



Research Article

Beta diversity patterns in Andean rodents: current and historical factors as drivers of turnover and nestedness

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Abstract

The Andes are known to be one of the most species-rich regions on Earth, with their origination promoting formation of new habitats and acting as climatic barriers. This orogenic event was structured latitudinally with 3 major segments having different formation times and with different environmental and historical conditions. The Andean region has been historically important in the evolutionary history of small mammals and is considered the region of Earth with the highest values of rodent species richness and turnover. Therefore, the region provides an excellent opportunity to evaluate mechanisms involved in structuring rodent assemblages and beta diversity patterns. Here, we assessed spatial patterns of rodent beta diversity along the Andes Mountains, with specific goals of examining patterns of turnover and nestedness as 2 recognized processes that drive species composition. We explored the role of spatial, climate, and historical factors on beta diversity patterns using geographic range maps for 432 rodent species to construct a species presence-absence matrix. We used piecewise regressions to identify latitudinal breakpoints in turnover and nestedness, and conducted multiple regressions and variation-partitioning approaches to assess the contribution of each set of postulated drivers in shaping beta diversity patterns. Beta diversity decreases from north to south. The highest turnover was located at the Northern Andes (5°N and 10°S) and western-central Andes (20°S and 35°S). Nestedness was higher below 40°S and in some areas of the western-central Andes between 15° and 20°S. Turnover and nestedness registered breakpoints coincident with the Central and Southern Andes limit. Turnover explained most of the beta diversity for all segments, although within the Southern Andes there was also some contribution of nestedness. In all segments, beta diversity was mainly explained by spatial factors with minor contributions from spatially structured climate (Northern Andes), interaction of all factors (Central Andes), and the interaction between current climate and history (Southern Andes).

Key words: Andes, beta diversity, environmental drivers, historic processes, rodents, spatial processes.

Patrones de diversidad beta en roedores Andinos: factores actuales e históricos como determinantes del recambio y anidamiento de especies

Resumen

Los Andes son reconocidos como una de las regiones más ricas en especies de la tierra, ya que su levantamiento favoreció la formación de nuevos hábitats y actuó como barrera climática. Este evento orogénico se estructuró latitudinalmente en 3 segmentos, cada uno con tiempos de formación características ambientales y condiciones históricas diferentes. La región Andina ha sido un importante escenario en la historia evolutiva de los pequeños mamíferos y es considerada la región con mayor riqueza y recambio de especies. Por lo tanto, es un excelente escenario para evaluar los mecanismos que estructuran los patrones de diversidad beta del ensamble de roedores. Aquí evaluamos el patrón espacial de la diversidad beta de roedores a lo largo de la Cordillera de los Andes, descomponiéndolo en recambio y anidamiento, con el fin de comprender los procesos subyacentes que determinan la composición de especies. Exploramos el papel de los factores espaciales, climáticos e históricos sobre los patrones de diversidad beta utilizando mapas de distribución geográfica para 432 especies de roedores obtenidos de la Base de Datos de Diversidad de Mamíferos y construimos una matriz de presencia-ausencia de especies (PAM). Utilizamos regresiones por tramos (piecewise) para identificar los puntos de quiebre latitudinales en recambio y anidamiento, y realizamos regresiones múltiples y partición de la varianza para evaluar la contribución de cada conjunto de factores en la conformación de los patrones de diversidad beta. La diversidad beta disminuye de Norte a Sur, con un mayor recambio en los Andes del Norte (5°N y 10°S) y en la zona central oeste (20°S y 35°S). El anidamiento fue más

alto por debajo de los 40° S y en algunas áreas del centro oeste entre los 15° y 20° S. Tanto el recambio como el anidamiento registraron puntos de quiebre coincidentes con el límite entre el segmento Central y el Sur. El recambio explica la mayor parte de la diversidad beta para todos los segmentos, aunque el anidamiento contribuye también a la diversidad beta de los Andes del Sur. En todos los segmentos andinos la diversidad beta se explicó principalmente por factores espaciales con una menor contribución del clima actual (NA), por la interacción de todos los factores (CA) y la interacción entre el clima histórico con el actual (SA).

Palabras clave: Andes, diversidad beta, factores ambientales, procesos históricos y espaciales, roedores.

The Andes, the longest mountain chain in the world (approximately 7,000 km long), are known to be one of the most species-rich regions on Earth (Myers et al. 2000). The Andean uplift process prompted the formation of new dry high-elevation habitats, produced a mosaic of montane and inter-Andean valleys, and acted as climatic barriers, among other effects (Brumfield and Edwards 2007; Orme 2007). This process embraced a progressive and complex sequence of orogenic events, which progressed from north to south and west to east, affecting different regions at different times (Gregory-Wodzicki 2000; Ramos and Alemán 2000; Antonelli et al. 2009; Ramos 2009). More than 60% of the current elevation of the Central Andes (CA) was attained within the last 10 Myr (Gregory-Wodzicki 2000; Garzzone et al. 2006). The Andes chain has been categorized into 3 different geological units—Northern Andes (NA), CA, and Southern Andes (SA; Ramos 2009), which evidence different uplift histories in shape and time, and show distinct geological and environmental characteristics. Andean orogeny has promoted a remarkable evolutionary radiation of the biota, from bellflowers (Lagomarsino et al. 2016), and angiosperms (Hughes and Eastwood 2006; Antonelli et al. 2009; Madriñán et al. 2013), to butterflies (Elias et al. 2009), birds (Brumfield and Edwards 2007; McGuire et al. 2014), and mammals (Ruggiero et al. 1998; Upham and Patterson 2012; Upham et al. 2013; Leite et al. 2014; Maestri et al. 2019).

