Geographic distribution modeling and taxonomy of *Stephadiscus lyratus* (Cothouny in Gould, 1846) (Charopidae) reveals potential distributional areas of the species along the Patagonian Forests

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Background: *Stephadiscus lyratus* (Couthouy in Gould, 1846), an endemic Charopidae from southern South America, was described from few dry shells. In the same way, species distribution is known on scatter occurrences, mainly from material deposited in Museum collections. We provide here new information on anatomy, habitat and microhabitat preferences and estimate the potential geographic distribution of the species to test if it is exclusively endemic to the Subpolar Magellanic Forest. **Methods:** Fieldwork was carried out in National Parks of the Patagonian Forests. Snails were photographed, measured and dissected for anatomical studies; shells studied with scanning electron microcopy. Estimation of the species geographical distribution (EGD) was obtained through correlative ecological niche modeling (ENM). We designed a calibration area a priori with known species points of occurrence in the Magellanic Subpolar Forests and borders of Patagonian steppe. Seven bioclimatic variables of WorldClim database were used. The best ENMs were calibrated and selected using a maximum entropy method with Maxent v3.3.3K through the R package "kuenm". Candidate models were created by combining 4 values of regularization multiplier and all possible combinations of 3 feature classes. We evaluated candidate model performance based on significance (partial ROC), omission rates (E = 5%), and model complexity (AICc). From the best models obtained, a final model was transferred to a region "G" consisting of the calibration area plus the Valdivian Temperate Forests and whole Patagonian steppe, where we hypothesize that the species could be present. Finally, we obtained binary presence-absence maps. We quantified the proportion of the occurrence points and distribution range of *S. lyratus* in different land cover categories. To explore the degree of protection of *S. lyratus*' EGD, we quantified the proportion of its distributional range within protected areas. **Results:** A be-lobed kidney, a close secondary ureter, the terminal portion of the uterus forming a compact glandular

mass and the vas deferens with a dilatation are new anatomical information provided. *Stephadiscus lyratus* inhabit cold native forest areas, mainly living on or under humid logs in contact with the ground. Main constraining variables to explain *S. lyratus* distribution in the EGD were BIO3, BIO12, BIO6 and BIO4. The potential area of distribution obtained

almost duplicates their original range (140,454 Km^2) extending to the Valdivian Temperate forests mainly in Chile. Natural and semi-natural terrestrial vegetation was predominant in the potential area of distribution of *S. lyratus.* However, only 14.7% of this area occurs within current protected areas from Argentina and Chile. The ectothermic physiological traits of this species, low dispersal capacity, and its narrow habitat requirements turns *S. lyratus* into a vulnerable species.

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17 **Abstract**

18 **Background:** *Stephadiscus lyratus* (Couthouy in Gould, 1846), an endemic Charopidae from

19 southern South America, was described from few dry shells. In the same way, species

20 distribution is known on scatter occurrences, mainly from material deposited in Museum

21 collections. We provide here new information on anatomy, habitat and microhabitat preferences

22 and estimate the potential geographic distribution of the species to test if it is exclusively

23 endemic to the Subpolar Magellanic Forest. **Methods:** Fieldwork was carried out in National

24 Parks of the Patagonian Forests. Snails were photographed, measured and dissected for

25 anatomical studies; shells studied with scanning electron microcopy. Estimation of the species

26 geographical distribution (EGD) was obtained through correlative ecological niche modeling

27 (ENM). We designed a calibration area a priori with known species points of occurrence in the

28 Magellanic Subpolar Forests and borders of Patagonian steppe. Seven bioclimatic variables of

29 WorldClim database were used. The best ENMs were calibrated and selected using a maximum

30 entropy method with Maxent v3.3.3K through the R package "kuenm". Candidate models were

31 created by combining 4 values of regularization multiplier and all possible combinations of 3

32 feature classes. We evaluated candidate model performance based on significance (partial ROC),

33 omission rates (E = 5%), and model complexity (AICc). From the best models obtained, a final

34 model was transferred to a region "G" consisting of the calibration area plus the Valdivian

