

1 **Running title:** Diversity and Biogeography of Chilean millipedes

2 **Filling gaps on the diversity and biogeography of Chilean millipedes (Myriapoda:**
3 **Diplopoda).**

4

5 Antonio Parra-Gómez¹ and Leonardo D. Fernández^{2,3,*}

6 ¹Facultad de Ciencias, Universidad Austral de Chile, Av. Rector Eduardo Morales Miranda
7 23, Valdivia, Chile

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

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

12 *Corresponding author: Leonardo D. Fernández; limnoleo@gmail.com

13

14 **Abstract**

15 Research on the diversity and biogeography of Chilean millipedes (Diplopoda) represents a
16 severe gap in knowledge. To reduce this gap we conducted a study to: (1) investigate the
17 state of knowledge of millipede diversity, and (2) assess the pattern and causes underlying
18 the latitudinal diversity gradient in Chilean millipedes. After combining the number of
19 described species with those that have not yet been formally described, we concluded that
20 there are 95 native millipede species in Chile. A diversity estimate suggested that in the future
21 this number could increase to 125 or 197 species. However, this estimate is based on limited
22 data. Therefore, the number of millipede species inhabiting Chile probably exceeds our
23 estimate. Consistently, rarefaction-extrapolation curves revealed that we have not yet
24 recorded a substantial fraction of millipede diversity and that increased sampling effort will
25 reveal the presence of a greater number of millipede species in Chile. Most millipede species
26 exhibited narrow geographic ranges in Chile. The north-south distribution of their species
27 richness followed a bell-shaped latitudinal gradient of diversity, i.e. diversity peaked at the
28 temperate climate of central Chile and then decreases towards the arid and polar climates of

29 northern and southern Chile, respectively. The causes underlying this biogeographical pattern
30 were water availability, ambient energy input and climate stability. This finding provided
31 support for two of the five biogeographic hypotheses we tested: water-energy balance and
32 climate stability. Thus, Chilean millipedes were more diverse at sites that exhibit warm and
33 humid (temperate) climates for much of the year.

34

35 **Keywords**

36 Beta diversity, biodiversity hotspot, biogeographic hypothesis, latitudinal diversity gradient,
37 millipede biogeography, niche conservatism, rarefaction-extrapolation curves.

38

39 **1. Introduction**

40 Diplopoda is the third largest class of terrestrial arthropods after Insecta and Arachnida
41 (Golovatch and Kime 2009). Its diversity is close to 12,000 species although it is estimated
42 that there could be as many as 80,000 species worldwide (Golovatch and Kime 2009).
43 Although diplopods are commonly referred to as millipedes, their representatives have only
44 hundreds (or fewer) pairs of legs distributed along their body segments (Adis 2002). So far
45 the only known exception to this rule is the species *Eumillipes persephone*, which boasts
46 1,306 pairs of legs (Marek et al. 2021). Found on all continents except Antarctica, millipedes
47 inhabit a wide range of terrestrial biomes although they are most diverse in those with warm
48 and humid climates, such as temperate forests (Minelli 2015).

49 The diversity and distribution of millipedes is poorly known compared to that of other
50 historically better studied metazoans (Sierwald and Bond 2007). These gaps in knowledge
51 are severe in Chile (Golovatch 2014; Parra-Gómez submitted), a long and narrow country in
52 southwestern South America (Fig. 1a). Chile stretches from 17° S to 56° S covering c. 4,300
53 km from north to south and yet it only averages 177 km from east to west. Chile's extensive
54 latitudinal distribution is coupled with a strong north–south climatic gradient. Broadly
55 speaking, the north at low latitudes is arid, the centre at mid-latitudes is temperate, while the
56 south at high latitudes is polar (Beck et al. 2018).

57 The Chilean north–south climatic gradient emerged during the Pleistocene as a consequence
58 of desertification and glaciation events that modified the original warm and humid conditions
59 of northern and southern Chile respectively (Fig. 1b) (Gregory-Wodzicki 2000; Davies et al.
60 2020). Driven by these historical contingencies many northern and southern mesophile taxa
61 became extinct or migrated to the temperate climate of central Chile, where they
62 subsequently diversified (Villagrán and Hinojosa 1997). Today, the diversity of most taxa
63 peaks in mid-latitudes and then decreases towards low and high latitudes (Villagrán and
64 Hinojosa 1997; Samaniego and Marquet 2009; Fernández et al. 2015; Moreno et al. 2021;
65 Campello-Nunes et al. 2022).

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

73 The insular condition of Chile and the historical contingencies experienced by its territory
74 probably favoured the occurrence of a particular millipede diversity (Fig. 1c). Chilean
75 millipedes are mainly Gondwanan relicts (Shelley and Golovatch 2011). They share more
76 taxonomic and possibly evolutionary affinities with millipedes from South Africa, Australia,
77 Tasmania, New Caledonia and New Zealand than with other South American taxa
78 (Golovatch 2014). Families such as Dalodesmidae and Eudigonidae are widely represented
79 in Chile and only marginally in Argentina, while the family Iulomorphae is only found in
80 Chile.

81 The goal of the present study is to investigate the state of knowledge and biogeography of
82 Chilean millipedes. Specifically, we investigated the temporal variation in the number of
83 published studies, the number of sites investigated, and the number of new species reported
84 in Chile over the last 175 years. We also constructed rarefaction, extrapolation and
85 asymptotic diversity curves to assess the number of species that have not yet been described

86 in Chile. Finally, we tested six biogeographic hypotheses (Table 1) to investigate the pattern
87 and causes underlying the latitudinal diversity gradient in Chilean millipedes.