The Andean region has been an important scenario in the evolutionary history of small mammals (Hershkovitz 1969; Reig 1981, 1986; Marquet 1994; Ojeda et al. 2000; Palma et al. 2005; Maestri and Patterson 2016; Vallejos-Garrido et al. 2023). Among these, rodents are the most diverse of all mammalian groups worldwide (accounting for more than 42% of all species; Burgin et al. 2018; D'Elia 2019) and occupy most terrestrial environments (including subterranean, semiaquatic, arboreal, scansorial, and cursorial forms; Ojeda et al. 2016; D'Elia et al. 2019). In South America, rodents encompass almost 50% of all mammals, and their evolutionary history differs between the 2 most diverse groups—i.e. caviomorphs (Upham and Patterson 2015; Ojeda et al. 2016) and sigmodontines (Patterson and Costa 2012; Lacher et al. 2016).

In western South America (east of the Andes), multiple dispersal events occurred into the Andes, which promoted diversification of modern taxa within several tribes (i.e. Abrothrichini, Andinomiyini, Euneomyini, and Phyllotini). Within the Andes region, rodent species richness and turnover across geographic and elevational gradients (i.e. beta diversity) are among the highest on Earth (Maestri and Patterson 2016; Vallejos-Garrido et al. 2023). Moreover, it is considered one of the regions where the most species ranges overlap, and where several small or restricted-range species coexist (Maestri and Patterson 2016), leading to high levels of local (i.e. alpha) diversity.

Mountain environments are known to promote high beta diversity—frequently due to allopatric speciation events—but also due to current and historical factors, including sharp environmental gradients (Badgley et al. 2017; Antonelli et al. 2018). There are 2 major patterns of beta diversity—spatial turnover

and nestedness (Baselga et al. 2007; Baselga 2012; Legendre 2014). Spatial turnover is the replacement of some species by others (Qian et al. 2005; Leprieur et al. 2011), while nestedness reflects a process of species loss, in which species at more depauperate sites are subsets drawn from species assemblages at richer sites (Ulrich and Gotelli 2007; Baselga 2012). In general, beta diversity patterns are addressed by 1 or more of 3 hypotheses. First, spatial patterns may determine species composition as a consequence of dispersal limitations (Hubbell 2001; Condit et al. 2002; Leibold et al. 2004)—however, spatial patterns may also result from several other unknown processes. Second, the historical hypothesis suggests that long-term abiotic and biotic events related to the area and taxon history control diversity patterns (Hewitt 2004; Wiens and Donoghue 2004; Svenning and Skov 2005; Leprieur et al. 2011), e.g. climatic conditions that vary through time, large-scale environmental changes such as mountain formation and glaciation, among others. Third, the environmental control hypothesis emphasizes that variation in current climatic conditions determines species distributions and coexistence due to species–habitat associations (Hawkins et al. 2003; Whittaker et al. 2007; Baselga et al. 2012b). These hypotheses are not mutually exclusive, and may act together to determine species diversity patterns.

The Andes have a sharp elevational gradient and broad latitudinal extent that result in large-scale climatic and topographic variation, frequent volcanic activity, and glaciation below 40° S (Hulton et al. 2002; Marín et al. 2013). These features make the range an excellent region in which to evaluate the relative roles of sequential episodes of uplift through time, historical formation of barriers to dispersal, and current climate conditions on patterns of rodent species distribution and beta diversity.

Our research aims to achieve 2 primary objectives: (i) to characterize regional beta diversity patterns in rodents across the Andes—assessing the relative roles of turnover and nestedness components; and (ii) to evaluate the role of climate and historical/geological long-term processes in their distributions. Our approach is 2-fold. First, we aim to assess whether beta diversity patterns are influenced by the Andes historical sequence of segmentation into NA, CA, and SA regions, which can serve as a proxy for historical effects. We predict that the NA and CA segments, relative to the SA segment—will be predominantly characterized by turnover due to factors including: greater stability and complex topography (including major differences in elevation) resulting from older formation time; historically higher average temperature; and absence of glaciation events. Conversely, SA will exhibit higher levels of nestedness facilitated by environmental filtering and selective recolonization, resulting from Pleistocene glaciations and generally lower temperatures.

Second, we seek to identify the drivers associated with beta diversity patterns along each Andean segment. We expect that beta diversity in NA and CA will register higher associations with current climate and historical drivers mainly related to

topographic heterogeneity. Regions with high spatial/topographic heterogeneity promote several microclimates and therefore high species turnover (Rahbek and Graves 2000). Conversely, we expect that beta diversity in SA will be primarily explained by historical drivers such as climate variation through time, and dispersal limitations associated with Pleistocene glaciations driving range retraction and expansion events.

Materials and methods

The study area includes the Andean Cordillera, from 10°N in Venezuela to 55°S in southern Argentina and Chile (Nagy and Grabherr 2009; Körner et al. 2011). The 3 Andean segments (NA 10°N to 5°S, CA 5°S to 46°S, and SA 46°S to 55°S) differ in their uplift genesis, with subsequent regional differences in climate, and resulting in an historical and current climatic latitudinal gradient (Ramos 1999; Horton 2018) and Pleistocene glaciations restricted to the SA (Heusser et al. 2006).

