SENCKENBERG
world of biodiversity

Filling gaps in the diversity and biogeography of Chilean millipedes (Myriapoda: Diplopoda)

Antonio Parra-Gómez[1] and Leonardo D. Fernández[2,3]

1 *Facultad de Ciencias, Universidad Austral de Chile, Av. Rector Eduardo Morales Miranda 23, Valdivia, Chile*

2 *Centro de Investigación en Recursos Naturales y Sustentabilidad (CIRENYS), Universidad Bernardo O'Higgins, Avenida Viel 1497, Santiago, Chile*

3 *Centro de Investigación de Estudios Avanzados del Maule, Universidad Católica del Maule, Talca 3466706, Chile*

http://zoobank.org/1B3CEECD-EFCE-49AD-B715-24BDFAC35C72

Corresponding author: Leonardo D. Fernández (limnoleo@gmail.com)

Received 29 May 2022
Accepted 16 September 2022
Published 14 October 2022

Academic Editors Lorenzo Prendini, Marianna Simões

Citation: Parra-Gómez A, Fernández LD (2022) Filling gaps in the diversity and biogeography of Chilean millipedes (Myriapoda: Diplopoda). Arthropod Systematics & Phylogeny 80: 561–573. https://doi.org/10.3897/asp.80.e86810

Abstract

Research on the diversity and biogeography of Chilean millipedes represents a significant gap in knowledge. To reduce this gap we conducted a study: (1) to investigate the current state of knowledge of millipede diversity, and (2) to assess the pattern and causes underlying the latitudinal diversity gradient in Chilean millipedes. In Chile, 95 native millipede species have been recorded. However, rarefaction and extrapolation curves showed that increased sampling effort will reveal more species. An asymptotic estimate of diversity predicted that millipede diversity fluctuates between 125 and 197 species. The estimate, though, was based on a limited data set. Therefore, millipede diversity is probably higher than predicted. Chilean millipedes were categorized as micro-range endemics because they all have latitudinal ranges of less than 1,000 km (with 78% of species exhibiting latitudinal ranges of only ~222 km). Millipede species richness also exhibited a bell-shaped latitudinal diversity gradient, i.e. diversity peaks in the temperate climate of central Chile and decreases towards the arid and polar climates of northern and southern Chile. A multiple regression analysis revealed that this biogeographic pattern is shaped by environmental variables related to water availability, ambient energy inputs and climatic stability. These environmental variables are proxies for two of the five biogeographic hypotheses we tested in this study, i.e. the water-energy balance hypothesis and climatic stability hypothesis. Both hypotheses suggest that millipedes need stable, humid and warm climates to grow, survive and reproduce (niche conservatism). These climatic conditions are only found in central Chile, which is consistent with the diversity peak observed in that region.

Keywords

Beta diversity, biodiversity hotspot, biogeographic hypothesis, latitudinal diversity gradient, microendemic millipedes, millipede biogeography, niche conservatism

1. Introduction

Diplopoda is the third largest class of terrestrial arthropods after Insecta and Arachnida (Golovatch and Kime 2009). Currently, the global diversity of this taxon is represented by ~12,000 species, though it is estimated that there may be as many as 80,000 species (Golovatch and Kime 2009). Diplopoda are commonly referred to as mil-

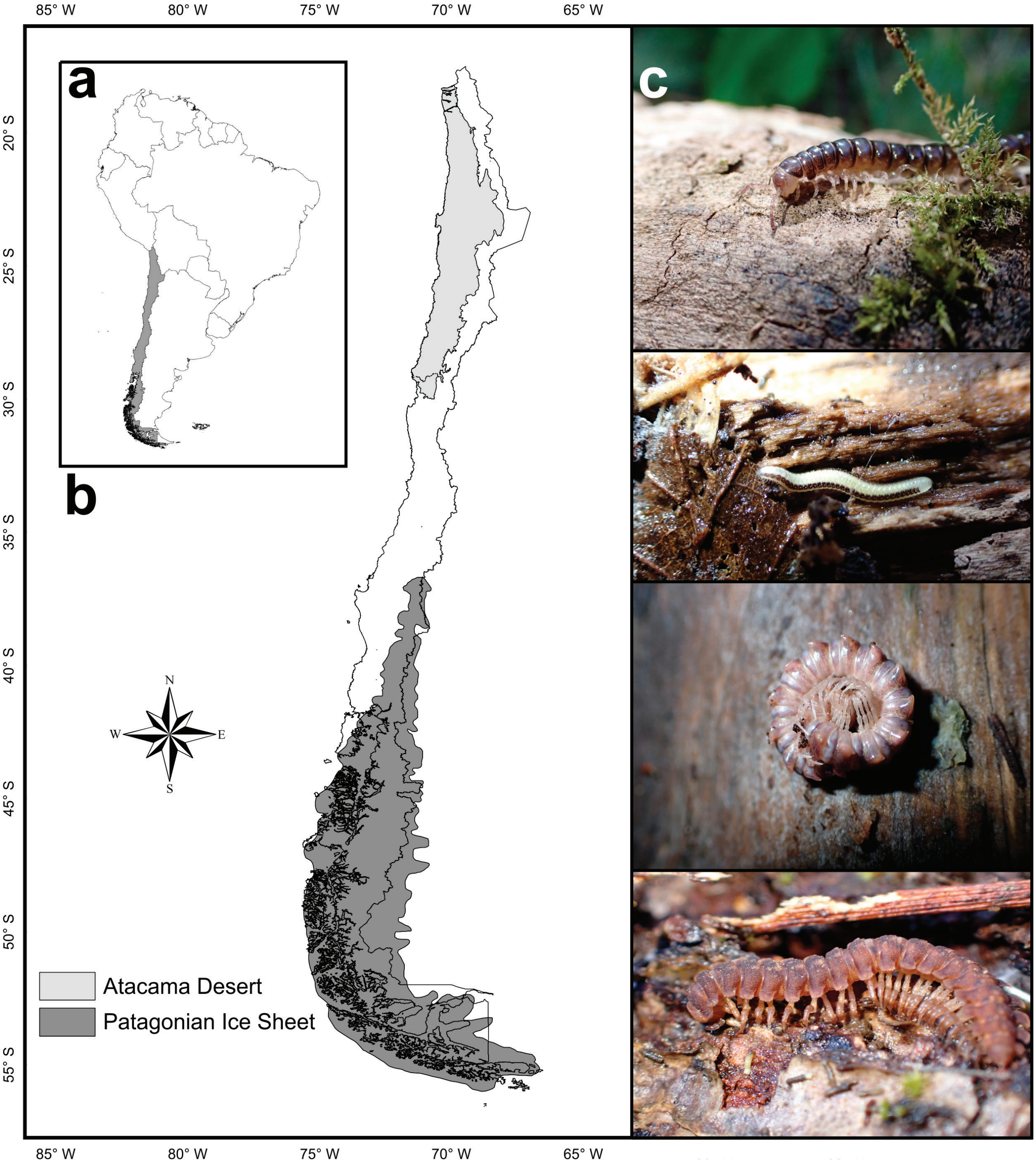

Figure 1. Map and representative millipedes of Chile. **a** Chile in southwestern South America stretches from ~17°S to 56°S. **b** During the Pleistocene, a series of geological events (e.g. the uplift of the Andes) and climatic changes (e.g. the Last Glacial Maximum) shaped the Atacama Desert in the north (area shaded in light grey) and the Patagonian Ice Sheet in the south (area shaded in dark grey) in Chile. Since then, the Atacama Desert has favoured an arid climate at low latitudes while at the end of the Last Glacial Maximum the retreat of the Patagonian Ice Sheet set up a polar climate at high latitudes. The mid-latitudes of central Chile exhibit a temperate climate and acted as a refuge for biota during the occurrence of the historical contingencies described. **c** Examples of millipedes endemic to Chile. From top to bottom: *Tsagonus* aff. *valdiviae* Chamberlin, 1957; *Siphonotus parguaensis* Mauriès and Silva, 1971; *Monenchodesmus inermis* Silvestri, 1903 and *Mikroporus granulatus* Attems, 1898.

lipedes, yet almost all of these invertebrates have only hundreds or fewer pairs of legs (Adis 2002). So far the only known exception to this rule is the Australian species *Eumillipes persephone*, which boasts up to 1,306 pairs of legs (Marek et al. 2021). Found on all continents except Antarctica, millipedes inhabit a wide range of terrestrial biomes, though they are most diverse in those with warm and humid environmental conditions, such as temperate or tropical rainforests (Minelli 2015).