88

89 **2. Methods**

90 2.1. Data source

91 The database used in this study consists of 95 native species recorded in continental Chile
92 between 1847 and 2022. We constructed the database based on species records obtained by
93 the first author and species records included in a recent checklist of Chilean millipedes
94 (Parra-Gómez submitted). Our database is the most up-to-date and comprehensive database
95 for millipedes in Chile. We excluded from the original database (109 species) a total of eight
96 exotic species and six *nomina dubium* species. We used our database to construct a binary
97 matrix (i.e. columns as samples and rows as taxa) on which all subsequent statistical analyses
98 were based.

99

100 2.2. State of knowledge of Chilean millipedes

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

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

107 Second, we estimated a rarefaction curve to investigate whether the sampling effort invested
108 in Chile (measured as the number of sites investigated between the 1840s and 2020s) has
109 contributed to the completion of the checklist of Chilean millipede species. If the rarefaction
110 curve reaches a plateau, we will conclude that the investment of additional sampling effort
111 will not reveal a substantial number of new species in Chile. If the rarefaction curve does not
112 reach a plateau, then we will conclude that the investment of additional sampling effort will
113 reveal new species in Chile. We also estimated an extrapolation curve to investigate whether

114 an increase in sampling effort will contribute to the completeness of the checklist of Chilean
115 millipede species. If the rarefaction curve reaches a plateau, we will conclude that an increase
116 in sampling effort will contribute to completing the checklist of Chilean millipede species. If
117 the rarefaction curve does not reach a plateau, we will conclude that a significant increase in
118 sampling effort is needed to complete the checklist of Chilean millipede species. We
119 estimated the rarefaction and extrapolation curves based on the approach proposed by Chao
120 et al. (2014). The rarefaction curve was estimated using the number of sites surveyed in Chile
121 from the 1880s onwards as a proxy for sampling effort ($n = 140$ sampling sites). The
122 extrapolation curve was estimated by doubling the sampling effort ($n = 280$ sampling sites).
123 The rarefaction and extrapolation curves and their lower and upper confidence limits (95%
124 CI) were estimated based on 10,000 bootstrap replicates in the R package iNEXT version
125 2.0.20 (Hsieh et al. 2016).

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

131

132 2.3. Millipede biogeography

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

139 To investigate the latitudinal diversity gradient we divided Chile into bins of 3° latitudinal
140 bands. We then counted the number of species recorded in each latitudinal bin and correlated
141 species richness against latitude by fitting linear and non-linear functions in PAST version

142 4.09 (Hammer et al. 2001). We used the Akaike information criterion to select the model that
143 best fitted the data.

144 To investigate the distribution ranges of millipede species we plotted and classified the
145 latitudinal distribution of each species into one of the following categories: (a) species with
146 small distributions, occurring only within two latitudinal bands; (b) species with narrow-
147 medium ranges of distribution, ranging from three to 10 latitudinal bands; (c) species with
148 medium-large distributions, ranging from 11 to 19 latitudinal bands; and (d) species with
149 large distributions, ranging from 20 to 39 latitudinal bands.

150 We investigated the relationship between species richness and 25 environmental variables
151 frequently used as proxies for ecological hypotheses proposed to explain the occurrence of
152 latitudinal diversity gradients (Table 1). We obtained the environmental variables from
153 various sources such as WorldClim, among others. Based on scatter plots for all variable
154 pairs (Draftsman Plot) we $\log(x + 1)$ transformed all variables and removed highly correlated
155 variables to avoid skewed trends. This process resulted in 19 environmental variables (Table
156 1). We then normalized all selected variables to compare variables with different unit
157 measures (Clarke et al. 2005). To investigate the relationship between these 19 variables and
158 millipede richness we conducted a BioEnv procedure, which used a multiple regression
159 approach to determine which environmental variables best explain the latitudinal diversity
160 gradient in millipedes (Clarke and Ainsworth 1993). We estimated BioEnv and its statistical
161 significance (1,000 permutation) in PRIMER version 6 (Clarke and Gorley 2006).

162 To investigate beta diversity or the latitudinal variation in species composition we estimated
163 beta diversity (β_{SOR}) as well as its underlying additive components, i.e. spatial turnover (β_{SIM})
164 and nestedness (β_{SNE}), as described by Baselga (2012). In brief β_{SOR} is a measure of
165 (di)similarity based on Sørensen's index and represents a global metric of beta diversity. β_{SIM}
166 is a measure of (di)similarity based on Simpson's index and describes the fraction of beta
167 diversity that corresponds only to the spatial turnover of species. β_{SNE} is estimated as the
168 difference between β_{SOR} and β_{SIM} and describes the spatial loss of diversity among sites.
169 These metrics range from zero (perfect similarity) to one (perfect dissimilarity). We
170 estimated β_{SOR} , β_{SIM} and β_{SNE} using the R package betapart (Baselga and Orme 2012).

171 We also conducted an analysis of similarity (ANOSIM) to investigate the variation in species
172 composition between arid, temperate and polar climates at low, mid and high latitudes,
173 respectively. ANOSIM compares the mean of ranked dissimilarities between groups to the
174 mean of ranked dissimilarities within groups based on the R–statistic. An R–statistic close to
175 "1" suggests dissimilarity between groups, an R–statistic close to "0" suggests an even
176 distribution of high and low ranks within and between groups, while an R–statistic below "0"
177 suggest that dissimilarities are greater within groups than between groups. The ANOSIM and
178 significance value of the R–statistic were estimated based on 1000 permutations in PRIMER
179 version 6 (Clarke and Gorley 2006).

