The colonization of the Puna and Atacama Biogeographic Province by sister clades of *Psectrascelis* (Coleoptera: Tenebrionidae): Synchronous expansion without spatial overlap

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Abstract

**Aim:** We investigated the biogeographic pattern of the species-rich genus *Psectrascelis* (Coleoptera: Tenebrionidae) in the Central Andes and the Chilean Atacama Desert as an example for insect evolution in such a geologically and climatically highly dynamic arid region. The main aim was to test two alternative hypotheses about the main drivers of diversification of biotas from deserts in the region: Andean uplift versus Pleistocene fragmentation/dispersal.

**Location:** South America, Central Andes, Atacama Desert.

**Taxon:** *Psectrascelis* (Coleoptera: Tenebrionidae).

**Methods:** A phylogenetic tree based on cytochrome oxidase I, 16S and Wg genes was prepared for multiple individuals from 36 populations of the region representing 14 species or subspecies. Divergence times, ancestral ranges and biogeographic events that may have led to the current distribution and species diversity were estimated.

**Results:** The first split within the genus is not directly related to the Andean uplift but began at the time of global cooling at ~3.5 Ma, when the Andes had already reached their current altitude. Further differentiations of *Psectrascelis* lineages were mostly caused by common and more global drivers resulting in major clusters of diversifications at ~2.6–2.2 Ma, ~1.3–0.7 Ma and several subsequent events during the mid- to late Quaternary. Today, the two main clades of *Psectrascelis* almost meet each other after presumably synchronous range expansions along the Western Cordillera.

**Main conclusions:** Diversification of *Psectrascelis* has primarily been affected by global climate changes since the mid-Pliocene and has involved multiple vicariance and jump dispersal events. We hypothesize that jump dispersal events have occasionally been accompanied by adaptation to stronger aridity, which paved the way for range expansion into previously unsuitable habitats and eventually led to synchronous colonizations without spatial overlap along different isohyets in the Western Cordillera during the late Pleistocene.

**KEYWORDS**
Atacama, Central Andes, Chile, hyperaridity, non-adaptive radiation, Nyctellini, Phylogeny

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Understanding and characterizing thresholds for biological colonization and speciation and their potential causes, such as species diversification in response to climate and geological processes (e.g. Gillespie & Roderick, 2014) or interplay between geographical barriers and species dispersal (e.g. Burrows et al., 2014) is a major topic in biogeography. We are particularly interested in biological evolution and speciation at the transition from aridity to hyperaridity. In deserts, simple food webs and limited biological interactions offer ideal conditions for detailed research into key factors in the past that may have influenced the current distribution and diversification of organisms. Such analyses can then be used to model future trends in regions with increasing aridity, including possible time scales for adaptation and speciation processes.