The diversity and distribution of millipedes is poorly known compared to that of other historically better studied metazoans (Sierwald and Bond 2007). These

Table 1. Ecological hypotheses tested with respect to the diversity of native millipedes in Chile and their respective predictions and predictors.

	Hypothesis	**Prediction**	**Predictors**	**Reference examples**
1	Species-energy	Diversity increases with energy inputs (including plant productivity)	UVB, NPP, NDVI, PET, AMT, MTW, MTQ, MWQ, MCQ	Currie (1991), Evans et al. (2005)
2	Water availability	Diversity increases with water inputs	APR, PDM, PWQ	Rodríguez et al. (2005), Samaniego and Marquet (2009)
3	Water energy-balance	Diversity increases with energy and water inputs	AET, UVB, NPP, NDVI, PET, APR, PDM, PWQ	Hawkins et al. (2003), Rodríguez et al. (2005), Fernández et al. (2016)
4	Climatic stability	Diversity increases in climatically stable areas	ISO, TS, MDR, TAR, MTC,	Currie (1991), Kerr and Packer (1997)
5	Habitat heterogeneity	Diversity increases with habitat heterogeneity	ELE	Pianka (1966), Kerr and Packer (1997)
UVB: Ultraviolet Radiation B, NPP: Net Primary Productivity, NDVI: Normalized Difference Vegetation, PET: Potential Evapotranspiration, AMT: Annual Mean Temperature, MTW: Max Temperature of Warmest Month, MTQ: Mean Temperature Of Wettest Quarter, MWQ: Mean Temperature of Warmest Quarter, MCQ: Mean Temperature of Coldest Quarter, APR: Annual Precipitation, PDM: Precipitation of Driest Month, PWQ: Precipitation of Warmest Quarter, ISO: Isothermality, TES: Temperature Seasonality, MDR: Mean Diurnal Range, TAR: Temperature Annual Range, MTC: Min Temperature of Coldest Month, ELE: Topographic Elevation				

gaps in knowledge are significant in Chile (Golovatch 2014; Parra-Gómez 2022), a long but narrow strip of land stretching from 17°S to 56°S, spanning 4,300 km from north to south and an average of 177 km from east to west (Fig. 1a). Chile's extensive latitudinal distribution is coupled with a strong north–south climatic gradient. Broadly speaking, the north at low latitudes is arid, the centre at mid-latitudes is temperate, while the south at high latitudes is polar (Beck et al. 2018).

The Chilean north–south climatic gradient emerged during the Pleistocene as a consequence of desertification and glaciation events that modified the original warm and humid conditions of northern and southern Chile respectively (Fig. 1b) (Gregory-Wodzicki 2000; Davies et al. 2020). Driven by these historical contingencies many northern and southern mesophilic taxa became extinct or migrated to the temperate climate of central Chile, where they subsequently diversified (Villagrán and Hinojosa 1997). Today, the diversity of most taxa peaks in mid-latitudes and then decreases toward low and high latitudes (Villagrán and Hinojosa 1997; Samaniego and Marquet 2009; Fernández et al. 2015; Moreno et al. 2021; Campello-Nunes et al. 2022).

Chile is often referred to as a biogeographic island because its political boundaries overlap with natural barriers to species dispersal. To the north Chile is bordered by the Atacama Desert, to the east by the Andes Mountains, to the west by the Pacific Ocean and to the south by the end of the South American continent (Figs 1a-b). The Chilean biota therefore evolved largely in isolation, and today Chile is a well-known hotspot of biodiversity and endemism for macro- and microscopic organisms (Arroyo et al. 2004; Fernández et al. 2015; Campello-Nunes et al. 2022), including millipedes (Parra-Gómez 2022).

The insular condition of Chile and the historical contingencies experienced by its territory probably favoured the occurrence of a peculiar millipede fauna (Fig. 1c). Native Chilean millipedes are mainly Gondwanan relicts (Shelley and Golovatch 2011). They share more taxonomic and possibly evolutionary affinities with millipedes from South Africa, Australia, Tasmania, New Caledonia and New Zealand than with other South American taxa (Golovatch 2014). Families such as Dalodesmidae and Eudigonidae are common in Chile and occur only marginally in Argentina and Brazil, while the family Iulomorphidae is only present in Chile (Golovatch 2014; Parra-Gómez 2022).

The goal of the present study is to investigate the state of knowledge and biogeography of Chilean millipedes. Specifically, we investigated the temporal variation in the number of published studies, the number of sites investigated, and the number of new species reported in Chile over the last 175 years. We also constructed rarefaction, extrapolation and asymptotic diversity curves to assess the number of species that have not yet been described in Chile. Finally, we tested five biogeographic hypotheses (Table 1) to investigate the pattern and causes underlying the latitudinal diversity gradient in Chilean millipedes.

2. Methods

2.1. Data source

The database used in this study consists of 95 native species recorded in continental Chile between 1847 and 2022. We constructed this database by merging records obtained by the first author with information recently published in Parra-Gómez (2022). We excluded from the original database (109 species) a total of eight exotic species and six *nomina dubia* species. The name, scientific authority and records (localities) of each of the species used in this study are provided in a Darwin core CSV file (Suppl. file 1). The database was used to construct a binary matrix (i.e. columns as samples and rows as taxa) on which we based all subsequent statistical analyses.

2.2. State of knowledge of Chilean millipedes

We used three complementary approaches to investigate the state of knowledge of Chilean millipedes following Fernández et al. (2015) and Campello et al. (2022).

First, we estimated the number of published studies, the number of new sites sampled, the number of new species reported, and the cumulative number of new species reported in each decade from the 1840s onwards. We then correlated each indicator against time to investigate its trend over years using the R package spdep version 1.1–12 (Bivand et al. 2013).

Second, we estimated a rarefaction curve to investigate whether the sampling effort invested in Chile (measured as the number of sites investigated between the 1840s and 2020s) has contributed to the completion of the checklist of Chilean millipede species. If the rarefaction curve reaches a plateau, we will conclude that the investment of additional sampling effort will not reveal a substantial number of new species in Chile. If the rarefaction curve does not reach a plateau, then we will conclude that the investment of additional sampling effort will reveal new species in Chile. We also estimated an extrapolation curve to investigate whether an increase in sampling effort will contribute to the completeness of the checklist of Chilean millipede species. If the extrapolation curve reaches a plateau, we will conclude that an increase in sampling effort will contribute to completing the checklist of Chilean millipede species. If the extrapolation curve does not reach a plateau, we will conclude that a significant increase in sampling effort is needed to complete the checklist of Chilean millipede species. We estimated the rarefaction and extrapolation curves based on the approach proposed by Chao et al. (2014). The rarefaction curve was estimated using the number of sites surveyed in Chile from the 1880s onwards as a proxy for sampling effort (n = 140 sampling sites). The extrapolation curve was estimated by doubling the sampling effort (n = 280 sampling sites). The rarefaction and extrapolation curves and their lower and upper confidence limits (95% CI) were estimated based on 10,000 bootstrap replicates in the R package iNEXT version 2.0.20 (Hsieh et al. 2016).

Third, we constructed an asymptotic diversity profile to estimate the number of species we have yet to discover at the sites we have so far surveyed in Chile. We estimated the asymptotic diversity profile and its upper and lower 95% confidence intervals (10,000 bootstrap replicates) based on the method proposed by Chao and Jost (2015) implemented in the R package iNEXT version 2.0.20 (Hsieh et al. 2016).

2.3. Millipede biogeography

We used a range interpolation approach to standardise species richness and reduce the effects of spatial sampling biases (McCain 2009; Fernández et al. 2022). Range interpolation assumes that species have continuous latitudinal ranges between their lowest and highest latitudinal occurrences. Standardised species richness was subsequently used to investigate the latitudinal diversity gradient, the size of geographic ranges and beta diversity of Chilean millipedes.

To investigate the latitudinal diversity gradient we divided Chile into bins of 3° latitudinal bands. We then counted the number of species recorded in each latitudinal bin and correlated species richness against latitude by fitting linear and non-linear functions in PAST version 4.09 (Hammer et al. 2001). We used the Akaike information criterion to select the model that best fit the data.