180

181 3. Results

182 3.1. State of knowledge of Chilean millipedes

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

187 Our analysis revealed that between 1847 and 2022 (175 years) native millipede species were
188 described or reported in 30 studies. The number of published studies exhibits two peaks over
189 time, i.e. one in the 1970s and another in the 2010s with eight and seven published studies,
190 respectively. The remaining decades exhibit between one and three published studies. While
191 we recorded an increase in the number of studies on Chilean millipedes over time, we also
192 noted extended periods without published studies. These include the periods between 1848
193 and 1897 (49 years); 1906 and 1915 (nine years) and more recently between the 1989 and
194 2011 (22 years) (Fig. 2a).

195 The review of the 30 published studies on Chilean millipedes revealed that researchers have
196 explored the diversity of these invertebrates at 140 unique sites. Eleven studies (37%) are
197 based on a single study site, four (13%) on three sites, three (10%) on two sites, three (10%)
198 on eight sites, two (7%) on 13 sites, two (7%) on six sites, two (7%) on five sites, one (3%)
199 on 19 sites, one (3%) on 11 sites and one (3%) on nine sites. The number of new sites sampled

200 exhibits a peak in the 1970s with 30 new sites sampled. The 1900s, 1950s and 2010s also
201 stand out with 22, 20 and 21 new sites sampled. The number of new sites sampled during the
202 remaining decades range between 1 and 11 sites. Overall our analysis suggests that, even
203 though there are extended periods without published studies, the number of new sites
204 investigated has increased over time, particularly after the 1900s (Fig. 2b).

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

210 Although the number of new species reported varies significantly between decades, the
211 cumulative number of new species has increased exponentially over time. Between the 1840s
212 and 2020s the number of native species known for Chile has increased from three to 95
213 (including species that have yet to be formally described; Parra-Gómez, personal
214 observation). This suggests that conducting further studies and exploring more sites will
215 reveal new species in Chile (Fig. 2d).

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

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

229 3.2. Millipede biogeography

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

233 Analysis of geographic range size revealed that most millipedes (78 species) have narrow
234 geographic ranges, while the rest (28 species) have narrow-medium ranges (Fig. 3b). We did
235 not record species with medium and medium-large geographic ranges in Chile. Our analysis
236 also revealed that the diversity peak observed in mid-latitudes is a product of the
237 accumulation (and overlap) of species with narrow geographic ranges in central Chile.

238 The bell-shaped latitudinal diversity gradient of Chilean millipedes is positively and
239 significantly correlated with a subset of five environmental variables, including Ultraviolet
240 Radiation B (UVB), Normalised Difference Vegetation (NDVI), Annual Precipitation
241 (APR), Mean Diurnal Range (MDR) and Isothermality (ISO) (BioEnv, $R = 0.787$, $p = 0.01$).
242 UVB and NDVI are proxies for energy, APR is a proxy for water availability, while MDR
243 and ISO are proxies for climatic stability. The observed correlation between millipede
244 diversity and these proxies lends support to the water–energy balance and the climate stability
245 hypotheses. Thus, our results suggest that millipede diversity is high in mid-latitudes because
246 they exhibit a continuous trade-off between water availability and ambient energy inputs
247 throughout the year.

248 Millipedes have a high beta diversity in Chile ($\beta_{\text{SOR}} = 0.94$; Fig. 4). The most important
249 underlying phenomenon was species turnover ($\beta_{\text{SIM}} = 0.78$; Fig. 4), suggesting high
250 latitudinal variation in species composition. Nestedness was less important ($\beta_{\text{SNE}} = 0.16$; Fig.
251 4), suggesting that few species co-occur latitudinally in Chile. We also observed that species
252 composition varies significantly between the arid, temperate and polar climates of low, mid
253 and high latitudes, respectively (ANOSIM, Global $R = 0.395$, $p = 0.043$).

254

255 4. Discussion

256 Millipedes are a poorly known group in Chile and represent a severe gap in knowledge for
257 myriapodology worldwide (Golovatch 2014; Parra-Gómez submitted). In this study we

258 investigated the state of knowledge, as well as the patterns and causes underlying the spatial
259 distribution of their diversity across an extensive latitudinal gradient. To our knowledge, our
260 study represents the first attempt to investigate the diversity and biogeography of these
261 organisms in Chile.

262

263 4.1. State of knowledge of Chilean millipedes

264 Our analyses revealed that sampling effort and the number of published studies have
265 increased, albeit only modestly, over the last 175 years. Both indicators are particularly low
266 between the mid-19th and mid-20th centuries, probably because during that period it was
267 very difficult to obtain samples from Chile. Researchers from Europe and North America
268 travelled months to get to Chile and usually the samples did not arrive in good condition back
269 to the laboratory (Certes 1889; Jung 1942). Other times researchers did not travel to Chile
270 but analysed limited numbers of samples collected and granted by colleagues (Attems 1898;
271 1903) or scientific expeditions (Chamberlin, 1957). These limitations surely hindered the
272 sampling effort, as well as the number and frequency of publications during that period. In
273 fact, there is a gap of 51 years between the publication of the first study (Gervais 1847) and
274 the second study (Attems 1898) on Chilean millipedes.