We used geographic range maps for 432 species of rodents (Suborders Myomorpha and Hystricomorpha) taken from the Mammal Diversity Database (MDD, <https://www.mammaldiversity.org/index.html>; Marsh et al. 2022) to construct species richness maps and a species per cell presence-absence matrix (PAM; Supplementary Data SD1). Species ranges were overlapped into a 0.5° × 0.5° grid, with the `lets.presab` function of the “letsr” package (Vilela and Villalobos 2015) in R (R Core Team 2022). The PAM encompasses 1,009 grid cells and each species was considered present in a cell if at least 40% of a cell was included in its range. Beta diversity was calculated as the mean turnover partition of Sorensen’s index (Melo et al. 2009; Baselga 2012; Baselga and Orme 2012) between a focal cell and its 8 neighbor cells. We used the function `betagrid` (available at: <http://rfunctions.blogspot.com/>), developed by José Hidasi-Neto (from Universidade Federal de Goiás, Brazil), to calculate beta diversity of each cell and also to partitioned it into spatial turnover and nestedness according to Baselga (2010) framework. Maps of beta diversity were prepared using the `rasterize` function of the “raster” package (Hijmans and Van Etten 2012).

Regional overall beta diversity was calculated using the `betadiv.comp` function of the package “adespatial” (Dray et al. 2023), and beta diversity for each Andean segment was calculated to identify the relative contributions of components of beta diversity for each of the 3 regions. Bootstrap analysis, selecting random samples equivalent to 50% of the cells, was carried out to calculate the fraction of nestedness explained in each Andean region and to assess significant differences, if any, among them.

Piecewise regressions were performed between each component of beta diversity versus latitude to identify breakpoints and associate components of beta diversity with each Andean segment, using the function `selgmented` of the R package “segmented” (Muggeo 2008)—optimal number of breakpoints was determined according to the BIC criterion (Muggeo 2020). We plotted a bivariate map of turnover and nestedness quantiles using the `bivariate.map` function (available at: <http://rfunctions.blogspot.com/>), to graphically identify latitudinal breakpoints. We analyzed the synergistic effect between latitude and elevation in structuring beta diversity patterns, using a generalized regression model (GLM) and plotting its results using the `predictorEffects` function of the R package “effects.”

To analyze which variables better explained turnover and nestedness patterns in each Andean segment, we used linear regression models and variance partitioning analysis. We analyzed 3

different sets of variables: (1) current climate; (2) historic, and (3) spatial explanatory variables. Current climate consisted of 4 bioclimatic variables (mean annual temperature, mean annual precipitation, precipitation seasonality, and temperature seasonality) obtained from the Worldclim database (<http://www.worldclim.org/bioclim>) with a resolution of 30 arc-seconds (~1 km). We generated the normalized difference vegetation index, and 1 variable that accounts for vegetation complexity (CanopySD—1-km resolution—Simard et al. 2011)—for each of these metrics, we extracted the standard deviation between each cell canopy height and its 8 surrounding cells (by doing so, we attempted to account for variability among vegetation complexity in each region).

Historic variables account for past events such as the Andean uplift orogenic process and Pleistocene glaciations. We used a digital elevation model (GTOPO30; US Geological Survey 2023), and the topographic ruggedness index (Riley et al. 1999) to account for topographic elevation variation. As proxies for Pleistocene climate conditions, we used the difference in annual mean temperature, annual mean precipitation, temperature seasonality, and precipitation seasonality between the present and mid-Holocene (~6,000 BP) climatic conditions (modeled by CCSM4, Community Climate System Model—Version 4; Gent et al. 2011).

The spatial structure of our data was modeled using distance-based Moran’s eigenvector maps (dbMEMs; Borcard and Legendre 2002; Dray et al. 2006), which decompose spatial distances into orthogonal variables (eigenvectors). We used the function `quickMEM` (provided in Numerical Ecology with R pp.327), to select significant dbMEMs with positive eigenvalues (NA: 7 dbMEM; CA: 46 dbMEM; SA: 12 dbMEM).

Variance partitioning seeks to quantify the unique and combined fractions explained by each data set. Therefore, we independently stepwise selected each set of environmental data with turnover and nestedness, and determined the percentage (%) of variation explained by each. We used the `stepAIC` function of the “mass” package (Ripley et al. 2013) with direction “both” for variable selection and the `varpart` function of the “vegan” package (Oksanen et al. 2018) for variance partitioning.

Results

Our findings indicate a noticeable decline in mean beta diversity moving from the NA to SA segments. Higher values of beta diversity are located between 9° and 35° South latitude, toward the western region of the Andes, which encompass ecotones between the Sechura Desert (West) and the Puna (Central, dry and wet Puna) and the Peruvian Yungas (Olson et al. 2001)—beta diversity values are also high at the ecotone between the Atacama Desert and Puna, and between the northern portion of the Chilean Matorral and the southern Andean Steppe. Lower values are located between 15° and 28°S and toward the central region of the Andes chain—an area including the Puna ecoregion (including the Altiplano) and other arid regions (Fig. 1). The highest values in turnover occur in the NA (between 10°N and 12°S) and in the western portion of the CA (between 25°S and 35°S). Nestedness values were higher in the SA, below 40°S and in small areas of the western portion of CA between 15°S and 20°S (Fig. 1).