Our study area is part of the South American Transition Zone (SATZ; Morrone, 2014, 2015) and includes the Chilean Atacama Desert, adjacent regions of the Pacific coast of Chile and the Central Andes. The area of the Central Andes considered here, including the Western and Eastern Cordilleras, the Altiplano and the Puna south of the Altiplano, is known as the Puna Biogeographic Province (Puna BP; Morrone, 2014). It is well established that the uplift of the Andes to its current altitude during the Miocene (Garzione et al., 2017) caused significant climatic changes during the Pliocene with strong impacts on the biodiversity throughout South America (Graham, 2009). Since then, the Andes have functioned as an effective east-west migration barrier for fauna and flora and thus a major driver for the diversification of many plant and animal taxa that have been studied from this region so far (e.g. Antonelli & Sammartin, 2011; Bohnert et al., 2019; Ceccarelli et al., 2016; Pocco et al., 2013), including insects (e.g. Cigliano, 1989; Roig-Juñent, 2002). The interplay of tectonic activity and changing climate led to the proliferation of arid environments in the southern cone known as Arid Diagonal of South America (ADSA; Abraham et al., 2000; Hinojosa & Villagrán, 1997), providing favourable conditions for the dispersal of organisms adapted to aridity (e.g. Ceccarelli et al., 2016; Zúñiga-Reinoso & Predel, 2019). In the eastern part of the ADSA, the Andes uplift was accompanied by hyperaridity in coastal Pacific regions (Jordan et al., 2014), caused in part by the rain shadow effect of the mountain ranges. Species diversification was also affected by global climate changes that overlapped temporally with the Andes uplift. These climate changes have repeatedly interconnected or fragmented suitable habitats. In addition, the emergence of arid habitats favoured adaptive radiations as a result of the availability of new ecological niches (Hughes & Eastwood, 2006; Antonelli & Sammartin, 2011). Taking all this into account, the complex geoclimatic structure in our focus area seems to provide a very suitable starting point to test effects of tectonic and/or climate changes on the diversification of organisms under conditions of increasing aridity. For the present study, we used wingless beetles of the family Tenebrionidae (Insecta: Coleoptera), which generally have low dispersal abilities. The Tenebrionidae belong to the most species-rich animal families with about 20,000 species and, in contrast to most animal groups, show an increasing species diversity with increasing aridity (Koch, 1962). In deserts, which in the past were often colonized in a convergent scenario by different lineages of Tenebrionidae, they are among the ecologically most important consumers. It is still unclear which genetic predisposition of Tenebrionidae favours worldwide desert colonization, but it is known that such colonization is usually followed by subsequent radiations in new and often still unoccupied ecological niches, which is then accompanied by numerous adaptations that affect morphology, physiology and behaviour (Cloudsley-Thompson, 2001).

Our main objective is, therefore, the examination of the biogeographic history of *Psectrascelis* to determine the driving forces behind the distribution and diversification of taxa adapted to high altitudes and aridity. We have used tenebrionid species as they form the largest radiation of insects in hyperarid deserts worldwide, and *Psectrascelis* is considered as a taxon with progressive adaptation to hyperaridity. In this context, we tested whether the distribution and molecular diversity of *Psectrascelis* can be related to historical geoclimatic events. In particular, we tested two alternative hypotheses about the main drivers of diversification of biotas from deserts in the region: Andean uplift versus Pleistocene fragmentation and/or dispersal.

### 2 MATERIALS AND METHODS

#### 2.1 Insect collection

Sampling of Tenebrionidae was carried out in the focus area in the Chilean Atacama Desert and Chilean Puna BP from 2016 to 2019 with hand collecting and pitfall traps from 17.6°S to 27°S.
addition, we collected at locations in adjacent areas: in the south in the Coquimban BP to Guanaqueros (30.2°S), in the north to Lake Titicaca in Peru (15.7°S; −70.15°W) and in the east in the Bolivian Altiplano (21.74°S; 67.48°W). The hand-collected beetles were directly transferred to 96% ethanol, whereas the pitfalls were filled with propylene glycol. The beetles caught with these traps were transferred to 96% ethanol during the trap control (2–6 weeks after trap installation). For the species determination, we used Peña (1985, 1994) and Vidal and Guerrero (2007).

2.2 | DNA extraction, amplification and sequencing

DNA was extracted from thoracic muscles using the EZNA® Insect DNA Kit (Omega Bio-tek, Inc., Norcross, U.S.A). First, the mitochondrial gene cytochrome oxidase I (COI) was amplified for 87 specimens. To facilitate the detection of different haplotypes in more conserved genes, we selected the genetically more distant specimens of each Psectrascelis lineage (see Zúñiga-Reinoso & Méndez, 2018) and subsequently amplified the ribosomal RNA 16S and the nuclear gene wingless (Wg) from these samples. The primers used to amplify each gene are listed in Table S1. The thermal polymerase chain reaction (PCR) steps were 94°C for 2 min, followed by 36 cycles at 94°C for 30 s, 56°C for 45 s and 72°C for 1 min, with a final extension at 72°C for 2 min. The PCR products were purified using peqGOLD Cycle-Pure kit (Peqlab Biotechnologie GmbH, Erlangen, Germany), and both forward and reverse products were sequenced at Eurofins Genomics GmbH (Germany) using the Sanger sequencing method. The DNA sequence of each sample was reviewed, and all orthologous sequences were aligned using the Clustal W algorithm implemented in BIOEDIT version 7.0.5.3 (Hall, 1999) and then manually checked for inconsistencies. In addition, Xia’s test (Xia et al., 2003) implemented in DAMBE, v5.1.5 (Xia & Xie, 2001) was used to evaluate the saturation of each gene matrix.