275 The sampling effort and the number of publications increased notably during the second half
276 of the 20th century thanks to the contributions of the Chilean myriapodologist Francisco
277 Silva. This researcher remained active for 13 years until his premature death in the 1990s
278 (Silva et al. 1968; Demange and Silva 1971a, 1971b; Mauriés and Silva 1971; Silva and
279 Vivar 1973, 1974; Silva and Sáiz 1975; Demange and Silva 1976a, 1976b; Urzua and Silva
280 1981). The studies of Krabbe (1982) and Shear (1988) are also added to this period. Finally,
281 after a hiatus of 24 years, new studies on Chilean millipedes were published (Korsos and
282 Read 2012; Golovatch 2014; Spelda 2015; Mesibov 2017; Short and Vahtera 2017; Vega-
283 Román et al. 2019; Parra-Gómez and Faúndez 2021; Parra-Gómez 2022). Taken together,
284 these studies represent a significant increase in sampling effort by exploring the diversity of
285 Chilean myriapods at 36 new sites.

286 In Chile, there are 96 native millipede species. This value includes 68 described species in
287 the last 175 years, species that have not yet been formally described and subspecies that will
288 be promoted to species in the near future (Parra-Gómez submitted). However, the number of
289 millipede species inhabiting Chile is possibly higher. Based on available data we estimated
290 the diversity of native Chilean millipedes to be between 125 and 197 species. These values
291 represent between two and three times the number of described species.

292 Although we used a robust method to assess millipede diversity (see Chao et al. 2015), we
293 believe that we have underestimated the diversity of Chilean millipedes. Our estimate is
294 based on diversity data collected at 140 sites, which represents a small fraction of the area
295 included within Chile's extensive latitudinal and altitudinal gradients. Each of these gradients
296 contains thousands of sites where millipede diversity has never been investigated. In turn,
297 each of these sites represents a myriad of microhabitats with local environmental conditions
298 that could contain an imponderable number of native species unknown to Chile and science
299 (Fernández 2011). Thus, the number of millipede species that have not yet been recorded in
300 Chile probably exceeds our estimate. Our rarefaction and extrapolation curves suggest that
301 we need to significantly increase sampling effort to record these species. Fortunately, there
302 is renewed interest in investigating the diversity and distribution of Chilean millipedes
303 (Vega-Román et al. 2019; Parra-Gómez and Faúndez 2021; Parra-Gómez submitted, present
304 study). Therefore, our knowledge about Chilean millipedes could increase significantly in
305 the coming years.

306

307 4.2. Millipede biogeography

308 After accounting for spatial bias in sampling effort we observed that millipede species
309 richness follows a bell-shaped latitudinal diversity gradient, i.e. diversity peaks at mid-
310 latitudes and decreases monotonically towards low and high latitudes. The observed
311 latitudinal diversity gradient is not unique to these invertebrates. Many macro- (e.g. Villagrán
312 and Hinojosa 1997; Samaniego and Marquet 2009; Moreno et al. 2021) and microorganisms
313 (i.e. protists; Fernández et al. 2016; Campello-Nunes et al. 2022) also exhibit a bell-shaped
314 latitudinal diversity gradient in Chile. This finding suggests that millipede species richness
315 covaries latitudinally with that of other Chilean taxa. Probably all Chilean taxa share a

316 common biogeographic history determined, for example, by historical contingencies
317 (desertification at low latitudes, glaciations at high latitudes) that originated Chile's climatic
318 gradient.

319 Millipedes are recognized for their low vagility and for occupying narrow geographic ranges
320 (Sierwald and Bond 2007; Golovatch and Kime 2009). Consistently, we observed that most
321 millipede species have narrow geographic ranges in Chile. Many of the species with narrow
322 ranges accumulate in central Chile, contributing to the diversity peak we observed in mid-
323 latitudes. This area is a known hotspot of diversity and endemism (Arroyo et al. 2004;
324 Fernández 2010; Fernández et al. 2015; Campello-Nunes et al. 2022). Many of these
325 organisms are threatened by habitat fragmentation and other human activities (Arroyo et al.
326 2004; Fernández et al. 2009) and possibly millipedes are no exception. The mid-latitudes
327 harbor about 65 endemic millipede species with very narrow geographic ranges (Parra-
328 Gómez submitted). Unfortunately, there is no information on the conservation status of
329 Chilean millipedes. We presume that rare species, i.e. uncommon, scarce or infrequent
330 species (e.g. *Siphonotus jacqueminae* Mauriès and Silva, 1971, *Myrmekia karykina* Attems,
331 1898, *Oligodesmus nitidus* Attems, 1898, *Polyxenus rossi* Chamberlin, 1957), are those
332 facing the greatest risk of extinction in Chile.