Millipedes have low vagility and consist largely of micro-range endemic species, i.e. animals with geographic range (area where a particular species can be found) smaller than 1,000 km^2 (Means and Marek 2017) and short-range endemic species, i.e. animals with geographic range smaller than 10,000 km^2 (Harvey 2002). In Chile there is no information on the geographic range size of millipedes. We therefore used the latitudinal range size of species as a proxy for their geographic range size. The use of this approach is common in biogeography (Fernández et al. 2016), as there is usually no information for the geographic ranges of poorly studied organisms (Geisen et al. 2017). To categorise the latitudinal range size of species into micro-range and short-range endemics, we multiplied the latitudinal range of each species by the approximate distance between each latitudinal band (~111 km). We categorised as micro-range endemics all species with latitudinal ranges less than 1,000 km (species distributed between 1 and 9 latitudinal bands); and as short-range endemics all species with latitudinal ranges less than 10,000 km (species distributed between 10 and 44 latitudinal bands).

We tested a set of alternative hypotheses to investigate the causes underlying the latitudinal diversity gradient of Chilean millipedes. The null hypothesis is that millipede species richness is randomly distributed in Chile. Then, we tested five biogeographical hypotheses to explain the spatial distribution of Chilean millipede species richness (Table 1). The species-energy hypothesis proposes that sites that receive more solar energy or have high levels of primary productivity exhibit high species richness (Currie 1991; Evans et al. 2005). Alternatively, the water availability hypothesis gives greater prominence to the water resource and proposes that species are more numerous at sites that receive higher annual water inputs (Rodríguez et al. 2005; Samaniego and Marquet 2009). The water-energy balance hypothesis integrates the two previous hypotheses and proposes that species richness is high at sites that exhibit high energy and water inputs during the year (Hawkins et al. 2003; Rodríguez et al. 2005; Fernández et al. 2016). The climatic stability hypothesis proposes that species richness is high at sites with relatively invariant climates throughout the year (Currie 1991; Kerr and Packer 1997). This hypothesis argues that species numbers are high at sites with climatic stability because biotic interactions favour species specialisation in stable environments. Similarly, the habitat heterogeneity hypothesis proposes that species richness is high at sites with many available habitats because this would favour niche partitioning through competitive exclusion (Currie 1991; Kerr and Packer 1997).

To test the five biogeographical hypotheses we investigated the relationship between millipede species richness and 25 environmental variables often used as surrogates for the mechanisms proposed by these hypotheses. These environmental variables were obtained from various sources, which are detailed in Suppl. file 2. Based on scatter plots for all variable pairs (Draftsman Plot) we log (x + 1) transformed all variables and removed highly correlated variables to avoid skewed trends. This process resulted in 18 environmental variables (Table 1). We then normalized all selected variables to compare variables with different unit measures (Clarke et al. 2005). To investigate the relationship between the selected variables and millipede richness we conducted a BioEnv procedure, which used a multiple regression approach to determine which environmental variables best explain the latitudinal diversity gradient in millipedes (Clarke and Ainsworth 1993). We estimated BioEnv and its statistical significance (1,000 permutation) in PRIMER version 6 (Clarke and Gorley 2006).

To investigate beta diversity or the latitudinal variation in species composition we estimated beta diversity (β_{SOR}) as well as its underlying additive components, i.e. spatial turnover (β_{SIM}) and nestedness (β_{SNE}), as described by Baselga and Orme (2012). β_{SOR} is estimated based on the Sørensen's similarity index, a metric that investigates variation in species composition between sites in terms of both turnover and gain (or loss) of species between sites. It should be noted that the gain or loss of species between sites is known as nestedness. Therefore, Sørensen's index is considered a global metric of beta diversity (the ratio of gamma and alpha diversity) as its interpretation includes the effect of both phenomena underlying beta diversity (i.e. turnover and nestedness). β_{SIM} is estimated on the basis of Simpson's similarity index, a metric that investigates spatial variation in species composition only in terms of turnover. This index does not measure the effect of nestedness on beta diversity formation. Finally, β_{SNE} is estimated as the difference between β_{SOR} and β_{SIM}. This operation reveals the proportion of beta diversity that is the exclusive result of nestedness (gain or loss of species between sites). β_{SOR}, β_{SIM} and β_{SNE} range from zero (perfect similarity) to one (perfect dissimilarity) and were estimated using the R package betapart (Baselga and Orme 2012).

We also conducted an analysis of similarity (ANOSIM) to investigate the variation in species composition between arid, temperate and polar climates at low, mid and high latitudes, respectively. ANOSIM compares the mean of ranked dissimilarities between groups to the mean of ranked dissimilarities within groups based on the R–statistic. An R–statistic close to "1" suggests dissimilarity between groups, an R–statistic close to "0" suggests an even distribution of high and low ranks within and between groups, while an R–statistic below "0" suggest that dissimilarities are greater within groups than between groups. The ANOSIM and significance value of the R–statistic were estimated based on 1,000 permutations in PRIMER version 6 (Clarke and Gorley 2006).

3. Results

3.1. State of knowledge of Chilean millipedes

We recorded a positive, significant correlation between time and the number of published studies, the number of sites sampled, the number of new species reported, and the cumulative number of new species reported in each decade (Fig. 2). These results suggest that primary knowledge on Chilean millipede diversity has increased (albeit modestly) from the 1840s onwards.

Our analysis revealed that between 1847 and 2022 (175 years) native millipede species were described or reported in 30 studies. The number of published studies exhibits two peaks over time, i.e. one in the 1970s and another in the 2010s with eight and seven published studies, respectively. The remaining decades exhibit between one and three published studies. While we recorded an increase in the number of studies of Chilean millipedes over time, we also noted extended periods without published records. These include the periods between 1848 and 1897 (49 years); 1906 and 1915 (nine years) and more recently between the 1989 and 2011 (22 years) (Fig. 2a).

A review of the 30 published studies on Chilean millipedes revealed that researchers have explored the diversity of these invertebrates at 140 unique sites. Eleven studies (37%) are based on a single study site, four (13%) on three sites, three (10%) on two sites, three (10%) on eight sites, two (7%) on 13 sites, two (7%) on six sites, two (7%) on five sites, one (3%) on 19 sites, one (3%) on 11 sites and one (3%) on nine sites. The number of new sites sampled exhibits a peak in the 1970s with 30 new sites sampled. The 1900s, 1950s and 2010s also stand out with 22, 20 and 21 new sites sampled. The number of new sites sampled during the remaining decades ranges between 1 and 11 sites. Overall our analysis suggests that, even though there are extended periods without published records, the number of new sites investigated has increased over time, particularly since the 1900s (Fig. 2b).

The number of new millipede species also increased significantly over time, although the correlation coefficient is low. This is because the number of new species reported varies significantly from decade to decade, with values ranging from one to 17 species. The highest number of new species was recorded in the 1950s (17 species), and the lowest number of species was recorded in the 1910s and 1940s (1 species each time) (Fig. 2c).

Although the number of new species reported varies significantly between decades, the cumulative number of new species has increased exponentially over time. Between the 1840s and 2020s the number of native species known for Chile has increased from three to 95 (including described species and species that have yet to be formally described; see the species list provided in Suppl. file 1). This suggests that conducting further studies and exploring more sites will reveal new species in Chile (Fig. 2d).

