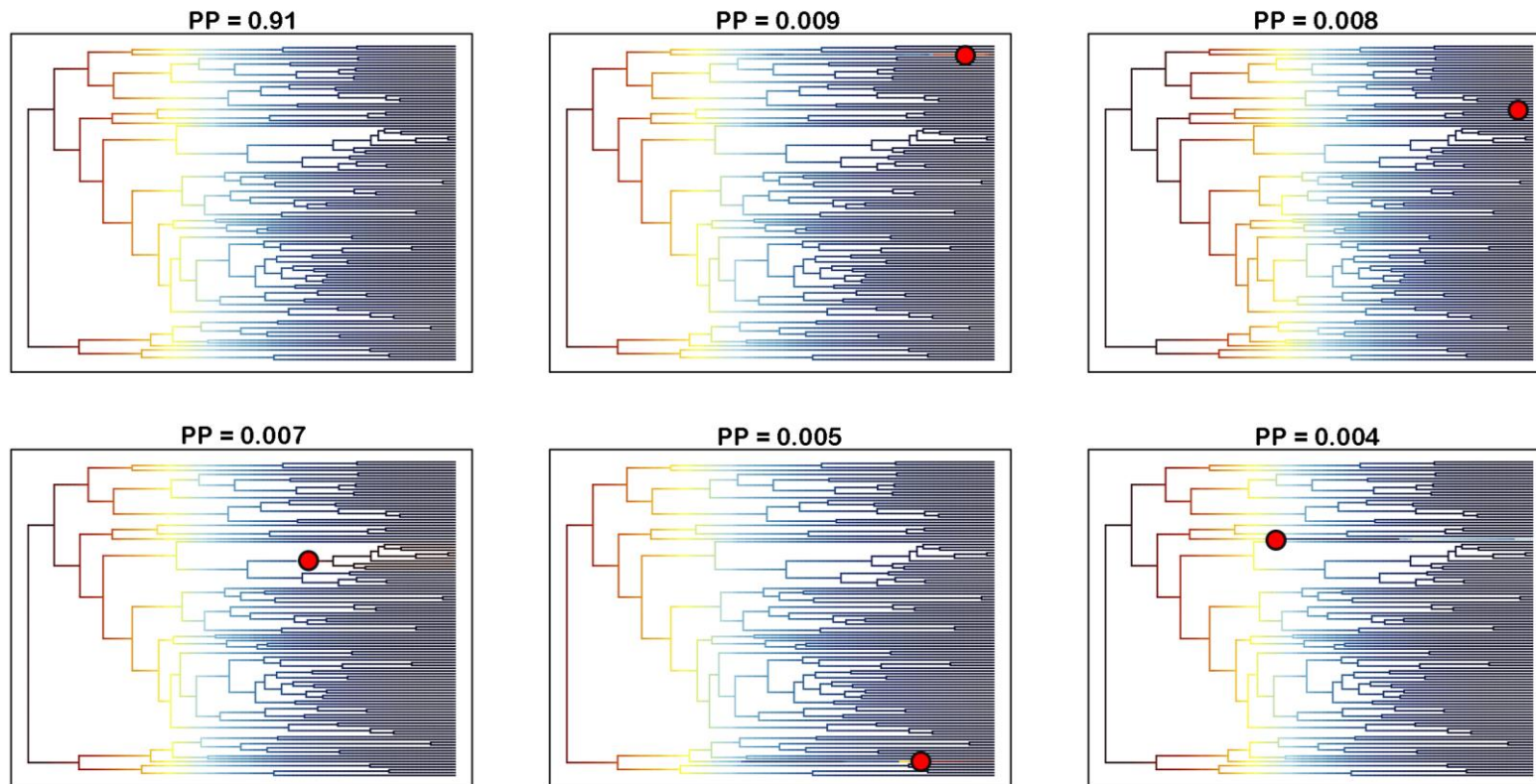
Annex 8. Comparisons among curvilinear area correction method (solid circles and solid lines) and empirical diversity patterns (open squares and dotted lines) for each main mountain range where significant curvilinear species-area effects were detected. (A) Merida Andes, Venezuela. (B) Eastern Cordillera, Colombia. (C) Central Cordillera, Colombia. (D) Eastern Cordillera, Ecuador. (E) Western Cordillera, Ecuador.



Annex 9. Time-calibrated maximum clade (MCC) credibility (modified from Pinto-Sánchez et al., 2012; see Materials and Methods for more details about the tree) showing the 10 clades identified for historical analyses (for more details see Padial et al., 2014). Time before present is indicated in million years.



Annex 10. Speciation dynamics during the evolutionary history of *Pristimantis* frogs. Plots illustrate the six most-probable configurations sampled with BAMM. Warmer colors denote faster rates of speciation. Red circles denote locations of rate shifts for each configuration. The upper left plot (see Figure 5) with no shifts shown the maximum posteriori probability (PP) configuration.



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