333 Millipede diversity exhibited a positive correlation with a subset of climatic variables related
334 to climatic seasonality, water availability and ambient energy inputs. Thus, millipedes are
335 more diverse in latitudinal bands that exhibit a mesophilic or temperate climate (i.e. warm
336 and humid) during most of the year, supporting two of the biogeographic hypotheses tested,
337 i.e. climate stability and water-energy balance, respectively. In Chile, the mesophilic or
338 temperate climate is present during most of the year in mid-latitudes (Veblen et al. 2007),
339 explaining the diversity peak we have observed. Consistently, millipede diversity in other
340 regions is also predicted by environmental variables used as surrogates for water-energy
341 balance such as precipitation and temperature (Cooper 2022a; Cooper 2022b). Possibly the
342 need for warm, humid climates is a phylogenetically conserved trait in millipedes
343 (Kadamannaya et al. 2009; Cooper 2022b). Therefore, these arthropods may have
344 evolutionary constraints that prevent them from adapting to new climates (Wiens et al. 2010;
345 Fernández et al. 2022). Of course, this does not mean that there are no millipede species

346 adapted to live in harsh climates. In Chile, the arid and polar climates of low and high
347 latitudes, respectively, also harbor millipede species. However, the habitats of these areas are
348 of post-Pleistocene origin and are therefore more recent than the habitats of mid-latitudes
349 (Villagrán and Hinojosa 1997). These areas also have fewer millipede species than mid-
350 latitudes. Therefore, the species composition present in high and low latitudes possibly
351 represents cases of post-Pleistocene recolonization and/or cases of recent adaptation to severe
352 climates. Among the adaptations that millipedes inhabiting the low and high latitudes of
353 Chile may exhibit are a fossorial lifestyle and conglobation, which allow them to conserve
354 moisture and survive in suboptimal sites (Golovatch 2009).

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

372

373 **5. Conclusions**

374 There are 96 native millipede species in Chile (considering described species, species that
375 have not yet been formally described and subspecies that will be promoted to species),

376 although we estimate that the diversity is between 125 and 197 species. On the other hand,
377 our estimate is based on limited data so that the real diversity of Chilean millipedes could be
378 much higher. In line with this conclusion, rarefaction and extrapolation curves suggest that
379 the sampling effort invested in the last 175 years has been insufficient to record a substantial
380 number of millipede species inhabiting Chile. To reverse this situation we need to
381 significantly increase sampling effort across the extensive latitudinal and altitudinal gradients
382 that characterize Chile.

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

397

398 **6. Competing interests**

399 The authors have declared that no competing interests exist.

400

401 **7. Authors' contributions**

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

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410

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619 **Table 1.** Ecological hypotheses tested with respect to the diversity of native millipedes in Chile and their respective predictions and
 620 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)
5 Climatic variability	Diversity increases in climatically stable areas	ISO, TS, MDR, TAR, MTC,	Currie (1991), Kerr and Packer (1997)
6 Habitat heterogeneity	Diversity increases with habitat heterogeneity	ELE	Pianka (1966), Kerr and Packer (1997)

621
 622 UVB: Ultraviolet Radiation B, NPP: Net Primary Productivity, NDVI: Normalized Difference Vegetation, PET: Potential
 623 Evapotranspiration, AMT: Annual Mean Temperature, MTW: Max Temperature of Warmest Month, MTQ: Mean Temperature Of
 624 Wettest Quarter, MWQ: Mean Temperature of Warmest Quarter, MCQ: Mean Temperature of Coldest Quarter, APR: Annual
 625 Precipitation, PDM: Precipitation of Driest Month, PWQ: Precipitation of Warmest Quarter, ISO: Isothermality, TES: Temperature
 626 Seasonality, MDR: Mean Diurnal Range, TAR: Temperature Annual Range, MTC: Min Temperature of Coldest Month, ELE:
 627 Topographic Elevation

628 **Figure 1.** Map and millipedes of Chile. (A) Chile in southwestern South America stretches
629 from $\sim 17^{\circ}\text{S}$ to 56°S . (B) During the Pleistocene, a series of geological events (e.g. the uplift
630 of the Andes) and climatic changes (e.g. the Last Glacial Maximum) shaped the Atacama
631 Desert in the north (area shaded in light grey) and the Patagonian ice sheet in the south (area
632 shaded in dark grey) in Chile. Since then, the Atacama Desert has favoured an arid climate
633 at low latitudes while at the end of the Last Glacial Maximum the retreat of the Patagonian
634 Ice Sheet set up a polar climate at high latitudes. The mid-latitudes of central Chile exhibit a
635 temperate climate and acted as a refuge for biota during the occurrence of the historical
636 contingencies described. **c.** Examples of millipede species endemic to Chile. From top to
637 bottom: *Tsagonus* aff. *valdiviae* Chamberlin, 1957; *Siphonotus parguaensis* Mauriès and
638 Silva, 1971; *Monenchodesmus inermis* Silvestri, 1903 and *Mikroporus granulatus* Attems,
639 1898.

640

641 **Figure 2.** State of knowledge of Chilean millipedes. (A) number of studies published per
642 decade. (B) number of new sites sampled per decade. (C) number of new species reported
643 per decade. (D) cumulative number of new species per decade. (E) rarefaction curves (solid
644 trend line) and extrapolation curves (dash-dotted line). The point between both curves
645 represents the number of sites where millipedes have been sampled in Chile. (F) Asymptotic
646 estimate of millipede diversity in Chile (solid trend line).