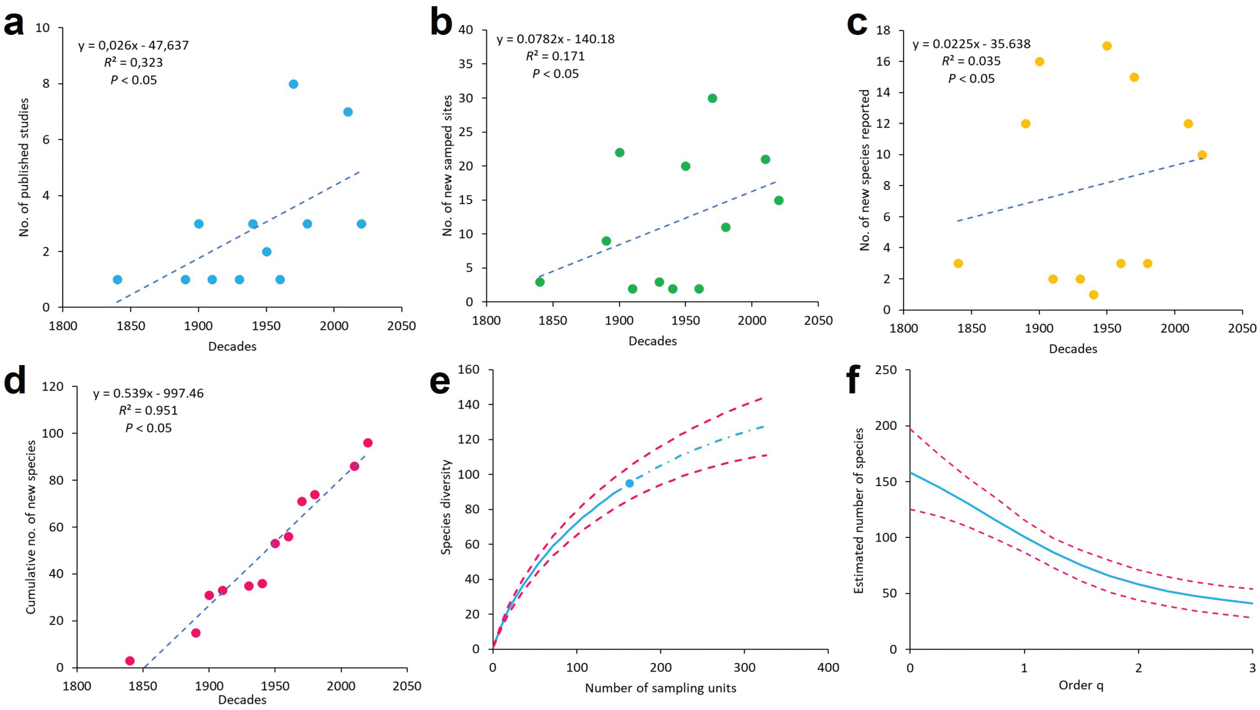

Figure 2. State of knowledge of Chilean millipedes. **a** Number of studies published per decade. **b** Number of new sites sampled per decade. **c** Number of new species reported per decade. **d** Cumulative number of new species per decade. **e** Rarefaction curves (solid trend line), extrapolation curves (dash-dotted line) and their lower and upper 95% confidence intervals (dashed line). The point between both curves represents the number of sites where millipedes have been sampled in Chile. **f** Asymptotic estimate of millipede diversity in Chile (solid trend line) and its lower and upper 95% confidence intervals (dashed line).

Rarefaction and extrapolation curves confirmed the above result. The rarefaction curve did not reach a plateau suggesting that the sampling effort has been insufficient to record a substantial number of the species inhabiting Chile. So, future studies will add new species to the checklist of Chilean millipedes. The extrapolation curve also did not reach a plateau, suggesting that doubling the sampling effort would also not contribute to recording a significant fraction of the millipede species present in Chile. Therefore, we need to invest a greater sampling effort over time to complete the checklist of Chilean millipedes (Fig. 2e).

The diversity estimate suggests that altogether, the sites surveyed between the 1840s and 2020s harbour at least 158 native species (considering 95% lower and upper confidence intervals of 125 and 197 species). Thus, our analysis suggests that we have missed at least one-third of the millipede species that actually inhabit the sites surveyed between the 1840s and 2020s. Therefore a significant increase in sampling effort could reveal up to 102 additional species (Fig. 2f).

3.2. Millipede biogeography

Millipedes exhibit a bell-shaped (unimodal) latitudinal diversity gradient in Chile. Thus, species richness exhibits a peak in the mid-latitudes (central Chile) and then decreases towards low (northern Chile) and high (southern Chile) latitudes (Fig. 3a).

Analysis of the geographic ranges of millipedes revealed that their latitudinal ranges can be categorised as micro-range endemics as all species exhibit latitudinal ranges of less than 1,000 km. Of the 95 native species included in our study, 74 (78%) exhibit latitudinal ranges of ~220 km, 17 (18%) have ranges of ~550 km and 4 (4%) have ranges of ~880 km (Fig. 3b).

The bell-shaped latitudinal diversity gradient of Chilean millipedes is positively and significantly correlated with a subset of five environmental variables, including Ultraviolet Radiation B (UVB), Normalised Difference Vegetation (NDVI), Annual Precipitation (APR), Mean Diurnal Range (MDR) and Isothermality (ISO) (BioEnv, $R = 0.787$, $p = 0.01$). UVB and NDVI are proxies for energy, APR is a proxy for water availability, while MDR and ISO are proxies for climatic stability. The observed correlation between millipede diversity and these proxies lends support to the water–energy balance and the climatic stability hypotheses. The water-energy balance states that species richness is high at sites that exhibit high energy and water inputs during the year (Hawkins et al. 2003; Rodríguez et al. 2005; Fernández et al. 2016). The climatic stability hypothesis states that species richness is high at sites with relatively invariant climates throughout the year (Currie 1991; Kerr and Packer 1997). Therefore, our results suggest that millipede diversity is high in mid-latitudes because they exhibit a continuous (stable) trade-off between water availability and ambient energy inputs throughout the year. This climatic stability might be favouring the coexistence of several species via biotic interactions.

Millipedes have a high beta diversity in Chile ($\beta_{SOR} = 0.94$; Fig. 4). The most important underlying phenome-

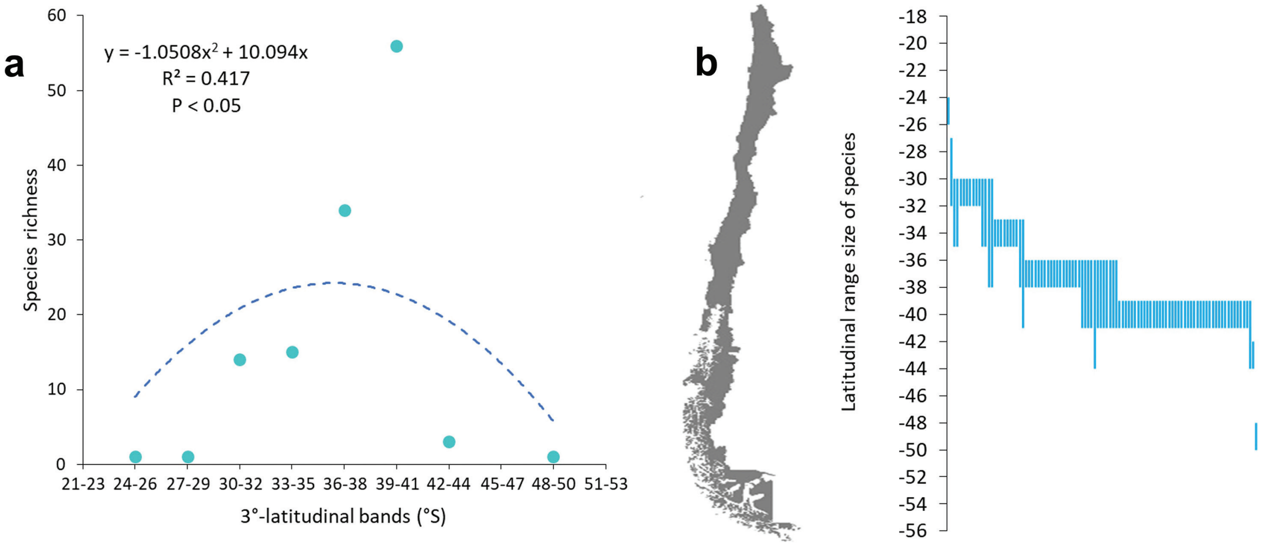

Figure 3. Biogeography of Chilean millipedes. **a** Bell-shaped latitudinal diversity gradient. The second-degree polynomial function (segmented line) reveals that millipede diversity peaks in central Chile and then decreases significantly towards northern and southern Chile. **b** Latitudinal range size of millipede species. All species were categorized as micro-range endemics because they all have latitudinal ranges of less than 1,000 km (with 78% of species exhibiting latitudinal ranges of only ~222 km).