35 Temperate Forests and whole Patagonian steppe, where we hypothesize that the species could be

36 present. Finally, we obtained binary presence-absence maps. We quantified the proportion of the

37 occurrence points and distribution range of *S. lyratus* in different land cover categories. To

38 explore the degree of protection of *S. lyratus'* EGD, we quantified the proportion of its

39 distributional range within protected areas. **Results:** A be-lobed kidney, a close secondary ureter,

40 the terminal portion of the uterus forming a compact glandular mass and the vas deferens with a

41 dilatation are new anatomical information provided. *Stephadiscus lyratus* inhabit cold native

42 forest areas, mainly living on or under humid logs in contact with the ground. Main constraining

43 variables to explain *S. lyratus* distribution in the EGD were BIO3, BIO12, BIO6 and BIO4. The

44 potential area of distribution obtained almost duplicates their original range (140,454 Km^2)

45 extending to the Valdivian Temperate forests mainly in Chile. Natural and semi-natural

46 terrestrial vegetation was predominant in the potential area of distribution of *S. lyratus*. However,

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49 requirements turns *S. lyratus* into a vulnerable species.

50

51 **Introduction**

52 Charopidae is a family of Punctoidea land gastropods with an extensive distribution that includes

53 South America, South Africa, Australia, New Zealand, and Oceania (Salvador et al., 2020).

54 Southern Argentina and Chile are particularly rich in endemic species of Charopidae (Miquel &

55 Cádiz Lorca, 2008). Hylton Scott (1964, 1968, 1970, 1973, 1981) was the researcher that most

56 studied and described Charopidae species in South America. Unfortunately, most of her

57 descriptions were based on a single or few dry shells, which resulted in the absence of

58 intraspecific shell variability studies. The lack of species anatomical data constitutes a barrier for

59 intra family taxonomy. Also, adequate fieldwork to estimate the current distributional range of

60 Charopidae genera and species in South America has not been done.

61 *Stephadiscus* Hylton Scott, 1981 originally included some species that are currently classified in

62 *Stephanoda* Albers, 1860, and *Stephacharopa* Miquel & Araya, 2013 (Miquel & Barker, 2009;

63 Miquel & Araya, 2013). At present, the genus is formed by six species, *Stephadiscus lyratus*

64 [designated as the genus type species], *S. celinae* (Hylton Scott, 1969), *S. mirabilis* (Hylton

65 Scott, 1968), *S. perversus* (Hylton Scott, 1969)*, S. rumbolli* (Hylton Scott, 1973)*, and S. stuardoi*

66 Miquel & Barker, 2009. The taxonomic position of *Stephadiscus striatus* Hylton Scott, 1981

67 from northeastern Argentina and Venezuela, should have to be reconsidered, as it appears to

68 belong to Punctidae (Miquel & Barker, 2009). Known *Stephadiscus* distribution is restricted to

69 Patagonia at both sides of the Andes from S 36° towards the southernmost portion of the

70 continent, including Malvinas islands (=Falklands) and southern archipelagos (Miquel & Barker,

71 2009; Miquel & Araya, 2013) and belong to the Andean region (Morrone, 2018). This

72 biogeographic area has a closer relationship to the Austral region in the Austral kingdom

73 (Morrone, 2015, 2018). Current distributional range of *Stephadiscus lyratus* (Couthouy in Gould,

74 1846) had been established on scattering points of occurrences taken from its original

75 description, and subsequent species mentions (Gould, 1845-1848; Hylton Scott, 1972, 1981;

76 Miquel & Araya, 2013, see "Species remarks" section). Erroneous taxonomic identified material

77 from Museum Collections suggested the presence of this species in the forests of northern

78 Patagonia, even though Hylton Scott (1981) stated that *S. lyratus* could be a strictly Magellanic

79   species. While *Stephadiscus celinae*, *S. perversus,* and *S. mirabilis* also occur in the Valdivian

80   rainforest sub-ecoregion of northern Patagonia, *S. rumbolli* is exclusively from the southern sub-

81   ecoregions. For this reason, there are doubts as to whether the distribution of *S. lyratus* extends

82   naturally to the Valdivian rainforest or it is restricted to southern areas.