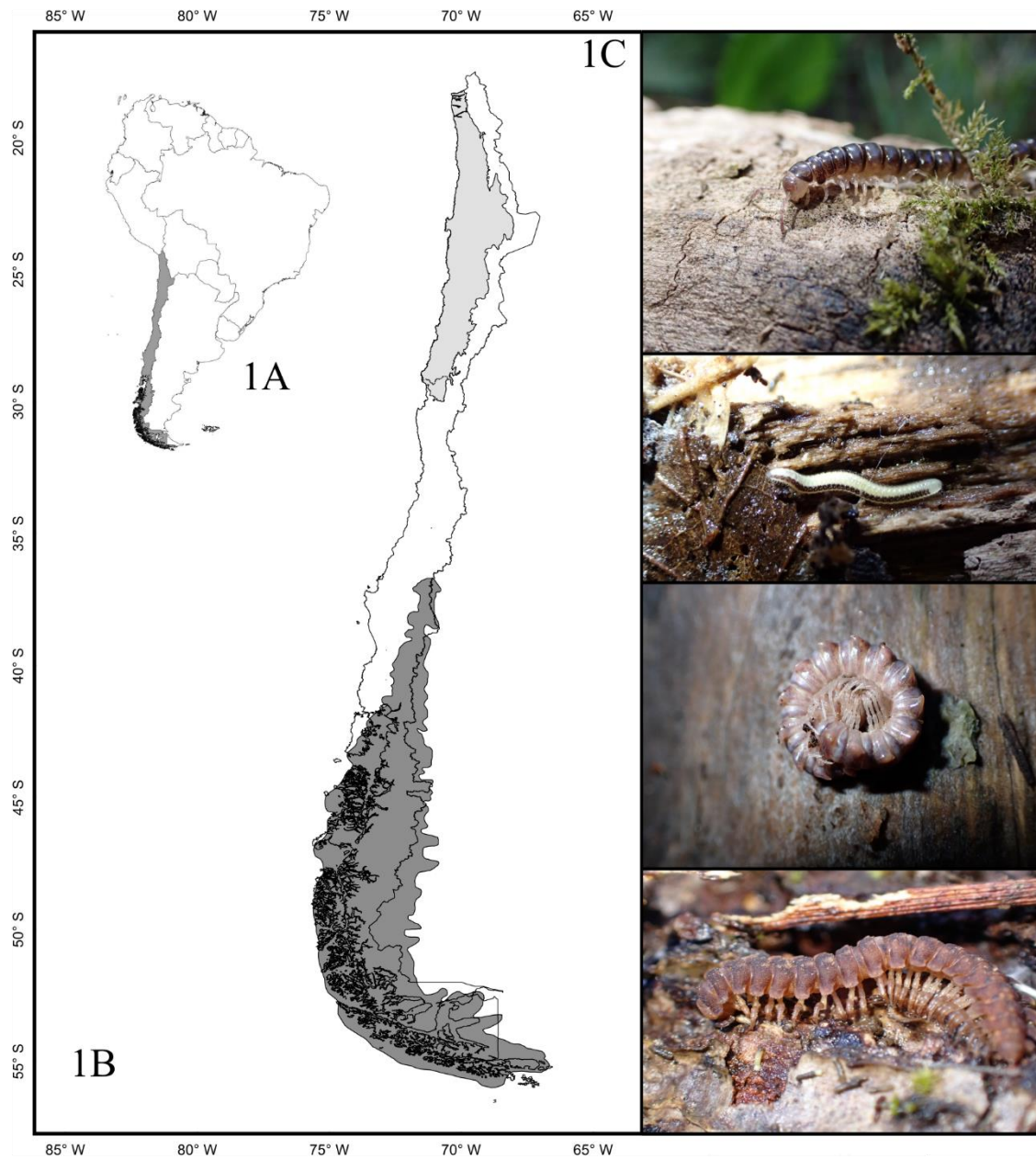
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648 **Figure 3.** Biogeography of Chilean millipedes. (A) Bell-shaped latitudinal diversity gradient.
649 The second-degree polynomial function (segmented line) reveals that millipede diversity
650 peaks in central Chile and then decreases significantly towards northern and southern Chile.
651 (B) Geographic ranges of Chilean millipedes. The geographic ranges of these invertebrates
652 are narrow or narrow-medium and are mainly concentrated in central Chile.