![Figure 1](image-url)  
**Figure 1** Overview of the collection sites of Psectrascelis. (a) South America with known distribution of Psectrascelis in grey; the two regions marked in orange represent the hotspots for diversity of this genus. The numbered red dots show the collection sites of Psectrascelis in this study. The orange biogeographic provinces are marked by colored lines: yellow, Western Puna BP; red, Eastern Puna BP; blue, Prepuna BP; green, Coquimban BP. The dotted blue line is the 4000 m.a.s.l. contour line in the west. (b) Coastal habitat of *P. pilosa* close to Tres Playitas. (c) Habitat of *P. laevigata* near Cariquima, at 3700 m.a.s.l. (d) Habitat of *P. intricaticollis* near the Huasco Salar, at 3800 m.a.s.l. (e) Habitat of *P. confinis* at the Salar Agus Calientes at 4200 m.a.s.l. (f) Habitat of *Psectrascelis* sp. nov. 2 near the Salar de Pedernales, at 3400 m.a.s.l.
2.3 | Phylogenetic reconstruction

Phylogenetic reconstructions were performed with the concatenated COI, 16S and Wg genes using Bayesian inference (BI) algorithms. The best model for sequence evolution was selected with the Akaike Information Criterion (AIC) in the program jModelTest 0.1.1 (Posada, 2008). The best models for the sequences were TIM2+I+G for COI and Wg and TIM2+G for 16S; these models were used for each partition in all analyses. The BI was performed with the program Mr. Bayes 3. 2. 6 (Huelsenbeck & Ronquist, 2001) implemented in the server CIPRES Science Gateway 3.3 (Miller et al., 2010). We conducted four independent runs, with a setting of four chains; starting with a random tree, running for 30 million generations and sampling every 1000 trees. The initial 25% of the resulting trees was discarded as burn-in. Once convergence of the four independent runs was confirmed by the average standard deviation of split frequencies and the potential scale reduction factor, results from the runs were combined to obtain a total of 30,004 trees. Finally, a consensus tree was constructed by a 50% majority rule; the node supports were evaluated using posterior probabilities.

2.4 | Divergence times and reconstruction of biogeographic history

For an estimation of the divergence times, we pruned the branches of the BI tree with the 24 specimens whose COI, 16S and Wg genes have been determined. Estimation of divergence times was performed with the software BEAST 1.8.2 (Drummond & Rambaut, 2007). The substitution models selected for the jModelTest in BI are not implemented in BEAST; these models were replaced by the complex models GTR+I+G for COI and Wg and GTR+G for 16S. In addition, lognormal relaxed clock and Yule speciation models were selected, and the analysis was then run for 30 million generations, sampling every 3000 generations. For the calibration of divergence times, the mutation rate for COI was set at 3.54%, according to the estimate for Tenebrionidae by Papadopoulou et al., (2010). Results were checked with TRACER 1.6 (Drummond & Rambaut, 2007) to determine the convergence of the chains and the effective sample size. The sampled trees were combined with TreeAnnotator 1.8.2 (Drummond & Rambaut, 2007) and used to plot the mean of the lineages through time and the respective 95% high posterior density (HPD) in TRACER 1.6. The tree was displayed and edited in FIGTREE 1.4.2 (Rambaut, 2009).