83   Modern methodologies to estimate a species distributional area involves the ecological niche

84   models (ENMs) that relate the species distribution data (species occurrence at known locations)

85   with information about the environment (abiotic factors) (Beltramino et al., 2015; Medina,

86   Ponssa & Aráoz, 2016). The environmental variables of the localities of occurrence are also

87   informative about the species' potential distribution. Estimates of geographic range obtained by

88   ENM techniques when data are scarce, or when species are rare, have proven to be more

89   successful than those obtained by traditional methods

90   (e.g., minimum convex polygon) (Marcer et al., 2013; Syfert et al., 2014; Pena et al., 2014).

91   These also allow avoiding the potential subjective bias of experts (Fourcade et al., 2014).

92   Furthermore, identifying the combination of environmental condition in the relevant scenopoetic

93   variables offers the opportunity to discover populations isolated (Wiens & Graham, 2005). On

94   the other hand, modeling species potential areas of distribution may also provide information on

95   the geographic distribution of unknown sister species (Peterson et al., 2011).

96   Invertebrates are recognized as indicators of human disturbance, due to their low dispersal

97   capacity and their dependence on microhabitats for survival and mating. Particularly, most snails

98   that are not arboreal are dependent on litter from deciduous trees and have higher abundances in

99   multispecies forests with strong broadleaf components (Addison & Barber, 1997; Niemelä,

100   1997). Taking into account that many natural areas to date are severely fragmented or threatened

101   by human activities, obtaining information on the ecological aspects of these species is very

102   useful for future biological conservation work (Barahona-Segovia et al., 2019). Previous studies

103   in *Stephadiscus lyratus* provided few data on habitat or microhabitat preferences and therefore

104   future evaluation on its risk of extinction will need ecological information on this species. The

105   objective of this research is to provide new information on the anatomy and ultrastructure of the

106   *Stephadiscus lyratus* shell, using recently collected material, identifying and describing the

107   microhabitat where it is found, and analyzing the environmental variables that are limiting its

108   distribution with ENMs techniques.

109   Finally, we estimate its potential geographic distribution to hypothesize if *S. lyratus* can also be

110   distributed in the Valdivian Temperate Forest or if this species is endemic exclusively to the

111   Magellanic Subpolar Forest.

112

113   **Material and Methods**

114   **Study area** (Fig. 1A, B)

115   Fieldwork was carried out in the Patagonian Forests, also known as the temperate forest of

116   southern South America that extends in a narrow strip of land over the Andes Mountain between

117   35° and 55° south latitude (Armesto et al., 2001). In Argentina, this region occupies the western

118   zone from the provinces of Neuquén to Tierra del Fuego and islands of the southern Atlantic.

119   The Patagonian Forests are divided into two different areas, the northern Valdivian Temperate

120   and the southern Magellanic Subpolar Forest ecoregions *sensu* Olson & Dinnerstein (1998),

121   Olson et al. (2001) and Morello et al. (2012) or sub-ecoregions *sensu* Dos Santos et al. (2020).

122   We followed here this last mentioned classification.

123   The Valdivian Temperate Forest (Fig. 1A) covers a narrow area running from 35º to 48º south

124   latitude between Chile and Argentina. Annual precipitation varies between 1,000 mm in the

125   north and more than 6,000 mm per year in the southern part of the sub-ecoregion. This seasonal

126   precipitation decreases significantly on the eastern slope of the Andes in Argentina, where

127   rainfall of less than 200 mm is recorded only 100 km east of the Andean peaks. Maximum

128   annual average temperatures vary between 21 ºC and 13 ºC in the northern and southern ends of

129   the sub-ecoregion. Minimum annual average temperatures range from 7 ºC to 4 ºC

130   (https://www.worldwildlife.org/ecoregions/nt0404). Biogeographically, these forests share

131   floristic similarities with other temperate forests in the southern hemisphere located in Australia

132   and New Zealand (McGlone et al., 2016). However, there is a high degree of endemism not only

133   in the flora but also in the fauna at species level.