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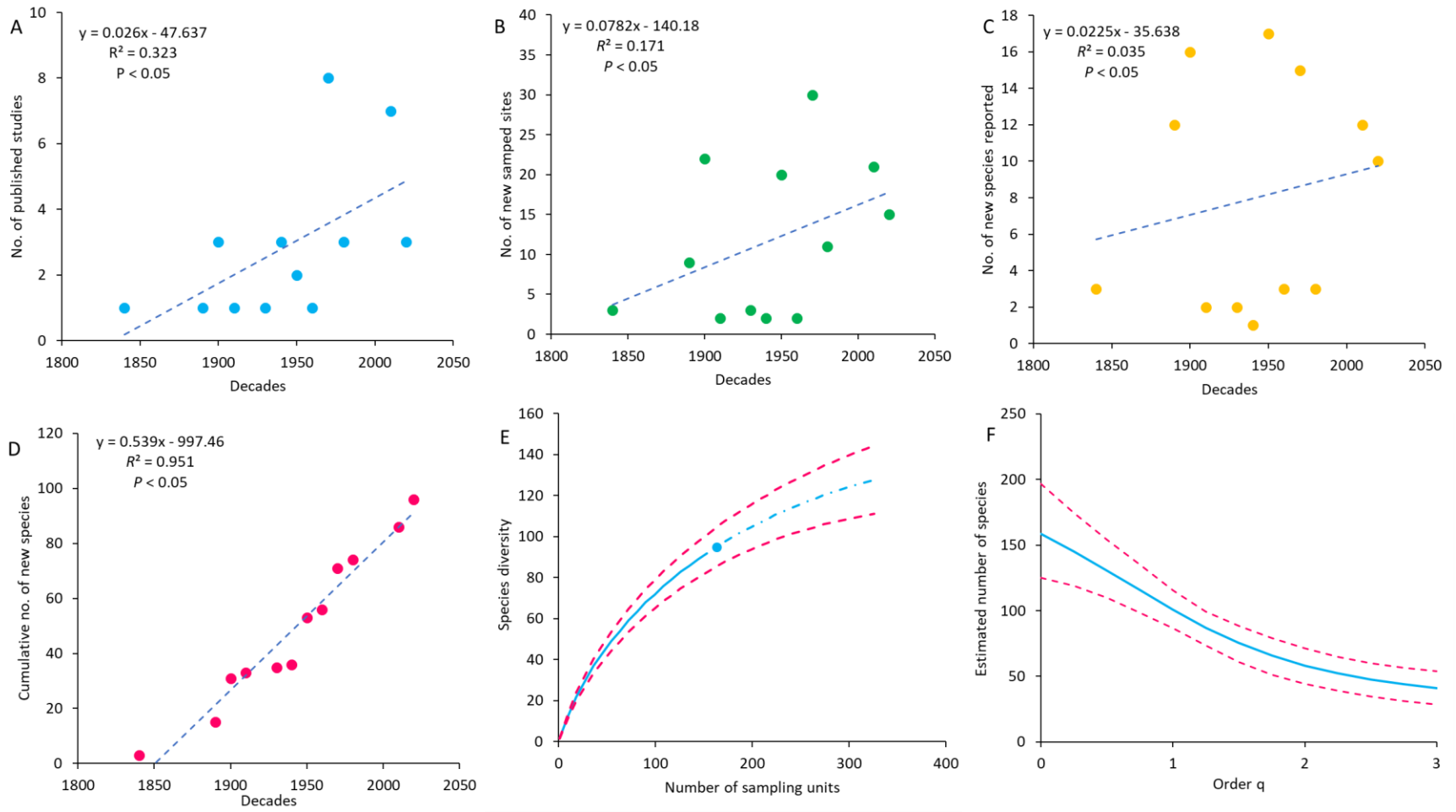
654 **Figure 4.** Beta diversity or latitudinal variation of Chilean millipede species composition.
655 The curves in the kernel density plot show the distribution of observed values for beta
656 diversity (β_{SOR} , solid curve) and its two additive components, spatial turnover (β_{SIM} ,

657 segmented curve) and nestedness (β_{SNE} , dotted curve). According to this analysis beta
658 diversity is mainly produced by millipede species turnover (β_{SIM}) among northern (arid),
659 central (temperate) and southern (polar) Chile.



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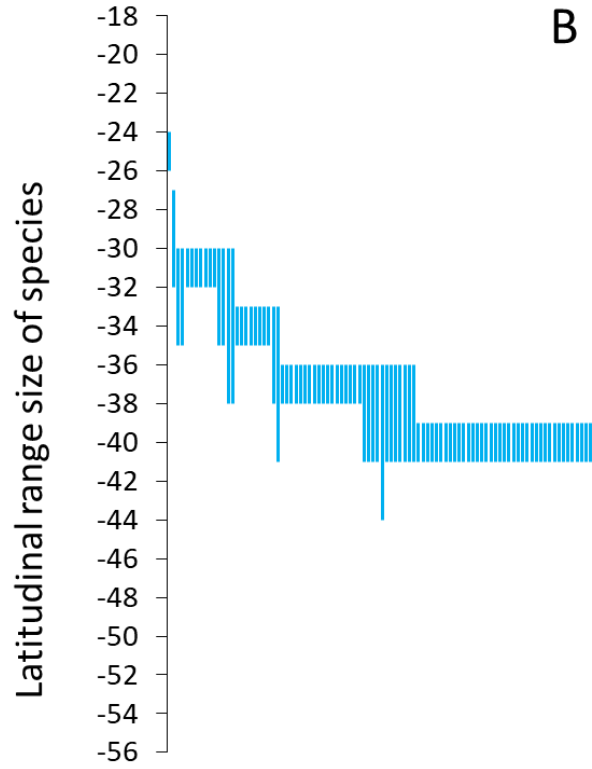
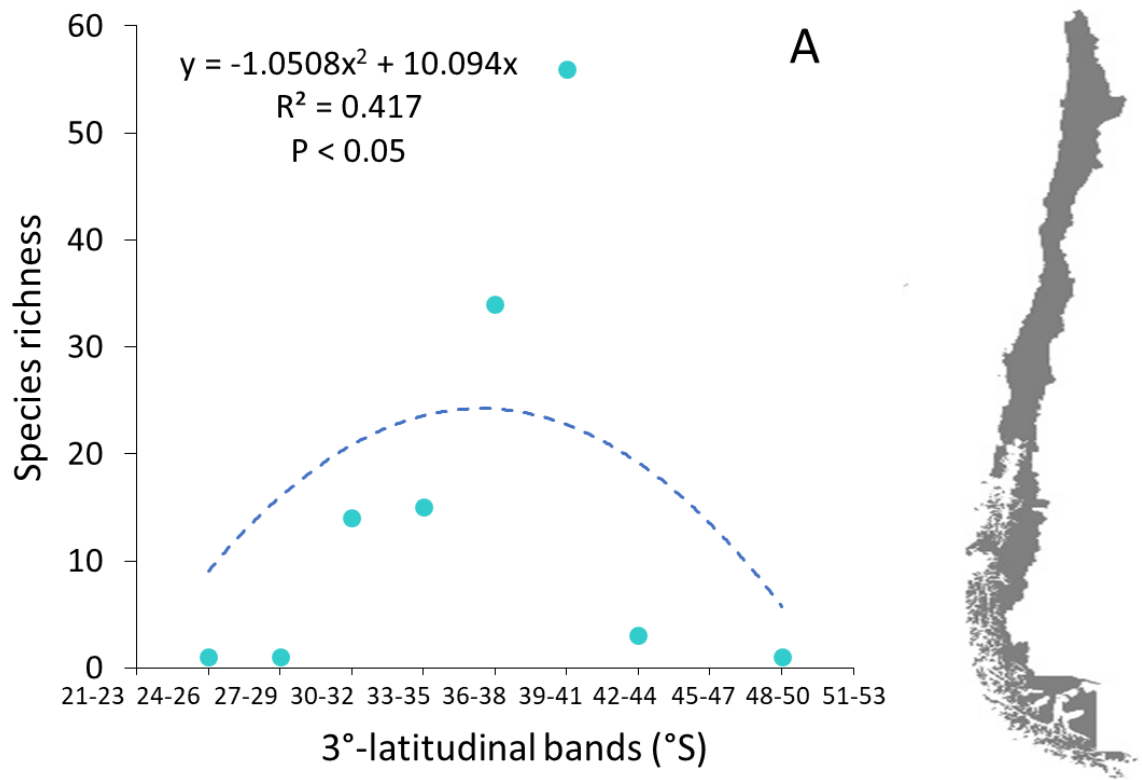
661 Fig. 1