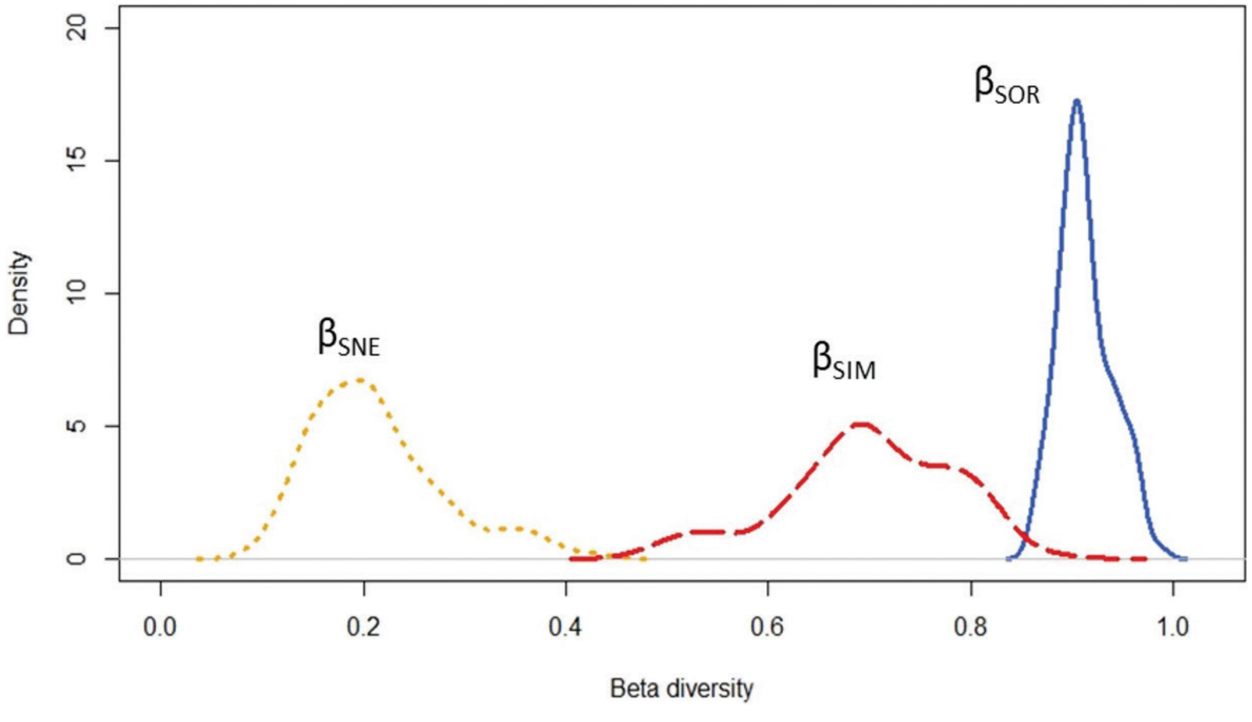

Figure 4. Beta diversity or latitudinal variation of Chilean millipede species composition. The curves in the kernel density plot show the distribution of observed values for beta diversity (β_{SOR}, solid curve) and its two additive components, spatial turnover (β_{SIM}, segmented curve) and nestedness (β_{SNE}, dotted curve). According to this analysis, millipede beta diversity is mainly modulated by species turnover between latitudinal bands. Therefore, species composition changes latitudinally following the north-south climatic gradient that characterizes Chile.

non was species turnover ($\beta_{SIM} = 0.78$; Fig. 4), suggesting high latitudinal variation in species composition. Nestedness was less important ($\beta_{SNE} = 0.16$; Fig. 4), suggesting that few species co-occur latitudinally in Chile. We also observed that species composition varies significantly between the arid, temperate and polar climates of low, mid and high latitudes, respectively (ANOSIM, Global $R = 0.395$, $p = 0.043$).

4. Discussion

Millipedes are a poorly known group in Chile and represent a significant gap in knowledge for myriapodology worldwide (Golovatch 2014; Parra-Gómez 2022). In this study we investigated the state of knowledge, as well as the patterns and causes underlying the spatial distribution of their diversity across an extensive latitudinal gradient. To our knowledge, our study represents the first attempt to investigate the diversity and biogeography of these organisms in Chile.

4.1. State of knowledge of Chilean millipedes

Our analyses revealed that sampling effort and the number of published studies have increased, albeit only modestly, over the last 175 years. Both indicators are low between the mid-19th and mid-20th centuries, probably because during that period it was very difficult to obtain samples from Chile. Researchers from Europe and North America travelled months to get to Chile and usually the samples did not arrive in good condition back to the laboratory (Certes 1889; Jung 1942). Other times, researchers did not travel to Chile but analysed limited numbers of samples collected and provided by colleagues (Attems 1898; 1903) or scientific expeditions (Chamberlin 1957). These limitations hindered the sampling effort, as well as the number and frequency of publications during that period. In fact, there is a gap of 51 years between the publication of the first study on Chilean millipedes (Gervais 1847) and the next one (Attems 1898).

The sampling effort and the number of publications increased notably during the second half of the 20th century thanks to the contributions of the Chilean myriapodologist Francisco Silva. This researcher remained active for 13 years until his premature death in the 1990s (Silva et al. 1968; Demange and Silva 1971a, 1971b; 1976a, 1976b; Mauriès and Silva 1971; Silva and Vivar 1973, 1974; Silva and Sáiz 1975; Urzua and Silva 1981). The studies of Krabbe (1982) and Shear (1988) are also added to this period. Finally, after a hiatus of 24 years, new studies on Chilean millipedes were published (Korsós and Read 2012; Golovatch 2014; Spelda 2015; Mesibov 2017; Short and Vahtera 2017; Vega-Román et al. 2019; Parra-Gómez and Faúndez 2021; Parra-Gómez 2022). Taken together, these studies represent a significant increase in sampling effort and productivity by exploring the diversity of Chilean Diplopoda at 36 new sites.

In Chile there are 95 native species of millipedes (Parra-Gómez 2022; see Suppl. File 1). The number of species known for Chile is similar to that of Argentina (65 species), a South American country where millipedes have also been poorly investigated (Mauriès 1998). However, the number of species inhabiting Chile is higher. An asymptotic estimate of diversity suggests that the diversity of Chilean millipedes is between 125 and 197 species. That is, the true diversity of Chilean millipedes is at least two times greater than known. Our estimate resembles the known diversity for Australia (240 species), a country where millipedes have been extensively investigated (Yeates et al. 2003).

Although we used a robust method to estimate millipede diversity (see Chao et al. 2015), we believe that we have underestimated the diversity of Chilean millipedes. Our estimate is based on diversity data collected at 140 sites, which represents a small fraction of the area included within Chile's extensive latitudinal and altitudinal gradients. Each of these gradients contains thousands of sites where millipede diversity has never been investigated. In turn, each of these sites represents a myriad of microhabitats with local environmental conditions that could contain a substantial number of native species still unknown to Chile and science (Fernández 2011). In fact, Chile has extensive and near-pristine ecosystems (e.g. peatlands, León et al. 2021) in which invertebrates such as millipedes have never been investigated. Thus, the number of millipede species that have not yet been recorded in Chile probably exceeds our estimate. Our rarefaction and extrapolation curves suggest that we need to significantly increase sampling effort to record these species. Fortunately, there is renewed interest in investigating the diversity and distribution of Chilean millipedes (Vega-Román et al. 2019; Parra-Gómez and Faúndez 2021; Parra-Gómez 2022, present study). Therefore, our knowledge of Chilean millipedes could increase significantly in the coming years.

4.2. Millipede biogeography

After accounting for spatial bias in sampling effort we observed that millipede species richness follows a bell-shaped latitudinal diversity gradient, i.e. diversity peaks at mid-latitudes and decreases monotonically towards low and high latitudes. The observed latitudinal diversity gradient is not unique to these invertebrates. Many macro- (e.g. Villagrán and Hinojosa 1997; Samaniego and Marquet 2009; Moreno et al. 2021) and microorganisms (i.e. protists; Fernández et al. 2016; Campello-Nunes et al. 2022) also exhibit a bell-shaped latitudinal diversity gradient in Chile. This finding suggests that millipede species richness covaries latitudinally with that of other Chilean taxa. Probably all Chilean taxa share a common biogeographic history determined, for example, by historical contingencies (desertification at low latitudes, glaciations at high latitudes) that formed Chile's climatic gradient.

Of the 95 species included in our study, 92 are endemic and three are native to Chile (Parra-Gómez 2022; see Suppl. file 1). All these species are micro-range endemics, i.e. they have latitudinal ranges of less than 1,000 km. This suggests that Chilean species have low vagility and very narrow habitat requirements. Our finding is consistent with the idea that Diplopoda exhibit high endemism and restricted distributions worldwide (Enghoff et al. 2011; Means and Marek 2017).

Most micro-range endemic species accumulate in central Chile, contributing to the diversity peak we observed in mid-latitudes. This area is known as a hotspot of diversity and endemism (Arroyo et al. 2004; Fernández 2010; Fernández et al. 2015; Campello-Nunes et al. 2022). Many of these organisms are threatened by habitat fragmentation and other human activities (Arroyo et al. 2004; Fernández et al. 2009) and millipedes are no exception. The mid-latitudes harbour about 65 endemic millipede species with narrow geographic ranges (Parra-Gómez 2022). Unfortunately, there is no information on the conservation status of Chilean millipedes. We presume that rare species (i.e. uncommon, scarce or infrequent species), are those facing the greatest risk of extinction in Chile. These rare species include *Siphonotus jacqueminae* Mauriès and Silva, 1971, *Myrmekia karykina* Attems, 1898, *Oligodesmus nitidus* Attems, 1898, and *Polyxenus rossi* Chamberlin, 1957.