The reconstruction of ancient distribution ranges and speciation events was performed with the software package ‘BioGeoBEARS’ (Matzke, 2013), which allows a probabilistic deduction of the biogeographic history of a taxon and has the advantage of comparing different biogeographical models. This approach considers both anagenetic events (i.e. dispersion, extinction and shift of range) and cladogenetic events (vicariance, founder events; Matzke, 2014). BioGeoBEARS was performed with the models DEC, DIVALIKE and BAYAREALIKE. Additionally, we performed the same models with the extra parameter ‘j’ (i.e. dispersion by jump; Matzke, 2014). All models implemented in the BioGeoBears were run independently, and the best model was selected using AIC. For our analyses, we used the ultrametric tree of BEAST and a presence/absence matrix with the biogeographic region where the species are currently distributed. Primarily, the biogeographic provinces proposed by Morrone (2014, 2015) were used. We have modified the data for the Puna BP according to the classification proposed for Chile based on the distribution of Tenebrionidae (Peña, 1966) and other terrestrial animals (Artigas, 1975).

Our sampling area includes the Coquimbo BP, the Prepuna BP, Western Puna BP (including Preccordillera and parts of the Western Cordillera of the Chilean Atacama Desert above ~2500 m and up to a maximum of ~3800 m) and the Eastern Puna BP (Puna and Altiplano plateau above ~3800 m, located mainly in Peru, Bolivia, Argentina and the north-easternmost parts of Chile) (Figure 1).

3 | RESULTS

Sampling in the Chilean Atacama Desert and Chilean Puna BP (Figure 1) yielded all species known from this region (P. intricaticollis, P. laevigata, P. escobari, P. confinis, P. izquierdoi) and added several locations not previously listed for Psectrascelis. The following morphologically determined species were collected from neighbouring regions: (1) P. laevigata (region Lake Titicaca, Peru). This species is one of the few Psectrascelis known to occur north of the focus area. (2) P. rotundata (Villa Mar, Bolivian Altiplano). This species belongs to several morphologically similar species in the region; most are known from the Argentinian Puna (Kulzer, 1954; Peña, 1994). (3) P. elongata, P. specularis, P. sublaevicollis, and P. pilipes. The latter species belong morphologically to Psectrascelis sensu stricto that become species-rich in the Coquimban BP south of the focus area and include coastal species. In total, 87 Psectrascelis individuals from 37 locations were included in our study (Table S2).

3.1 | Phylogenetic reconstruction

The combined matrix of COI, 16S and Wg genes has a length of 2460 bp and contains 572 polymorphic sites and 552 parsimony informative characters (for further details, see Table S3 and S4). No genetic saturation was observed for these genes.

The BI analysis with the concatenated data set recovered two main clades of Psectrascelis in the study area (posterior probability, pp =1). Clade A consists of species inhabiting the inner slopes of the Western Cordillera of the Altiplano and the Altiplano-Puna Plateau, whereas clade B contains all species inhabiting the western slopes of the Western Cordillera and Precordillera and reach further to the coast in the south of the focus area (Figure 2). Clade A is further divided into a northern lineage (A1) with P. laevigata and P. escobari and the southern lineage A2 (P. confinis, P. rotundata), whose sister group relationship to A1 was confirmed with maximum support (pp
Of these species, only *P. confinis* reaches the Chilean Altiplano but is restricted to altitudes above 4000 m.a.s.l.