134   The southern areas of the Magellanic Subpolar Forests are well represented in Tierra del Fuego,

135   where they occupy the entire south of the province (Fig. 1A, B). However, dominant vegetation

136   is a forest of less species diversity in comparison to the Valdivian rainforest due to the low

137   temperatures and rainfall.

138   Tierra del Fuego or Fueguia is the archipelago located south of the Strait of Magallanes between

139   52° 28'S and 55° 03'S; it occupies about 66,000 km² (Fig. 1A). The main island is Isla Grande,

140   with 48,000 km² representing 70% of the surface of the archipelago, from which 21,263 km²

141   belongs to Argentina (Frangi et al., 2004). The vegetation of the island is mainly formed by a

142   Patagonian steppe of grasslands and shrubs located at the northern part, and humid deciduous

143   and evergreen forests plus peat bogs located in the center and southern portion. The trees of the

144   genus *Nothofagus* dominate the forest composition in Tierra del Fuego and constitute the most

145   austral forest in the world as part of the Magellanic Subpolar forest sub-ecoregion. The highest

146   rainfall is recorded in the south of the island, decreasing to the east and center of it. In the south

147   and west of the island it is very windy, foggy and humid most of the year with few days without

148   rain, sleet, hail or snow. The average annual temperature on the island is 5.5 °C to the north and

149   5.9 °C to the south. Above the mountains, the temperature decreases with elevation, these

150   gradients determine temperatures below zero in the winter months (Frangi et al., 2004). The Big

151   Island of Tierra del Fuego and the Islas de Los Estados were modeled by the erosive action of

152   glaciers that covered large portions of land on several occasions. The glacial topography and the

153   temperate-cold and humid climate that prevail throughout the year, favored the formation of the

154   peat bogs that are now part of the Fuegian landscape.

155

156   **Fieldwork and specimen collections**

157   Fieldwork was carried out in the Magellanic Subpolar Forests of Tierra del Fuego National Park

158   (DRPA 146/2019) and other non-preserved areas in Isla Grande of Tierra del Fuego, Argentina,

159   during December 2018 - January 2019 (Figs. 1C, D). In the Valdivian Temperate Forests,

160   fieldwork was done within Los Alerces National Park and Puerto Blest in Nahuel Huapi National

161   Park (DRPA 1674, DFyFS1/19) during January 2020. We qualitatively searched for land snails

162   along transects for half an hour in each collecting site. Searching was mainly focused on

163   microhabitats that seem to be most favorable for snails, such as between exposed roots of trees,

164   under the bark of trees, under rocks, or under tree trunks lying on the forest floor in contact with

165   soil. In each collecting site, we recorded altitude and geographic coordinates. We also took

166   samples of 50x50 cm quadrats of leaf litter plus 2 cm of topsoil from moist microhabitats.

167   Samples were placed in plastic bags and posteriorly sieved through three decreasing mesh widths

168   (3, 1.5, and 0.5 mm) in the laboratory of the Centro Austral de Investigaciones Cientificas

169   (CADIC-CONICET, Tierra del Fuego) under a stereoscopic microscope. All snails collected

170   were photographed alive before relaxing them in water for 24 hours, posteriorly fixed in ethanol

171 96%, and preserved in ethanol 70% for anatomical studies. Several specimens were also fixed

172 directly in ethanol 96%, without relaxation in water, for future molecular studies. All the

173 material collected was deposited in the Malacological Collection of the Instituto de

174 Biodiversidad Neotropical (IBN, CONICET-UNT, Tucumán, Argentina).

175 **Morphology**

176 Ten adult shells were photographed using a Zeiss Stemi 508 with ActionCam and measured

177 using the software ImageJ 1.49 (Schneider, Rasband & Eliceiri, 2012). Shell measurements

178 selected, on dorsal and lateral views, are: major shell diameter (DM), shell minor diameter (Dm),

179 shell height (H), apertural height (Hap), and apertural diameter (Dap). The number of shell

180 whorls was calculated following the Kerney & Cameron (1979) methodology. Photographs and

181 shell measurements were carried out at the CADIC in Tierra del Fuego. For anatomical

182 information, dissections of 7 adult specimens were studied under a Leica MZ6 stereoscope.