For the most part, Andean rodent diversity was mainly determined by species turnover (Repl_s: 0.43), accounting for 94% of the diversity pattern, while the nestedness contribution was negligible (Nes_{BS}: 0.03) (Fig. 2a). Furthermore, turnover was the dominant feature among each Andean segment, whereas nestedness

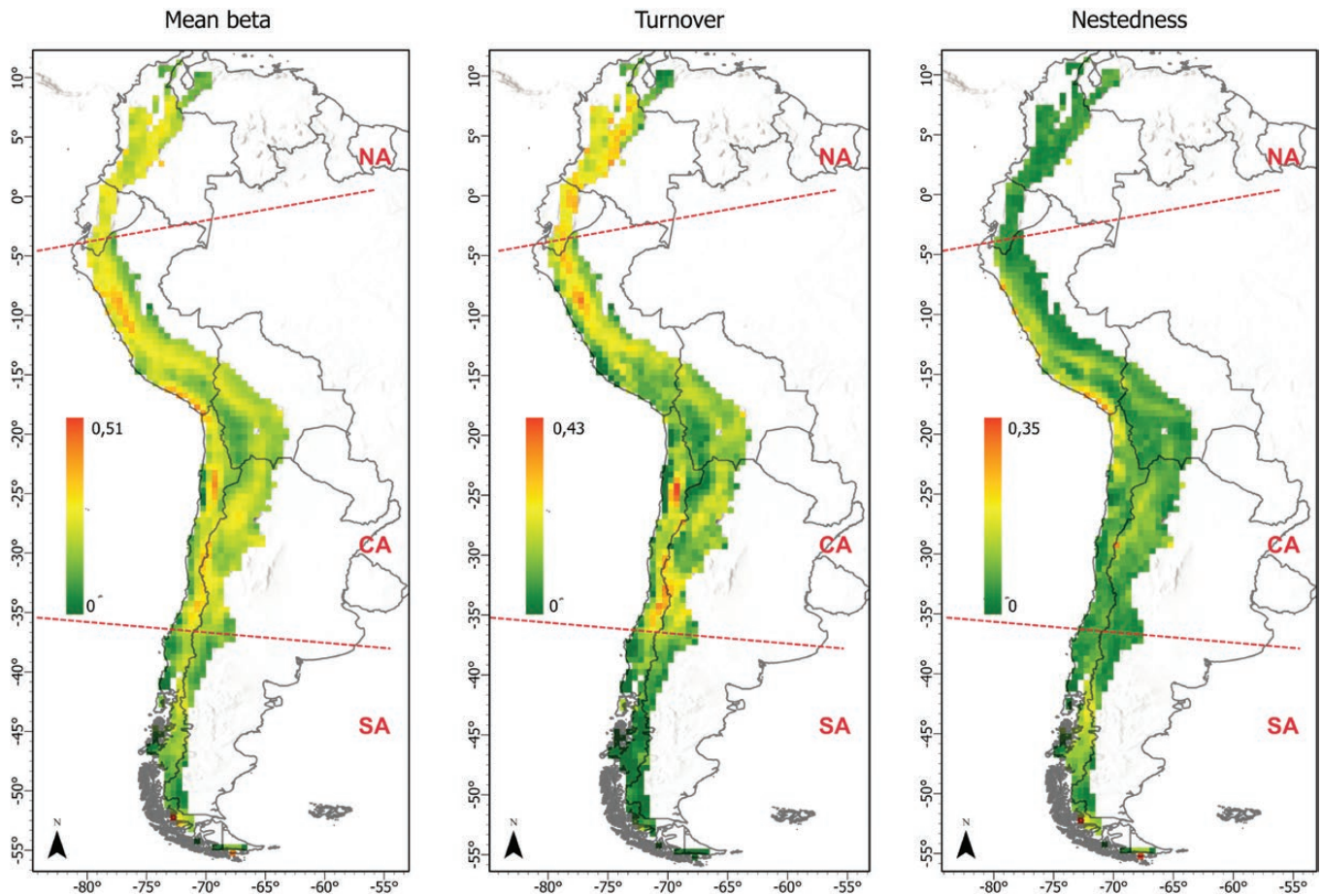


Fig. 1. Rodent beta diversity (mean beta), turnover, and nestedness pattern within the Andes region.

represents a significant contribution for the SA (Fig. 2b), where its proportion was almost 3 times higher than registered in NA and CA.

The analysis of rodent assemblage turnover revealed 3 latitudinal breakpoints. The first one occurred at 2°N, beyond which turnover decreased steadily until 20°S (Fig. 3a). At this point, the trend reversed, and turnover began to increase positively up to 33°S. However, from here, turnover sharply decreased toward the southern latitudes. The nestedness pattern showed 2 latitudinal breakpoints, at 18°S and 37°S. In general, nestedness increased with latitude. South from 37°S, nestedness increased markedly in association with latitude increase (Fig. 3a), whereas from 18°S to 37°S a reversed pattern was detected.

Bivariate plots showed a transition from dominant turnover in the NA to a more nestedness resultant pattern in the SA. The CA evidenced a more complex scenario with high turnover and nestedness synergy registered at the northern portion of the segment (Fig. 3b).