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663 Fig. 2.

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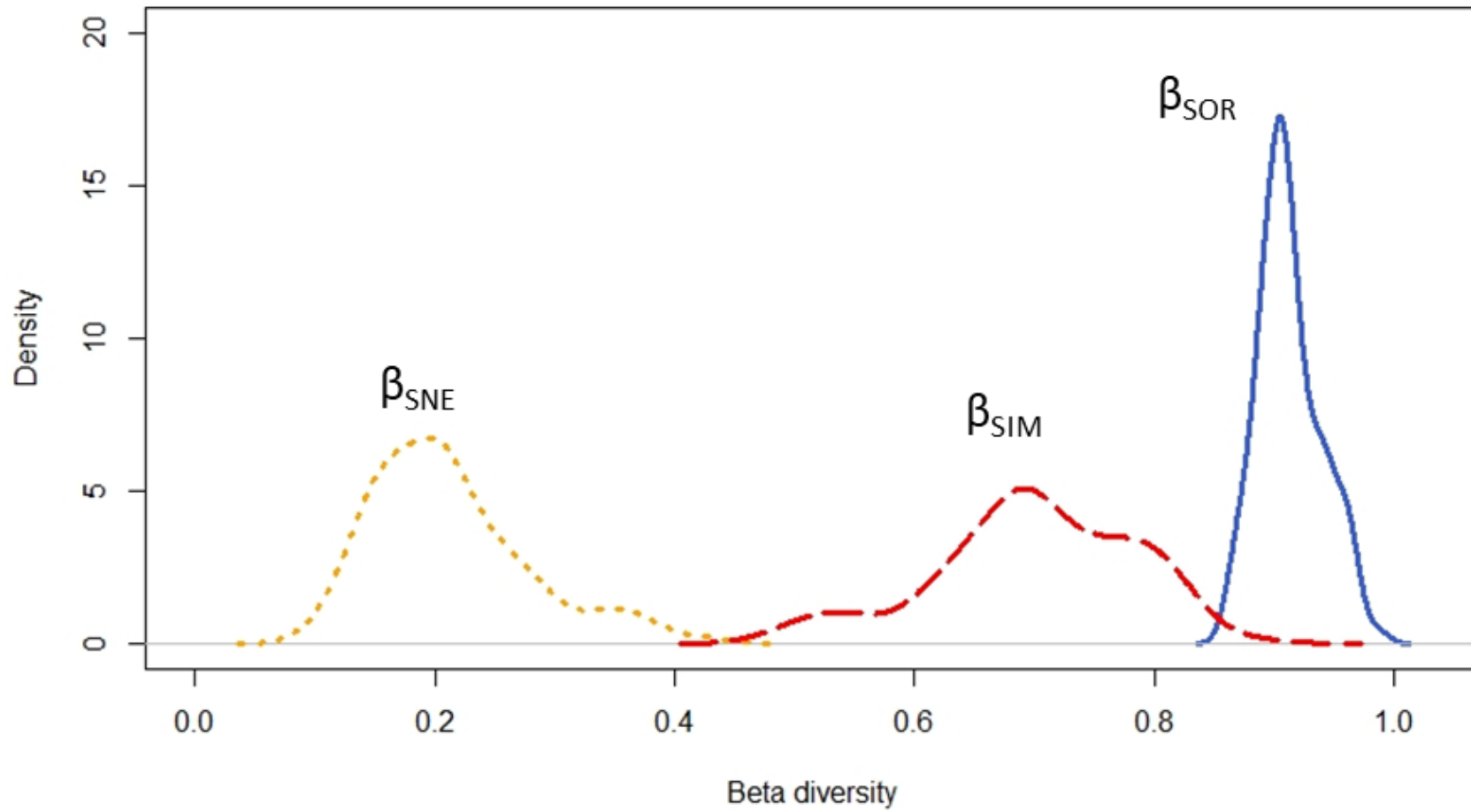
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666 Fig. 3

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671 Fig. 4

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