183 Illustrations of the dissected organs/systems were carried out with the aid of a camera lucida. The

184 terms proximal and distal refer to the position of an organ or part of an organ in relation to the

185 gamete flow from ovotestis (proximal) to genital pore (distal) as in previous works (Cuezzo,

186 2006; Cuezzo et al., 2018). The distinction of the limits between the epiphallus and penis is

187 based on the internal sculpture of their inner wall. Shell ultrastructure was studied and described

188 using a SEM Zeiss Supra 55VP at the Integral Center of Electron Microscopy (CIME) of the

189 National University of Tucumán, Argentina (UNT).

190

191 **Occurrence records**

192 We compiled a total of 60 geographic records of *Stephadiscus lyratus* from field surveys,

193 museum collections, and scientific articles (Fig. 1, Table S1). Twenty new reliable records were

194 obtained through fieldwork in Tierra del Fuego. To avoid primary taxonomic sources of error

195 from specimens deposited at different Museums, we corroborated the taxonomic identification of

196 specimens according to their shell morphology. The malacological collections of IBN (Instituto

197 de Biodiversidad Neotropical, Tucumán, Argentina), MACN-In (Museo Argentino de Ciencias

198 Naturales Bernardino Rivadavia, Buenos Aires, Argentina), and MLP (Museo de La Plata,

199 Buenos Aires, Argentina) were revised accordingly. Other sources of information were

200 electronic databases from the Smithsonian National Museum of Natural History (NMNH),

201 Museum of Comparative Zoology (MCZ), and Academy of Natural Sciences in Philadelphia

202 (ANSP). We used Google Earth to georeferenced localities of occurrences that lacked

203 geographic coordinates. From the total number of records, we removed duplicate records, which

204 left 37 unique sites with trustable geographic information. To avoid over-representation of

205 certain environmental combinations, we spatially filtered records based on a 5 km radius, which

206 left 24 localities, then we split them in 30% for test and 70% for train the ecological niche model,

207 both functions implemented in R-package "ellipsenm" (Cobos et al., 2020).

208

209 **Estimations of potential geographic distributions (EGDs)**

210 Estimates of the geographical distribution (EGD) of *S. lyratus* were obtained through correlative

211 ecological niche modeling (ENM). To adequately model the species niche, we used the

212 theoretical Biotic-Abiotic-Mobility framework (Soberón & Peterson, 2005). Only abiotic and

213 mobility factors were taken into account because the biotic components (i.e., biotic interactions)

214 are virtually impossible to spatially quantify thoroughly at regional scales (Peterson et al., 2011).

215 As for the mobility component, we designed a calibration area a priori "M" (Barve et al., 2011)

216 considering sub-ecoregions with known species points of occurrence, i.e., in the Magellanic

217 Subpolar Forest and the southern portion of Patagonian steppe. To delineate abiotic components,

218 we used 15 bioclimatic variables of the WorldClim database (Hijmans et al., 2005) at a spatial

219 resolution of 30 arc seconds (~1 km^2), excluding the four variables that combine temperature and

220 precipitation owing to be known artifacts (Escobar et al., 2014). We clipped the environmental

221 data layers to the calibration area defined. To eliminate one variable per pair of highly correlated

222 variables (r ≥ 0.85), we performed a correlation analysis through the "ntbox" package (Osorio-

223 Olvera et al., 2020). Thus, seven bioclimatic variables were selected for the analyses: BIO1 =

224 Annual Mean Temperature, BIO2 = Mean Diurnal Range (Mean of monthly (max temp - min

225 temp)), BIO3 = Isothermality (BIO2/BIO7) (* 100), BIO4 = Temperature Seasonality (standard