The combined effect of latitude and elevation was accounted for by a generalized regression model. Turnover pattern is correlated with latitude ($P < 0.001^{***}$) and the interaction between latitude and elevation ($P = 0.05^*$), while nestedness was only related to latitude ($P = 0.00261^{**}$). The interaction between latitude and elevation showed that in the NA (10°N to 5°S), turnover tends to decrease with elevation (Fig. 4), whereas below 5°S the relationship becomes negative. Furthermore, the slope in which turnover increases with elevation varies latitudinally, showing a marked increase south of 40°S.

Turnover pattern is mainly associated with spatial drivers and to a minor extent with current climate conditions. The NA turnover was explained by spatial drivers (58%), from which 23% represented spatially structured environmental variation and 25% was pure spatial effect. The CA turnover was also explained by pure spatial (45%), while current climate and historical drivers accounted for minor values. The interplay between current climate, history, and space accounted for 17% of the variation. SA turnover was also accounted for by spatial drivers (40%), but in this region, it was also explained by the combined effect of climate and history, which accounted for 26% of the variation (Fig. 5). The nestedness pattern was mainly explained by spatial drivers and also registered high values of unexplained variance (Fig. 5).

Discussion

The western portion of South America is known to host high alpha and beta diversity of rodents (Ruggiero and Lawton 1998; Maestri and Patterson 2016; Novillo and Ojeda 2021). This feature is mainly related to the topographic and climatic heterogeneity associated with the Andes mountain range (Maestri and Patterson 2016). When downscaling the focus of the study to the Andes chain (i.e. above 700 m a.s.l.), beta diversity of rodents decreased from north to south (this work), as also has been noted for other taxa including vascular plants, amphibians, and birds (Qian and Ricklefs 2007; Qian 2009; Baselga et al. 2012a; Qian et al. 2013). However, this decrease is not due to a

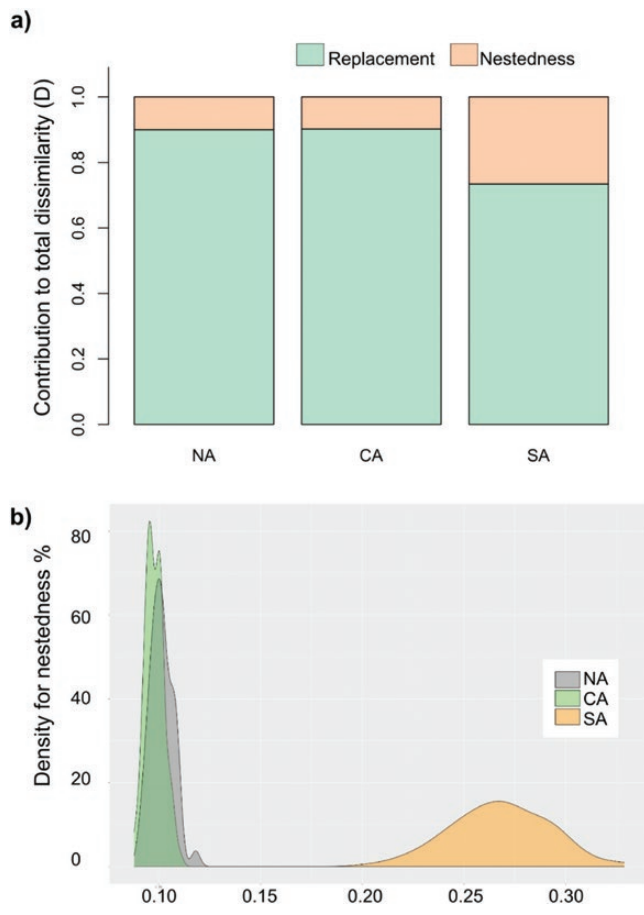


Fig. 2. (a) Contribution of turnover and nestedness to overall rodent beta diversity in each of the 3 Andean segments. (b) Comparison of nestedness percentage in each of the Andean segments, by adjustment of density function for nestedness percentage.

simple loss of species, but mainly to a high proportion of turnover. High turnover occurs in the NA (between 10°N and 12°S) and near to the limit between the CA and SA (between 25° and 35°S). The high turnover rate at the Andean flanks highlights the role played by the ecotonal zones between the dry Andean plateau (Puna–Altiplano) and the tropical forest (to the east), and the Sechura Desert and Atacama Desert to the northwest (Olson et al. 2001). These transitional zones between lowlands and highlands—with contrasting topographic and climatic features—promote allopatric isolation and the diversification of most endemic species (Ruggiero and Lawton 1998; Pacheco et al. 2007; Ortiz et al. 2012; Ferro 2013; Maestri and Patterson 2016; Maestri et al. 2017). Whereas low turnover was registered in the CA (Puna) from 15°S to 28°S, and in the Patagonia region of the SA (Valdivian Temperate Forest, Patagonian Steppe, and southern Chilean Matorral). Interestingly, this area of low turnover is convergent with a similar pattern of lower beta diversity in a central portion of the CA that is also flanked by areas of major beta diversity. This replicated pattern in different regions demonstrates changes in patterns of diversity that are abrupt from the periphery to the center, especially in the more longitudinally extensive central portion.