Clade B is divided into subclades B1 and B2 (pp =1; Figure 2). Subclade B1 contains all species occurring along a long and narrow strip with north-south orientation on the western slopes of the Precordillera and Western Cordillera; from Salar de Huasco to Salar Maricunga. *P. intricaticollis* as the northernmost species of clade B1 occurs with two described subspecies (*P. intricaticollis intricaticollis* and *P. i. ovata*) along a transect of about 550 km. The detailed analysis of many populations of *P. i. intricaticollis* and *P. i. ovata* supports a separation of both groups at species level (Figure 2). The sister of the *P. intricaticollis* group is *P. izquierdai* (pp =1), which is similarly distributed in north-south direction. Within B1 the above-mentioned *Psectrascelis* species are related to two undescribed species of *Psectrascelis* (*Psectrascelis* sp. 1; *Psectrascelis* sp. 2). While *P. sp. 1* as the southernmost (Prepuna BP) species of the clade B1 is the well-supported sister to the other taxa in clade B1 (pp =1), the position of *P. sp. 2* as sister to *P. izquierdai* +the *P. intricaticollis* group is not sufficiently supported (pp =0.52). The clade B2 contains solely species that are located in the Coquimban BP (from Chañaral to Guanaqueros). The only exception is *P. sublaevicollis*, which inhabits the same habitat as *P. sp. 1* (clade B1) along the Precordillera (Cordillera de Copiapó) of the Prepuna BP. The remaining species show a strict coastal proximity distribution (Figure 2). In the subclade B2, *P. pilosa* has the northernmost coastal distribution and is sister to the remaining taxa of clade B2 (pp =1). For the remaining species of subclade B2, our analyses revealed a sister group relationship of (*P. pilipes pilipes* +*P. sublaevicollis*) and (*P. elongata* +*P. pilipes* spicularis).

### 3.2 Divergence times and reconstruction of the biogeographic history

Different selection models for biogeographic estimations were tested (Table S5), and the best fit were obtained with DIVALIKE+J.
and DEC+J; both models yielded identical reconstructions. Clades A and B diverged at ~3.44 Ma (HPD: 2.7–4.4) (Figure 3A), probably due to vicariance. The subsequent divergence within clade A was at ~2.6 Ma (HPD: 1.8–3.4), separating the northern Altiplano species (clade A1) from the more southerly occurring species of clade A2. Divergence of taxa within clade B was at ~2.2 Ma (HPD: 1.7–2.9) into the Coquimban clade (B2) and the clade B1 inhabiting the Chilean Precordillera/Cordillera along the Atacama Desert (Figure 3B). This divergence could be associated with a founder event (jump dispersal), which led to the colonization of the Pre Puna region by clade B1. The spatial diversification of clade B2 through vicariance in the Coquimban region started at ~1.3 Ma (HPD: 1–1.7). A second colonization of the Precordillera from the Coquimban coastal region occurred at ~0.63 Ma (HPD: 0.9–0.35), presumably again by a founder event, and resulted in the species *P. sublaevicollis*. The clade B1 probably started its diversification at ~0.8 Ma (HPD: 1.1–0.55) with a founder event (jump) from the Precordillera north of the Pre Puna BP to the western slopes of the Western Cordillera region.

All data suggest that the migration and subsequent dispersal of the various *Psectrascelis* lineages along the Precordillera/Western Cordillera only started at ~0.98 Ma (HPD: 0.47–1.2). During these migrations, clade A2 colonized the eastern side of the Western Cordillera within the Puna BP and clade B1, starting in the southwestern Puna BP, colonized the Chilean Precordillera and the western slopes of the Western Cordillera adjacent to the Atacama Desert. In addition, clade A1 colonized at ~0.62 Ma (HPD: 0.43–0.9) the eastern side of the Western Cordillera in the northwestern Puna BP. This increase in lineages in the region over time indicates a good correlation with an exponential model (*R*^2^ = 0.94) whose inflection point is at ~1.5 Ma (Figure 3).