226 deviation *100), BIO6 = Min Temperature of Coldest Month, BIO12 = Annual Precipitation, and

227 BIO15 = Precipitation Seasonality (Coefficient of Variation).

228 The best ENMs were calibrated and selected using a maximum entropy method with Maxent

229 v3.3.3K (Phillips, Anderson & Schapire, 2006) through the R package "kuenm" (Cobos et al.,

230 2019). Then, candidate models were created by combining four values of regularization

231 multiplier (0.1, 0.5, 1, 2), and all possible combinations of three feature classes (linear = l,

232 quadratic = q, product = p). We evaluated candidate model performance based on significance

233 (partial ROC, with 100 iterations and 50 percent of data for bootstrapping), omission rates (E =

234 5%), and model complexity (AICc). Best models were selected according to the following

235 criteria: (1) significant models with (2) omission rates ≤5%. From among this set, models with

236 delta AICc values of ≤2 were chosen as final models. The final model was created using the

237 spatially filtered records (24 occurrences) and the selected parameterizations. We produced 100

238 iterations with five replicates by bootstrap, with logistic outputs. We ran the models with no

239 extrapolation or clamping to avoid artificial projections based on extreme values of the

240 bioclimatic variables (Elith et al., 2011; Owens et al., 2013; Merow et al., 2014; Guevara et al.,

241 2018). Then, the final model was transferred to a region "G" consisting of the calibration area

242 plus the Valdivian Temperate Forest and Patagonian steppe regions, where the species could be

243 also present as its congeners. To identify extrapolation risk areas in model transfers, we

244 performed MOP analyses (Owens et al., 2013). This function calculates multivariate

245 environmental distances between sites across the transfer region (G) and the nearest portion of

246 the calibration region to identify areas that have a condition of strict or combinational

247 extrapolation.

248 Finally, to obtain binary presence-absence maps, we used a minimum presence threshold,

249 modified to consider presence data errors (Peterson, Papeş & Eaton, 2007) implemented in R-

250 package "ENMGadgets" (Barve & Barve, 2019). This modified threshold included 100% of the

251 presence points minus the dataset error (E) (Phillips & Dudík, 2008); we assumed E = 5% based

252 on our experience of obtaining the presence data. This conservative method minimizes the

253 commission error rate.

254

255 **Spatial analysis**

256 To spatially characterize the distribution of *Stephadiscus lyratus* we quantified the proportion of

257 occurrences points and of their potential distribution in different categories of the land cover of

258 the Globcover 2009 dataset (Arino et al., 2012). The 22 land cover categories (e.g., Closed to

259 open (>15%) broadleaved evergreen or semi-deciduous forest (> 5m), Mosaic forest or shrubland

260 (50-70%) / grassland (20-50%)) are according to the UN Land Cover Classification System

261 (LCCS) (Di Gregorio, 2005).

262 To explore the degree of protection of *S. lyratus´* EGD, we quantified the proportion of its range

263 within protected areas. We take into account the protected areas categories I to VI assigned by

264 the International Union for Conservation of Nature (IUCN) (Dudley, 2008) and the National

265 Parks, even though these are not included in any IUCN category. Shapefiles of the protected

266 areas were obtained from the World Database of Protected Areas (IUCN & UNEP-WCMC,

267 2020) and http://mapas.parquesnacionales.gob.ar/.

268

269 **Results**

270 **Systematic account**

271 Superfamily Punctoidea Morse, 1864

272 Family Charopidae Hutton, 1884

273 Subfamily Charopinae Hutton, 1884

274

275 ***Stephadiscus*** Hylton Scott, 1981

276 *Type species*: *Helix lyratus* Couthouy "in" Gould, 1846, by original designation.

277

278 **Species description** (Figs 2, 3, 4)

279 *Stephadiscus lyratus* (Couthouy "in" Gould, 1846)

280   *Helix lyrata* Couthouy "in" Gould, 1846: 167; 1852: 39.

281   *Patula rigophila* Mabille, 1886: 123.

282   *Amphidoxa lirata* Pilsbry, 1894: 41.