Millipede diversity was positively correlated with a subset of climatic variables related to climatic seasonality, water availability and ambient energy inputs. Thus, millipedes are more diverse in latitudinal bands that have a mesophilic or temperate (warm and humid) climate for most of the year. This result supports two of the five biogeographical hypotheses tested in this study: the climatic stability hypothesis and the water-energy balance hypothesis.

Chile exhibits a mesophilic or temperate climate (humid and warm) in the mid-latitudes (Beck et al. 2018). In contrast, it exhibits arid and polar climates at low and high latitudes, respectively (Villagrán and Hinojosa 1997). This climatic gradient is consistent with the observed bell-shaped latitudinal diversity gradient: millipede diversity peaks at mid-latitudes because temperate conditions exist there almost all year round.

Our results are consistent with the conclusion of other authors. Minelli (2015) reports that millipedes are more diverse in hot, humid climates than in dry or cold climates. Cooper (2022a, 2022b) found that precipitation and temperature (environmental variables often used as surrogates for water and energy availability; see Fernández et al. 2015) are good predictors of millipede diversity.

The relationship between millipedes and water availability is because these invertebrates are vulnerable to desiccation. Their cuticle generally lacks a waterproof layer, their gas exchange system is not closed, and they lose a considerable amount of water through the mouth, in defecation, and during reproduction (Wolters and Ekschmitt 1997). Millipedes are also highly dependent on ambient energy inputs (e.g. organic matter via plant productivity) as most are scavengers that eat damp, decaying wood, leaf particles and other plant material (Golovatch and Kime 2009; Minelli 2015).

Possibly the need for warm, humid climates is a phylogenetically conserved trait in millipedes (Kadamannaya et al. 2009; Cooper 2022b); i.e. they have evolutionary constraints that prevent them from adapting to new climates (Wiens et al. 2010; Fernández et al. 2022). Of course, this does not mean that there are no millipedes adapted to live in harsh climates. In Chile, the arid and polar climates of low and high latitudes also harbour millipede species. However, the habitats of these areas are of post-Pleistocene origin and are therefore more recent than the habitats of mid-latitudes (Villagrán and Hinojosa 1997). These areas also have fewer millipede species than mid-latitudes. Therefore, the species composition present in high and low latitudes possibly represents cases of post-Pleistocene recolonization and/or cases of recent adaptation to severe climates. Among the adaptations that millipedes inhabiting the low and high latitudes of Chile may exhibit are a fossorial lifestyle and volvation, which allow them to conserve moisture and survive in suboptimal sites (Golovatch 2009).

Beta diversity or spatial variation in millipede species composition varies from north to south based on strong species turnover compared to nestedness. Species turnover or species replacement is particularly strong and significant between the arid climate of low latitudes, the temperate climate of mid-latitudes, and the polar climate of high latitudes. Species turnover is often more important than nestedness when species distributions occur in response to an environmental gradient or when there are spatial and historical constraints (Baselga 2012; Fernández et al. 2016). Therefore, the observed beta diversity pattern supports the idea that millipede diversity is distributed from north to south according to the latitudinal gradient of climatic stability and water-energy balance. Likewise, the pattern of beta diversity supports the existence of evolutionary constraints (niche conservatism) that limit the adaptation of millipedes to the more severe climates of northern and southern Chile. Possibly, diversity is lower in low and high latitudes because historical contingencies that established severe climatic conditions in those areas limited the colonization of most mesophilic millipede species. At least this is the explanation that has been postulated to explain the low diversity exhibited by plants, animals, and protists in northern and southern Chile (Villagrán and Hinojosa 1997; Samaniego and Marquet 2009; Fernández 2015; Fernández et al. 2016; Campello-Nunes et al. 2022).

5. Conclusions

There are 95 native millipede species in Chile (considering described species, species that have not yet been formally described and subspecies that will ultimately be promoted to species), although we estimate that the diversity is between 125 and 197 species. Our estimate is based on limited data and so, the diversity of Chilean millipedes could be higher than expected. In line with this conclusion, rarefaction and extrapolation curves suggest that the sampling effort invested in the last 175 years has been insufficient to record a substantial number of millipede species inhabiting Chile. To reverse this situation we need to significantly increase sampling effort across the extensive latitudinal and altitudinal gradients that characterize Chile.

The species richness of Chilean millipedes is distributed from north to south following a bell-shaped latitudinal diversity gradient, i.e. diversity peaks at mid-latitudes and decreases towards low and high latitudes. The diversity peak is caused by the accumulation of species with narrow geographic ranges in the mid-latitudes, a zone recognized as a hotspot of biodiversity and endemism for multi- and unicellular organisms. Species composition changes significantly between the arid climate of low latitudes, the temperate climate of mid-latitudes and the polar climate of high latitudes. Consistently, the variables that best predict the pattern and causes underlying the latitudinal diversity gradient of Chilean millipedes are climate stability, water availability and ambient energy inputs. Thus, Chilean millipedes are more diverse at sites that exhibit temperate (humid and warm) climates throughout much of the year. This result suggests that the biogeography of Chilean millipedes is predicted by the mechanisms proposed by two biogeographic hypotheses, i.e., climatic stability and water-energy balance. Possibly, water availability, ambient energy inputs, and climatic stability also predict broad-scale diversity patterns in millipedes from other regions of the planet.

6. Competing interests

The authors have declared that no competing interests exist.

7. Authors' contributions

APG and LDF conceived the idea. APG collected the data and LDF conducted the statistical and biogeographical analyses. Both authors wrote the manuscript and gave final approval for publication.

8. Acknowledgments

This manuscript was substantially improved by comments and suggestions provided by Sergei Golovatch, Paul Marek and an anonymous reviewer. Special thanks to Jackson Means who proofread the manuscript. APG thanks his parents for supporting his studies in BSc Biology. LDF is funded by the project Fondecyt Regular N° 1220605 awarded by the Agencia Nacional de Investigación y Desarrollo (ANID), Chile. Both authors thank Jorge Pérez, Francisco Urra, Juan Campodonico, José Contreras and Edgardo Flores for providing biological material for this study.

9. References

Adis J (2002) Amazonian Arachnida and Myriapoda identification keys to all classes, orders, families, some genera, and lists of know terrestrial species. Pensoft Publishers, Sofia, Bulgaria, 590 pp.

Arroyo MTK, Marquet PA, Marticorena C, Simonetti JA, Cavieres L, Squeo F, Rozzi R (2004) Chilean winter Rainfall–Valdivian forests. In: Mittermeier RA, Gil PR, Hoffmann M, Pilgrim J, Brooks T, Mittermeier CG, Lamoreux J, da Fonseca GAB (Eds), Hotspots revisted: Earth's biologically wealthiest and most threatened ecosystems. CEMEX, México D.F., 99–103.

Attems CG (1898) System der Polydesmiden. I. Theil. Denkschriften der Kaiserlichen Akademie der Wissenschaften / Mathematisch-Naturwissenschaftliche Classe 67: 221–482.

Attems CG (1903) Beiträge zur myriopodenkunde. Zoologische Jahrbücher Abteilung für Systematik, Geographie und Biologie der Tiere 18: 63–154.

Baselga A, Orme CDL (2012) betapart: an R package for the study of beta diversity. Methods in Ecology and Evolution 3(5): 808–812. https://doi.org/10.1111/j.2041-210X.2012.00224.x

Beck HE, Zimmermann NE, McVivar TR, Vergopolan N, Berg A, Wood EF (2018) Present and future Köppen-Geiger climate classification maps at 1-km resolution. Scientific Data 5(180214): 1–12. https://doi.org/10.1038/sdata.2018.214

Bivand R, Hauke J, Kossowski T (2013) Computing the Jacobian in Gaussian spatial autoregressive models: an illustrated comparison of available methods. Geographical Analysis 45(2): 150–179. https://doi.org/10.1111/gean.12008

Campello-Nunes PH, Woelfl S, da Silva-Neto ID, Paiva TS, Fernández LD (2022) Checklist, diversity and biogeography of ciliates (Ciliophora) from Chile. European Journal of Protistology 84(125892). https://doi.org/10.1016/j.ejop.2022.125892

Certes A (1889) Protozoaires. In: Mission Scientifique du Cap Horn 1882–1883. Zoologie. Paris, 1–53. Available from: https://doi.org/10.5962/bhl.title.2480

Chamberlin RV (1957) The Diplopoda of the Lund University and California Academy of Sciences expeditions. Lunds Universitets Arsskrift, Ny Följd, Avd. 2: 1–44.