### DISCUSSION

The present study provides the first detailed molecular analysis of the diversification and colonization history of insects across the SATZ, biogeographically covering the Puna BP and the Chilean...
Atacama Desert BP. The tenebrionid genus *Psectrascelis* serves as an example for evolutionary processes under the influence of temporarily increasing aridity, and our data allowed a chronological analysis of the diversifications and thus a correlation with orographic and climatic changes in the past. The most recent common ancestor (mrca) of the genus *Psectrascelis*, which belongs to the endemic South American tribe Nycetellini, probably inhabited semi-arid habitats at higher altitudes in the already uplifted Andean range. Because of the habitat preference of most Nycetellini living today and the current species richness of *Psectrascelis* in the southern Puna BP of Argentina, we assume that the mrca was widely distributed in this region. We hypothesize that before the first splitting of the mrca, the western distribution range of *Psectrascelis* was expanded to the Pacific Coast of the Coquimban BP (Figure 3A). The current distribution of *Psectrascelis* indicates two hotspots of diversification, one for each main lineage (Figure 1). The eastern clade A has the highest diversity in the southern Puna BP of Argentina, whereas clade B reaches the highest diversity in the Coquimban BP of Chile.

### 4.1 Forcing factors for species diversification

Diversification of species can have various causes, such as diversification in response to climate and/or geological processes. The generation of a comprehensive molecular data set related to the diversification of a biological taxon, as we have made it here exemplarily for *Psectrascelis*, can give significant insights on whether the spatial and temporal developments were more likely be due to common and more global forcing factors or whether the observed diversification events were more likely caused by local intrinsic dynamics or small-scale changes.

Our estimated diversification times all revealed that internal speciation of *Psectrascelis* took place during the past ~3.4 Ma. The high Andes already gained much of their recent elevation well before ~6 Ma (Garzione et al., 2017), and the Andean uplift can, thus, be excluded as a major forcing factor. Within the uncertainties of posterior time estimates, estimated diversification times indicate large-scale spatial coincidence, implying a common pacemaker for speciation of *Psectrascelis* in the Precordillera and Western Cordillera adjacent to the Atacama Desert, the high Central Andes and the Coquimbo region. Major clusters of diversifications could be observed at ~2.6–2.2 Ma, ~1.3–0.7 Ma and several subsequent events during the mid- to late Quaternary. To identify the potential forcing factors or events for biological diversification, molecular time estimates can be compared with global Plio-Pleistocene climate trends derived from variations in marine benthic δ¹³C records (Lisiecki & Raymo, 2005).

Diversification of the mrca already divided *Psectrascelis* into clade A (highland) and B (lowland) at the end of the Pliocene warm period. Ongoing global climate cooling (Zachos et al., 2001) may have promoted considerable geographical isolation and diversification. This most likely happened due to shrinking of suitable habitats. Expansion of glaciers in the Central and Southern Andes are evidence for climate cooling, which certainly affected the former habitats of *Psectrascelis* in the high Andes. The complex Andean orogeny might, thus, not have been the primary cause for the separation of the *Psectrascelis* species, but it presumably encouraged species separation by affecting potential migration corridors and thus gene exchange in response to climate change. Furthermore, climate models indicate that the reinforcement of the Humboldt Current, especially at the Pli- Plio-Pleistocene transition, was an important factor for the establishment of the widespread hyperarid conditions within the Atacama Desert (Garreaud et al., 2010). Several studies also indicate the transition of arid to hyperarid conditions upslope the Precordillera and the Western Cordillera (Evenstar et al., 2017; Jordan et al., 2014). The changing environmental conditions caused the separation into an eastern (Argentinian) and a western (Chilean) population of the mrca of *Psectrascelis*, which can be considered the origin of clade A and B, respectively (Figure 3). Following further cooling towards the Quaternary and throughout the Quaternary created the ADSA (Hinojos & Villagra, 1997), reinforcing potential gaps between the clades.