According to Andean orogenic evolution (Antonelli et al. 2009), we expected beta diversity patterns to differ among Andean segments, with turnover dominating the NA and CA, and nestedness prevailing at SA. However, our results showed that beta diversity

along the 3 Andean segments was mainly explained by turnover. Similar results were obtained in studies of beta diversity patterns along the Qinghai–Tibetan Plateau and the Hengduan Mountains in China (Wen et al. 2016), and across Europe (Svenning et al. 2011). However, within the SA segment, the nestedness proportion was significantly higher, which partially supports the hypothesis that harsh past climatic conditions act as environmental filters promoting species loss. On the other hand, a plausible explanation of the high turnover contribution in the SA could be related to species recolonization after ice sheets retractions (Sommer and Zachos 2009; Alexandri et al. 2012; Poljak et al. 2020) as well as local processes including within-region differentiation (Lessa et al. 2010).

Turnover breakpoints were not fully concordant with Andean segments. The first breakpoint was registered at 3°N which is almost 5° farther north than the NA and CA limit and occurs at the Amotape–Huancabamba deflection in northern Peru, which is considered an area of differentiation of several plant species (Anthelme et al. 2014; but see Mutke et al. 2014 for an opposite point of view). However, the limit between CA and SA was recovered by 1 breakpoint located at 35° to 36°S, which is coincident with the southern limit of the southern Andean Steppe and the tail of the Chilean Matorral. Previous studies of nonvolant mammal geographic ranges of South America (Castro-Insua et al. 2018) and the arid Andes (Novillo and Ojeda 2012) showed a beta diversity breakpoint at 29° to 30° S, which was coincident with changes in the slope of temperature decrease and also with lower elevation of the Andes chain. Most likely, the discrepancy among ours and previous results is a matter of spatial scale.

Nestedness shows higher values along the western flanks of the CA and at the southern portion of the continent (SA), with 2 latitudinal breakpoints, which evidence slope variation along different latitudes. The southern breakpoint is concordant with the CA and SA limit, and highlights the higher contribution of nestedness along this segment. This supports the idea of Pleistocene glaciation effect over diversity patterns, promoting species losses (Svenning et al. 2011; Baselga et al. 2012a).

Between 5° SL and 12° SL, there is a combination of high values of turnover and nestedness, which diminished downwards latitudinally. This area of high beta diversity and endemism represents a transitional mosaic where the Sechura Desert, Central Andean wet Puna, and the Peruvian Yungas meet (Olson et al. 2001). The nested pattern may have been favored by environmental filters (i.e. extreme cold and dry climatic conditions) of the Sechura Desert and Puna (Hartley 2003; Luebert and Weigend 2014), while the turnover pattern seems to be a consequence of allopatric speciation due to the marked zonation (i.e. vegetation and climate) between the Puna and the Yungas ecoregions (Patterson et al. 1998). The higher environmental heterogeneity and the larger continuous extent of the CA (area effect) are probably responsible for the high beta diversity of this region (Mena et al. 2011). Additionally, the interplay between latitude and elevation explained turnover patterns. In general, turnover increases with elevation (Maestri and Patterson 2016; Novillo and Ojeda 2021) but this pattern is reversed from 10°N to 5°S, where the limit between NA and CA is located. Finally, the slope of the variation of turnover with elevation varies according to latitude, being significantly steeper at lower latitudes.

Several studies analyzing beta diversity patterns in mid- to broad scales have shown that spatial processes are the primary drivers of beta diversity among several taxonomic groups (Qian 2009; Qian et al. 2009; Baselga 2010; Svenning et al. 2011;