Chao A, Jost L (2015) Estimating diversity and entropy profiles via discovery rates of new species. Methods in Ecology and Evolution 6(8): 873–882. https://doi.org/10.1111/2041-210X.12349

Chao A, Gotelli NJ, Hsieh TC, Sander EL, Ma KH, Colwell RK, Ellison AM (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecological Monographs 84(1): 45–67. https://doi.org/10.1890/13-0133.1

Clarke KR, Ainsworth M (1993) A method of linking multivariate community structure to environmental variables. Marine Ecology Press Series 92: 205–219. https://doi.org/10.3354/meps092205

Clarke KR, Gorley RN, Somerfield PJ, Warwick RM (2005) Change in marine communities: an approach to statistical analysis and interpretation, 3rd edn. PRIMER–E Ltda., Plymouth, UK.

Clarke KR, Gorley RN (2006) PRIMER v.6: User Manual / Tutorial. PRIMER–E Ltda., Plymouth, UK.

Cooper M (2022a) Assessment of latitudinal gradient in species richness of *Sphaerotherium*. New Visions in Biological Science 9: 14–20. https://doi.org/10.9734/bpi/nvbs/v9/1885A

Cooper M (2022b) The inverse latitudinal gradient in species richness of forest millipedes: *Centrobolus* Cook, 1897. New Visions in Biological Science 9: 82–88. https://doi.org/10.9734/bpi/nvbs/v9/1898A

Currie DJ (1991) Energy and large-scale patterns of animal- and plant-species richness. The American Naturalist 137(1): 27–49.

Davies BJ, Darvill CM, Lovell H, Bendle JM, Dowdeswell JA, Fabel D, García JL, Geiger A, Glasser NF, Gheorghiu DM, Harrison S, Hein AS, Kaplan MR, Martin JRV, Mendelova M, Palmer A, Pelto M, Rodés Á, Sagredo EA, Smedley RK, Smellie JL, Thorndycraft VR (2020) The evolution of the Patagonian Ice Sheet from 35 ka to the present day (PATICE). Earth-Science Reviews 204(103152): 1–77. https://doi.org/10.1016/j.earscirev.2020.103152

Demange J-M, Silva F (1971a) Nouvelle espèce chilienne du genre *Autostreptus* Silvestri et description du matériel type de *Iulus chilensis* Gervais, 1847, type du genre (Myriapode, Diplopode, Spirostreptoidea, Spirostreptidae, Spirostreptinae). Bulletin du Muséum National d'Histoire Naturelle, 2e série 42(4): 708–715.

Demange J-M, Silva F (1971b) *Abatodesmus velosoi* nov. sp., nouvelle espèce chilienne de la famille des Sphaerotrichopidae (Myriapode, Diplopodae: Polydesmoidea). Bulletin du Muséum National d'Histoire Naturelle 42(5): 881–886.

Demange J-M, Silva F (1976a) Etudes de quelques genres chiliens de la famille des Sphaerotrichopidae (Myriapodes, Diplopodes, Polydesmoidae). Bollettino del Laboratorio di Entomologia Agraria "Filippo Silvestri" di Portici 33: 15–33.

Demange J-M, Silva F (1976b) Contribution á la connaissance des espèces originaires du Chili par F. Silvestri en 1902. Bollettino del Laboratorio di Entomologia Agraria "Filippo Silvestri" di Portici 33: 34–43.

Enghoff H, Petersen G, Seberg O (2011) Phylogenetic relationships in the millipede family Julidae. Cladistics 27:606–616. https://doi.org/10.1111/j.1096-0031.2011.00360.x

Evans KL, Warren PH, Gaston KJ (2005) Species-energy relationships at the macroecological scale: a review of the mechanisms. Biological Reviews 80(1): 1–25. https://doi.org/10.1017/S1464793104006517

Fernández L (2010) Foraminíferos (Protozoa: Foraminiferida) del estuario del río Contaco (40° 33'S; 73° 43'O), Chile. Boletín de Biodiversidad de Chile 4: 18–62.

Fernández L (2011) Nuevos registros y ampliaciones de rango ¿Para qué? Boletín de Biodiversidad de Chile 5: 1–2.

Fernández LD (2015) Source-sink dynamics shapes the spatial distribution of soil protists in an arid shrubland of northern Chile. Journal of Arid Environments 113: 121–125. https://doi.org/10.1016/j.jaridenv.2014.10.007

Fernández L, Rau J, Arriagada A (2009) Calidad de la vegetación ribereña del río Maullín (41 28'S; 72 59'O) utilizando el índice QBR. Gayana Botánica 66(2): 269–278. https://doi.org/10.4067/S0717-66432009000200011

Fernández LD, Lara E, Mitchell EAD (2015) Checklist, diversity and distribution of testate amoebae in Chile. European Journal of Protistology 51(5): 409–424. https://doi.org/10.1016/j.ejop.2015.07.001

Fernández LD, Fournier B, Rivera R, Lara E, Mitchell EAD, Hernández CE (2016) Water–energy balance, past ecological perturbations and evolutionary constraints shape the latitudinal diversity gradient of soil testate amoebae in south-western South America. Global Ecology and Biogeography 25(10): 1216–1227. https://doi.org/10.1111/geb.12478

Fernández LD, Seppey CVW, Singer D, Fournier B, Tatti D, Mitchell EAD, Lara E (2022) Niche conservatism drives the elevational diversity gradient in major groups of free-living soil unicellular eukaryotes. Microbial Ecology 83(2): 459–469. https://doi.org/10.1007/s00248-021-01771-2

Geisen S, Mitchell EAD, Wilkinson DM, Adl S, Bonkowski M, Brown MW, Fiore-Donno AN, Heger TJ, Jassey VEJ, Krashevska V, Lahr DJG, Marcisz K, Mulot M, Payne R, Singer D, Anderson OR, Charman DJ, Ekelund F, Griffiths BS, Rønn R, Smirnov A, Bass D, Belbahri L, Berney C, Blandenier Q, Chatzinotas A, Clarholm M, Dunthorn M, Feest A, Fernández LD, Foissner W, Fournier B, Gentekaki E, Hájek M, Helder J, Jousset A, Koller R, Kumar S, La Terza A, Lamentowicz M, Mazei Y, Santos SS, Seppey CVW, Spiegel FW, Walochnik J, Winding A, Lara E (2017) Soil protistology rebooted: 30 fundamental questions to start with. Soil Biology and Biochemistry 111: 94–103. https://doi.org/10.1016/j.soilbio.2017.04.001

Gervais P (1847) Myriapodes. In: Walckenaer CA, Gervais P (Eds), Histoire naturelle des Insectes. Aptères. Librairie Encyclopédique de Roret, Paris, 1–330. Available from: https://doi.org/10.5962/bhl.title.61095

Golovatch SI (2014) On some new or poorly-known millipedes from Chile and Argentina (Diplopoda). Russian Entomological Journal 23: 249–281. https://doi.org/10.15298/RUSENTJ.23.4.02

Golovatch SI (2009) Millipedes (Diplopoda) in extreme environments. In: Golovatch SI, Makarova OL, Babenko AB, Penev LD (Eds), Species and Communities in Extreme Environments: Festschrift towards the 75th Anniversary and a Laudatio in Honour of Academician Yuri Ivanovich Chernov. Pensoft & KMK Scientific Press, Sofia-Moscow, 87–112.

Golovatch SI, Kime RD (2009) Millipede (Diplopoda) distributions: a review. Soil Organisms 81(3): 565–597.

Gregory-Wodzicki KM (2000) Uplift history of the Central and Northern Andes: A review. Geological Society of America Bulletin 112(7): 1091–1105. https://doi.org/10.1130/0016-7606(2000)112<1091:UHOTCA>2.0.CO;2

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: paleontological statistics software for education and data analysis. Paleontologia Electronica 4(1): 1–9.

Hawkins BA, Field R, Cornell HV, Currie DJ, Guégan J-F, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Porter EE, Turner JRG (2003) Energy, water, and broad-scale geographic patterns of species richness. Ecology 84(12): 3105–3117. https://doi.org/10.1890/03-8006

Hsieh TC, Ma KH, Chao A (2016 iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods in Ecology and Evolution 7(12): 1451–1456.

Jung W (1942) Südchilenische Thekamöeben. Archiv für Hydrobiologie 95: 253–356.

Kadamannaya BS, Sridhar KR, Sahadevan S (2009) Seasonal periodicity of pill millipedes (*Arthrosphaera*) and earthworms of the Western Ghats, India. World Journal of Zoology 4(2): 63–69.