283   *Amphidoxa (Stephanoda) lyrata* Smith, 1905: 339

284   *Stephanoda lyrata Pilsbry,* 1911, 518; Hylton Scott, 1972: 67.

285   *Stephadiscus lyratus* Hylton Scott, 1981: 124; Miquel and Araya, 2013: 230.

286

287 *Syntype*: MCZ 88297 MCZ: Museum of Comparative Zoology, Harvard University

288 *Type locality*: Orange Harbor, Tierra del Fuego [according to Johnson (1964): located at the west

289 side of Nassau Bay].

290

291 **Morphology** (Figs 2-4)

292 *External body morphology* (Fig. 2A-B)

293 Animal black with lighter foot and mantle collar around shell aperture. A deep longitudinal

294 furrow, the pedal groove, runs parallel to the foot edge on each side and above it. Dark irregular

295   spots are seen for transparency through the shell, although some specimens are lighter. Foot

296   short, triangular pointed, not to slightly surpassing the shell diameter.

297   *Shell* (Figs. 2 C-E; 3A-E): Discoidal, 3 ½ to 4 convex regularly expanded whorls, low spire

298   depressed, not planispiral as apex elevated, fragile (DM=4,247-5,041mm; Dm=3,444 -

299   4,487mm; H= 2,283-2,432mm) with brown caramel to light whitish color (Figs. 2 A-E).

300   Protoconch with 35 - 40 axial delicate, smooth, elevated ribs separated at regular intervals (Fig.

301   3A). Spaces between protoconch ribs with thinner axial costulae. Protoconch not clearly

302   delimited from the teleoconch, and similarly sculptured. Teleoconch surface with major axial

303   ribs (Figs. 3B-D), interspace between them of 4-7 μm filled with 5 to 7 micro radial costulas in

304   between major ribs, nodules at regular intervals supporting ribs, giving the appearance of radial

305   cords (Figs. 3B-C). Deep irregular suture (Fig. 3D). Circular aperture, not descendent, with sharp

306   peristome (Hap=1,861-2,110; Dap= 1,809-1,998). Umbilicus 1/3 or slightly less of body whorl

307   major diameter, with same sculpture as nepionic portion of the shell (Fig. 3E).

308   *Pallial system* (Fig. 4A): Pulmonary roof dark with black spots and whitish small granules over

309   the surface. Spots and granules visible through shell. Pulmonary sac short occupying 1/4 of body

310   whorl. Kidney triangular, bilobated, with pericardial side lobe overlapping pericardium. Rectal

311   side kidney lobe bigger than pericardial arm. Principal pulmonary vein short, slender, not

312   branched, smoothly marked. Remaining pulmonary roof smooth with no other veins. Secondary

313   ureter present, close along its length, parallel to rectum. Pallial gland absent.

314   *Jaw and radula*: Jaw consist on narrow vertical plates, slightly arched, cream colored. Radula as

315   described by Hylton Scott (1970).

316   *Reproductive system* (Figs. 4B-E): Albumen gland shapeless, roughly globular, rounded margins.

317   Spermoviduct formed by prostate and uterus fused together. Uterus divided in two portions,

318   proximal short, cylindrical, continuous to albumen gland, distal expanded in rounded glandular

319   chamber (Figs. 4B, C). Free oviduct cylindrical, short. Bursa copulatrix sac round, resting over

320   uterus distal portion. Duct of bursa copulatrix basally thickened, progressively decreasing in

321   diameter towards the sac (Fig. 4D). Vagina as long as bursa copulatrix duct, distally widened,

322   featuring three thick, longitudinal pilasters on the interior wall. Vas deferens cylindrical, narrow

323   in diameter, short, running from basal prostate towards peni-oviducal angle, inserting into

324   epiphallus. Penial retractor thin, inserted in penis. Penis cylindrical, thicker than epiphallus, with

325   a sac-like appendix in upper portion (Fig. 4C-E). Short verge in upper penial chamber, inner

326   penial wall with short pilaster noticeable towards middle penis length. Epiphallus reflected over

327   penis, shorter, thinner ending in a short finger-like flagellum (Fig. 4E). Vas deference delated

328   before inserting into epiphallus anteriorly of penial retractor insertion, dilatation as long as

329   flagellum, giving appearance of fork ending epiphallus.