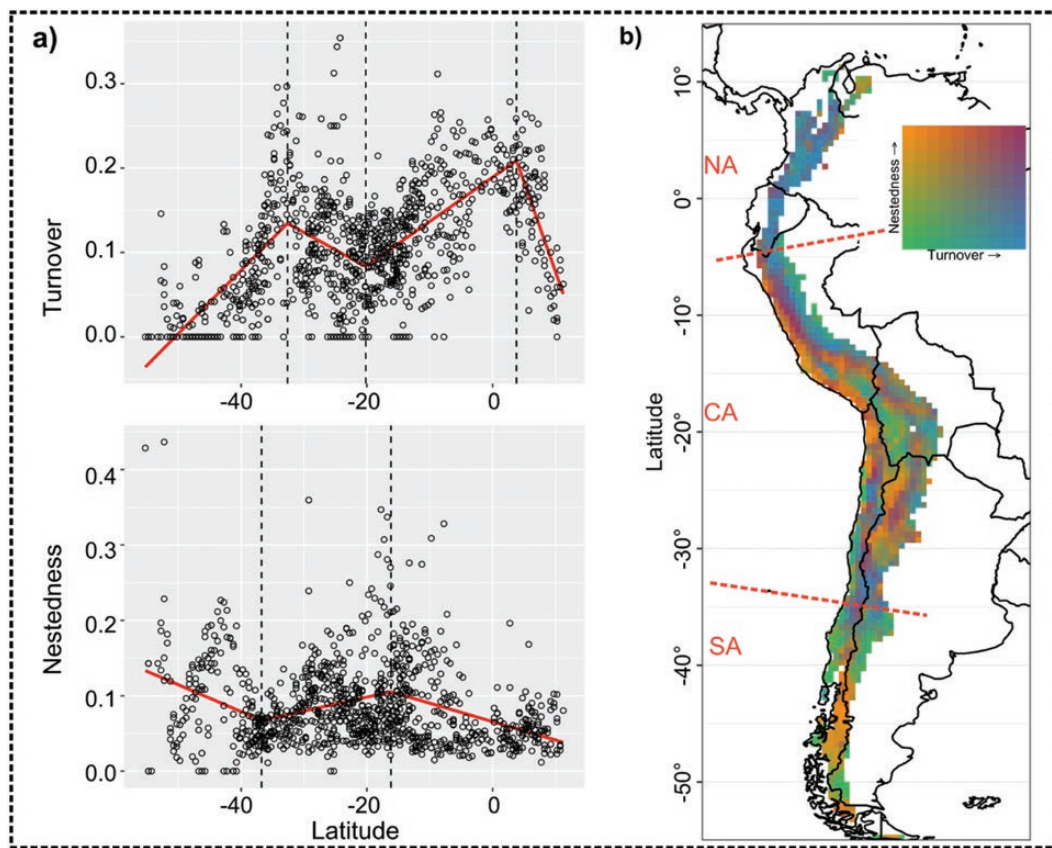


Fig. 3. (a) Latitudinal variation and breakpoints of turnover and nestedness. Dash lines indicate significant breakpoints, while red lines indicate a general latitudinal pattern. (b) Nestedness and turnover of rodent biplot across the Andes; dash lines indicate Andean segment limits. NA = Northern Andes; CA = Central Andes; SA = Southern Andes.

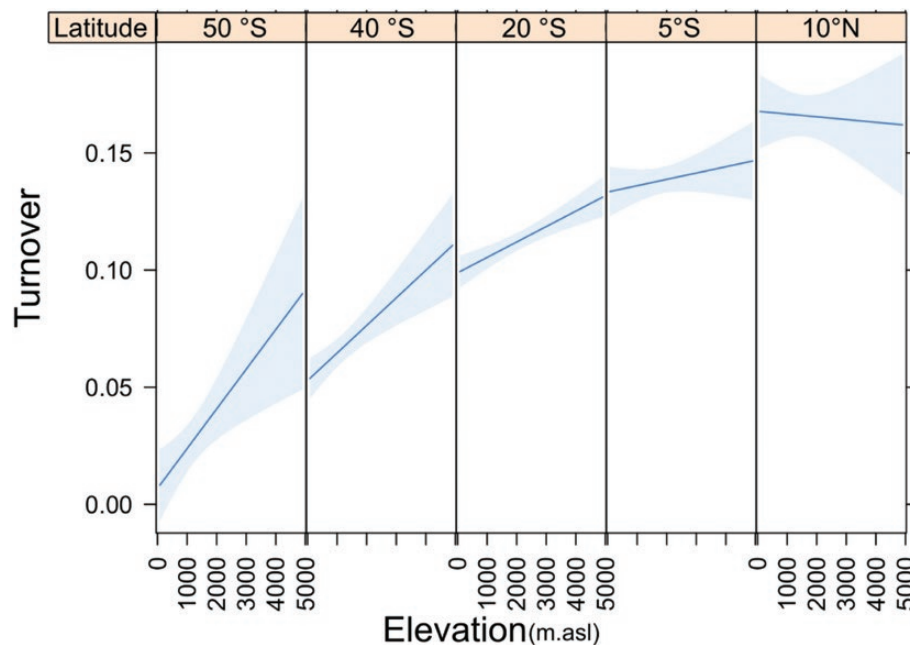


Fig. 4. Synergetic effect between latitude and elevation on rodent turnover pattern.

Varzinczak et al. 2018), including African rodent assemblages (Monadjem et al. 2023). The hypothesis that the spatial pattern results from dispersal limitations determined by historical effects has been commonly suggested (Cottiene 2005; Svenning and Skov

2005; Legendre et al. 2009). However, it is crucial to also consider alternative explanations for the observed pattern, such as neutral processes or the potential influence of environmental variables not considered in this study.