Both major clades of *Psectrascelis* (A, B) experienced a synchronous diversification into subclades ~2.6–2.2 Ma at the onset of the Quaternary. This diversification indicates a supraregional cause, which is most likely also connected to climate-induced isolation of habitats, cut-off of genetic exchange and/or development of new habitats in formerly unsuitable regions, promoting founder events. Cooling may have caused or favoured the separation of clades A1 and A2, leading to a northern and southern subclade. The colonization of the northern Central Andes by clade A could have already happened before. In this context, it should be noted that clade A2 likely comprises about 20 species of the subgenus *Cerostena* (Kulzer, 1954) and is distributed over the Argentinian Puna and adjacent regions further south (provinces of Salta, Catamarca, La Rioja). Probably, also the *Psectrascelis* species in the Arid Diagonal of eastern and south-eastern Argentina belong to this group. In our study, we only considered the two species *P. confinis* and *P. rotundata*, which live in close vicinity to *P.i. intricaticollis* and *P.i. ovata* (clade B1). For the *Psectrascelis* populations of clade B, which at that time probably inhabited mostly lowland areas adjacent to the southern Atacama Desert (Coquimban BP), it is very likely that they were exposed to an expansion and intensification of desert conditions. Such large-scale expansion of arid to hyperarid conditions to higher elevations and along latitudinal gradients in the north and south are reported for the beginning Quaternary (e.g. Evenstar et al., 2017; Jordan et al., 2014). Frequency and amplitude of climate changes and variability during this period are, compared with the mid-late Quaternary, relatively moderate, which a priori led to only a few diversifications of *Psectrascelis* within the B clade (Figure 3).

The significant emergence of diversification events at ~1.3–0.7 Ma coincides with the most fundamental change in global climate and climate variability in the Quaternary, referred to as the Mid-Pleistocene Transition (Zachos et al., 2001). During the Mid-Pleistocene Transition, the previous dominant periodicity of
climate cycles changed from a 41-kyr to a 100-kyr cycle, causing high-amplitude climate oscillations (e.g. Clark et al., 2006; Tziperman & Gildor, 2003; Zachos et al., 2001). Pronounced cold and warm cycles during the remaining Quaternary most likely caused the repeated cyclical closure of migration corridors during the warm (arid) periods, promoting further speciation of *Psectrascelis*. Dispersal of species, that are thought to have adapted over time to more arid conditions, to new, formerly not accessible habitats (the dry limit), led to founder events and extensive colonization of the western slopes of the Western Cordillera by subclade B1. These frequent high-amplitude changes of climate and environmental conditions most likely drove temporally rapid ‘species pumps’ (Rahbek et al., 2019).

### 4.2 | Allopatry and adaptation

Our results suggest that speciation in *Psectrascelis* was clearly linked to changes in global climate and climate variability in the last 3.5 Ma. Expansion and shrinking of suitable habitats might have regularly caused fragmentation of populations; primarily due to a failure to adapt to the changing environmental conditions. We hypothesize that such niche conservatism, which resulted in non-adaptive allopatric speciation (Predel et al., 2012; Rundall & Price, 2009; Wiens, 2004), is particularly typical for *Psectrascelis* clade A. The hypothetical origin of clade A is thought to be on the eastern slopes of the Central Andes in north-western Argentina; this is the proposed eastern retreat of the mrca of *Psectrascelis* during the major climate cooling after the Mid-Pliocene warm period, demonstrated by glaciation in the Central Andes 3.5 Ma (Haselton et al., 2002; Roberts et al., 2018). Today, clade A species more or less continuously occupy the entire high-altitude region of the Central Andes, except for the dry western slopes of the Western Cordillera, inhabited by the B clade (see below), and the Altiplano. All species of the A clade were collected in areas receiving precipitation of about 100 mm/year or more (Fick & Hijmans, 2017), including the northernmost species of this clade from an area west of Lake Titicaca that receives precipitation of more than 500 mm/year (Figure 2). The assumed non-adaptive radiations in *Psectrascelis* do not exclude subsequent adaptations or phenotypic changes, but speciations likely happened prior to these changes.