Kerr JT, Packer L (1997) Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. Nature 385: 252–254. https://doi.org/10.1038/385252a0

Korsós Z, Read H (2012) Redescription of *Zinagon chilensis* (Silvestri, 1903) from Chile, with a species list of Iulomorphidae from the Southern Hemisphere (Diplopoda: Spirostreptida: Epinannolenidea). Zootaxa 3493: 38–48. https://doi.org/10.11646/zootaxa.3493.1.4

Krabbe E (1982) Systematik der Spirostreptidae (Diplopoda, Spirostreptomorpha). Abhandlungen und Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg (N.F.) 24: 1–476.

León CA, Gabriel M, Rodriguez C, Iturraspe R, Savoretti A, Pancotto V, Benitez-Mora A, Valdes A, Diaz MF, Oberpaur C, Domínguez E, Fernández LD, Mackenzie R, Roland T, Mauquoy D, Silva C (2021) Peatlands of Southern South America: a review. Mires and Peat 27(3): 29 pp. https://doi.org/10.19189/MaP.2020.SNPG.StA.2021

Marek PE, Buzatto BA, Shear WA, Means JC, Black DG, Harvey MS, Rodriguez J (2021) The first true millipede-1306 legs long. Scientific Reports 11(23126): 8. https://doi.org/10.1038/s41598-021-02447-0

Mauriès J-P, Silva F (1971) Colobognathes du Chili. I. Espèces nouvelles du genre *Siphonotus* Brandt (Diplopoda). Bulletin du Muséum National d'Histoire Naturelle 2(42): 887–902.

Mauriès J-P (1998) Diplopoda. In: Morrone JJ, Coscarón S (Eds), Biodiversidad de Artrópodos Argentinos: Una Perspectiva Biotaxonómica. Ediciones SUR, La Plata, 475–484.

McCain CM (2009) Global analysis of bird elevational diversity. Global Ecology and Biogeography 18(3): 346–360. https://doi.org/10.1111/j.1466-8238.2008.00443.x

Means JC, Marek PE (2017) Is geography an accurate predictor of evolutionary history in the millipede family Xystodesmidae? PeerJ 5: e3854 https://doi.org/10.7717/peerj.3854

Mesibov R (2017) New records for millipedes from southern Chile (Polydesmida: Dalodesmidae; Polyzoniida: Siphonotidae). Biodiversity Data Journal 5: 1–5. https://doi.org/10.3897/BDJ.5.e15919

Minelli A (2015) Treatise on Zoology – Anatomy, Taxonomy, Biology. The Myriapoda, Volume 2. Brill, Leiden, The Netherlands, 482 pp. Available from: https://doi.org/10.1163/9789004188273

Moreno RA, Labra FA, Cotoras DD, Camus PA, Gutiérrez D, Aguirre L, Rozbaczylo N, Poulin E, Lagos NA, Zamorano D, Rivadeneira MM (2021) Evolutionary drivers of the hump-shaped latitudinal gradient of benthic polychaete species richness along the Southeastern Pacific coast. PeerJ 9(e12010): 1–24. https://doi.org/10.7717/peerj.12010

Parra-Gómez A (2022) Catálogo de los milpiés (Myriapoda: Diplopoda) de Chile. Revista Chilena de Entomología 48(3): 451–504. http://dx.doi.org/10.35249/rche.48.3.22.02

Parra-Gómez A, Faúndez EI (2021) First teratological case in *Pleonaraius pachyskeles* Attems, 1898 (Polydesmida: Dalodesmidae) including new distributional records in Chile. Boletín del Museo Nacional de Historia Natural del Paraguay 25(2): 144–149.

Pianka ER (1966) Latitudinal gradients in species diversity: a review of concepts. The American Naturalist 100(910): 33–46. https://doi.org/10.1086/282398

Rodríguez MÁ, Belmontes JA, Hawkins BA (2005) Energy, water and large-scale patterns of reptile and amphibian species richness in Europe. Acta Oecologica 28(1): 65–70. https://doi.org/10.1016/j.actao.2005.02.006

Samaniego H, Marquet PA (2009) Mammal and butterfly species richness in Chile: taxonomic covariation and history. Revista Chilena de Historia Natural 82: 135–151.

Shear WA (1988) The Chordeumatid millipeds of Chile (Diplopoda, Chordeumatida). American Museum Novitates (2912): 1–10. https://doi.org/2246/5171

Shelley RM, Golovatch SI (2011) Atlas of Myriapod Biogeography. I. Indigenous ordinal and supra-ordinal distributions in the Diplopoda: perspectives on taxon origins and ages, and a hypothesis on the origin and early evolution of the class. Insecta Mundi 0158: 1–134.

Short M, Vahtera V (2017) Phylogenetic relationships of millipedes in the subclass Penicillata (Diplopoda) with a key to the genera. Journal of Natural History 51(41–42): 2443–2461. https://doi.org/10.1080/00222933.2017.1380241

Sierwald P, Bond JE (2007) Current status of the myriapod class Diplopoda (Millipedes): taxonomic diversity and phylogeny. Annual Review of Entomology 52(1): 401–420. https://doi.org/10.1146/annurev.ento.52.111805.090210

Silva F, Vivar C (1973) Presencia de *Chilorus zapallar* Chamberlin, 1957, en el bosque nativo de Quintero. Anales Del Museo de Historia Natural de Valparaíso 6: 217–223.

Silva F, Vivar C (1974) Miriápodos: I diplópodos del Parque Nacional "Vicente Perez Rosales." Anales del Museo de Historia Natural de Valparaíso 7: 285–291.

Silva F, Sáiz F (1975) Investigaciones ecológicas de los diplópodos del Parque Nacional "Fray Jorge". Anales del Museo de Historia Natural de Valparaíso 8: 17–28.

Silva F, Veloso A, Solervicens J, Ortiz JC (1968) Investigaciones zoológicas en el Parque Nacional Vicente Pérez Rosales y zona de Pargua. Noticiario Mensual del Museo Nacional de Historia Natural: 3–12.

Spelda J (2015) The southernmost millipedes found on Guarello Island, southern Chile (Diplopoda, Polydesmida, Dalodesmidae). Spixiana 38(2): 186.

Urzua A, Silva F (1981) Componentes químicos de las secreciones defensivas de miriápodos-diplópodos del género *Autostreptus*, Silvestri, 1905 (Spirostreptida-Spirostreptidae). Anales del Museo de Historia Natural de Valparaíso 14: 271–273.

Veblen TT, Young KR, Ome AR (2007) The physical geography of South America. Oxford University Press, Oxford, 361 pp. Available from: https://doi.org/10.1093/oso/9780195313413.001.0001

Vega-Román E, Ruiz V, Arancibia-Ávila P (2019) First record of the genus *Polyxenus* Latreille (Diplopoda: Penicillata: Polyxenida) in the supralittoral zone of Cocholgüe, Biobío Region, Chile. Revista Chilena de Entomología 45(3): 399–402. https://doi.org/10.35249/rche.45.3.19.11

Villagrán C, Hinojosa LF (1997) Historia de los bosques del sur de Sudamérica, II: Análisis fitogeográfico. Revista Chilena de Historia Natural 70: 241–267.

Wiens JJ, Ackerly DD, Allen AP, Anacker BL, Buckley LB, Cornell HV, Damschen EI, Jonathan Davies T, Grytnes J-A, Harrison SP, Hawkins BA, Holt RD, McCain CM, Stephens PR (2010) Niche conservatism as an emerging principle in ecology and conservation biology. Ecology Letters 13(10): 1310–1324. https://doi.org/10.1111/j.1461-0248.2010.01515.x

Wolters V, Ekschmitt E (1997) Gastropods, isopods, diplopods, and chilopods: neglected groups of the decomposer food web. In: Benckiser G (Ed), Fauna in Soil Ecosystems: Recycling Processes, Nutrient Fluxes, and Agricultural Production. CRC Press, Boca Raton, 265–306.

Yeates DK, Harvey MS, Austin AD (2003) New estimates of terrestrial arthropod species-richness in Australia. Records of the South Australian Museum Monograph Series 7: 231–241.

Supplementary material 1

Names and occurrences of Chilean millipede species

Authors: Parra-Gómez A, Fernández LD (2022)
Data type: .csv
Explanation note: Database of the species used in this study.

Link: https://doi.org/10.3897/asp.80.e86810.suppl1

Supplementary material 2

Obtaining the environmental variables used in this study

Authors: Parra-Gómez A, Fernández LD (2022)
Data type: .docx
Explanation note: We provide the sources and methods used to estimate the environmental variables used in the present study.

Link: https://doi.org/10.3897/asp.80.e86810.suppl2