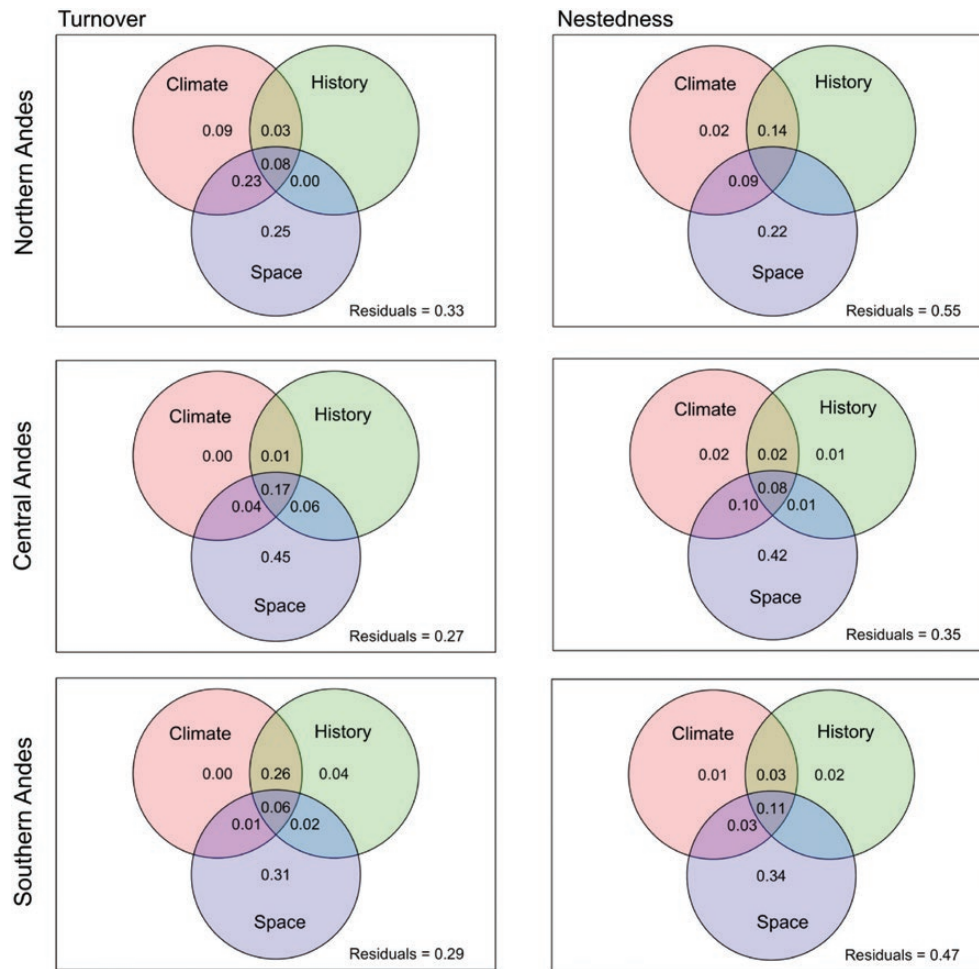


Fig. 5. Unique and shared contribution of climate, history, and spatial variables in explaining turnover and nestedness in each Andean segment.

The NA turnover predictors may be considered as a combination of deterministic process (niche-based process), and neutral mechanisms associated with the dispersal capabilities of the species (evidenced by pure spatial effect). Therefore, our prediction that current climatic conditions (climatic control hypothesis) determine beta diversity patterns along the NA was partially supported. NA, a warmer and subtropical region, which hosts in general more range-restricted species (Maestri and Patterson 2016), revealed more dispersal limitation effects (i.e. spatial process) than environmental filtering in structuring beta diversity. Climate may also contribute to the observed pattern of beta diversity, as a consequence of the high diversity of niches and microclimates registered in the region (Garreaud 2009).

The CA beta diversity was mostly explained by spatial effect and to a lesser extent by the interaction of space, history, and climate. Pure spatial effects may be caused by neutral mechanisms or a lack of other environmental variables not included in the present analysis, and could also be related to historical factors (Borcard and Legendre 1994; Svenning and Skov 2005). This segment is characterized by 2 very contrasting zones: a large and high-elevation Andean desert plain (Puna), and the heterogeneous topography and pronounced environmental gradients to the eastern and western slopes. It is in this matrix where species turnover seems to respond to the interaction between species dispersal limitations (neutral mechanism) and past orogenic and climatic events. Abrupt changes in species composition along the Andean

foothills were also registered for frugivorous birds (Dehling et al. 2014), and these rapid changes seem to be unrelated to climate, but rather probably associated with habitat structure, topography, and species radiations in lowlands and highlands. On the other hand, the nestedness pattern seems to result from environmental filtering due to species sorting into extreme cold and arid environments of the Puna ecoregion (Luebert and Weigend 2014).

SA turnover was explained by spatial effect and the interaction of current climate and history. Here, beta diversity patterns associated with the combined effects of mechanisms such as dispersal limitations and environmental filtering were likely driven by cycles of glaciation and deglaciation, in addition to orogenic processes and climate gradients. Additionally, the nestedness pattern was explained by an important spatial effect. Lessa et al. (2010) found that some rodent species from Patagonia evidenced demographic expansion signals, but several others showed a much older history of expansion (up to 500,000 years BP) than the last glacial maximum. The most probable processes related to beta diversity at the SA were pulses of contraction of geographic ranges, species extirpations during glacial time, recolonization after deglaciation, and local differentiation, which are evidenced by high values of turnover and nestedness along the region.

In conclusion, at a large scale, beta diversity of Andean rodents decreases as latitude increases. This pattern can be considered a general trend recorded for several taxa (Svenning and

Skov 2005; Qian and Ricklefs 2007; Baselga et al. 2012b; Qian et al. 2013). However, the processes involved to account for this pattern might be of different nature and magnitude along the Andes. In our study turnover was the dominant process controlling beta diversity pattern, while the contribution from nestedness increases in the SA. Beta diversity break points partially support Andean orogenic history reflected among latitudinal segments. Turnover and nestedness both evidence a breakpoint near the limit of CA and SA. But no breakpoint was registered at the NA and CA limit.

Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—List of 432 species of Andean rodents.

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Author contributions

AN conceived, designed the study, and drafted the initial manuscript. CL, JPJ, PT, and AAO contributed to data collection and analysis. LC contributed with specific analysis tools. RAO provided critical expertise and supervised the project. All authors edited and revised the final manuscript.

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Conflict of interest

None declared.

Data availability

Andean rodents list used in this manuscript can be found in [Supplementary Data](#).

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