The evolution and speciation within clade B, although affected by the same forcing factors as described above, are more complex and presumably involved adaptation to higher aridity. The Coquimban BP as biodiversity hotspot of clade B has a very complex geomorphology with a variety of different microhabitats and receives more precipitation than the core region of the Atacama Desert to the north. It is feasible that various adaptations played a significant role for the current diversity of *Psectrascelis* in that region. However, a single adaptation, survival under conditions of higher aridity, may have allowed the colonization of widespread habitats previously not suitable for *Psectrascelis*. Because both main lineages of clade B contain species currently living under conditions of high aridity, this presumably still ongoing adaptation probably started before the divergence of these lineages ~2.2 Ma.

The most xerophilous *Psectrascelis* species today is *P. pilosa*, which even inhabits the coast around Chañaral, with an average annual rainfall of about 20 mm and comparatively high temperatures throughout the year (Luebert & Pliscoff, 2016). The isolated and genetically deeply divergent populations along the coast (Figure 2) are probably the result of habitat fragmentation and thereby an impairment of gene flow between populations of *P. pilosa*. This current monotypic lineage of subclade B1 might expand the distribution of *Psectrascelis* in the future due to the colonization of previously unsuitable coastal habitats further north. During the last 0.8 Ma, however, it was the clade B2 that colonized after jump dispersals the Precordillera and arid western slopes of the Cordillera, thereby extending considerably the distribution of *Psectrascelis*. The 800-km long but narrow south-north distribution range suggests a northward range expansion of B1 along isohyets. It is likely that the suitable habitats in the mountain slopes are restricted by too low winter precipitation to the west and too much summer precipitation in the east. Because the region east of the distribution of B1 is inhabited by taxa of the A clade, we presume that the previous adaptation within the B clade to more arid conditions currently prevents a mutual intermingling of these lineages.

The vertical distribution of B1 species may have adapted in the past to the dynamic changes in annual precipitation on the western slopes of the Cordillera (*P. intricaticollis* group) or Precordillera (*P. izquierdoi*). This probably enabled the rapid colonization along a continuously inhabited transect, although local climatic conditions may have changed considerably over time. Such a scenario is supported by fossil records of *P. intricaticollis* (species identification by A. Zuniga-Reinoso; unpublished) in ~13,000-year-old rodent middens at the southern shore of the Salar de Atacama (Dézerald et al., 2019), a hyperarid area not currently inhabited by *Psectrascelis*.

### 5 | CONCLUSIONS

This study presents the first in-depth molecular data analysis of desert beetles inhabiting the arid SATZ including the Atacama Desert and Central Andes. The chosen genus *Psectrascelis* is widely distributed in this region but avoids hyperaridity. Therefore, these beetles appear to be very sensitive to changes from aridity to hyperaridity, and their current distribution may reflect past climatic changes particularly well. The molecular data presented here suggest that the Andean uplift itself had no direct effect on the divergence within *Psectrascelis*. Obviously, the diversification of *Psectrascelis* is mainly related to global climate changes since the mid- to late Pliocene, when the Andes had already reached their current altitude, and speciation increased exponentially with the frequency of climatic oscillations during the late Pleistocene. The estimated divergence times indicate a common pacemaker for speciation in the main clades A
and B, climate oscillation. Today, these clades almost meet each other without intermingling along the Western Cordillera. Thus, although the diversity and distribution of *Psectracelis* taxa have been forced by the same Pleistocene climate changes, the allopatric radiation in clade A and the presumed adaptation to higher aridity in clade B led to the phenomenon of synchronous range expansions in both clades without spatial overlap.

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**DATA AVAILABILITY STATEMENT**

The data sets generated during the current study are available in the NCBI repository (see table S2 for accession numbers), and the complete genes data set is available in the CRC1211 project repository under the https://doi.org/10.5880/CRC1211DB.37.

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Author contributions: A.Z.R. and R.P. conceived the study and collected the insects. A.Z.R. performed the laboratory work and analysed the data. A.Z.R., B.R. and R.P. contributed to the interpretation of the results and to writing the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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