330

331   **Microhabitat characterization**

332   Rainforests provide a variety of living spaces where snails can feed, crawl, and live. Although

333   micro snails are usually associated with leaf litter, *Stephadiscus lyratus* was mainly found living

334   on or under the bark of fallen trees or under humid logs in contact with the ground (Figs. 1C, D).

335   We found actively crawling snails only on tree barks or on moss logs. This species is not

336   considered to be arboreal or semi-arboreal. No specimens were found in living trees, nor in their

337   leaves or shrubs, the majority of alive snails were found under fallen decaying logs in contact

338   with the ground. During the hibernation period in wintertime, these microhabitats in contact with

339   soil can act as a buffer and help the species to survive during extreme freezing conditions. Dry

340   shells were recovered from soil samples, but in general, they were worn out. Feeding habits are

341   not known, but probably are associated to a diversity of fungi from the decaying wood, an

342   important food resource for snails. Species of the genus *Radiodiscus* occur in sympatry with *S.*

343   *lyratus*. In places outside protected areas where the forest shows some degree of alteration, living

344   snails were scarce or difficult to find.

345

346   **Species Remarks**

347   The history of the species discovery as well as the problem of the species authorship are

348   explained in Supplementary Material (See Appendix).

349

350   *Comparison with species of the same genus*: *S. lyratus* has the largest shell diameter (DM= 5.5

351   mm) among all species classified in *Stephadiscus*. It is a very conspicuous species regarding its

352   shell coloration and sculpture. Although *S. perversus* is similar in shell coloration, it cannot be

353   confused with *S. lyratus* because it is sinistrorse and has a smaller shell (DM=2, 8; H= 1.5mm).

354   *S. lyratus* is also similar in shell sculpture and general shape to *S. stuardoi* (DM= 2.0-2.02, H=

355   0.85), but clearly differs from this species in its larger shell diameter and the absence of weak

356   spiral threads in the teleoconch. In the original description, Couthouy in Gould mentioned that *S.*

357 *lyratus* could be a synonym of *Helix costellata* d'Orbigny, 1835 (now *Zilchogyra costellata*

358 (d'Orbigny, 1835)). However, *H. costellata* is distributed in the Humid Pampa ecoregion in

359 Buenos Aires, Argentina, an extra Patagonian area with completely different ecological

360 requirements. *H. costellata* (DM=4 mm, H= 2 mm) is smaller in shell diameter and height than

361 *S. lyratus* and its protoconch is a smooth surface.

362 *Stephadiscus lyrata* and *S. mirabilis* are the only species of the genus with known anatomies.

363 Both show a rounded glandular mass, identified as a "dilated sac" by Hylton Scott (1970) at the

364 base of the spermiduct, in the distal genitalia. A similar structure is also present in

365 *Stephacharopa testalba* (Hylton Scott, 1970). Most of the described species of the genus have

366 been originally established only on single or two dry shells (Table S2), and after their discovery,

367 rarely fresh specimens have been collected in their area of distribution.

368

369 *Comparison with related genera*: *Stephadiscus* is defined by having plane-convex whorls,

370 presence of a protoconch, and teleoconch with similar ornamentation consisting of thin, nodulose

371 ribs, without a marked limit between the protoconch and the teleoconch (Hylton Scott, 1981;

372 Miquel & Araya, 2013). Therefore, the transition of protoconch towards teleoconch is barely

373 distinguished. These ribs increase in height towards the body whorl, with thinner costula in the

374 interspaces. *Stephadiscus* is different from *Stephacharopa* Miquel & Araya, 2013 because in the

375 latter genus, the sculptured protoconch is dissimilar to the teleoconch ornamentation while in the

376 former, the sculptured protoconch is similar to the one present in the teleoconch. *Stephadiscus*

377 differs from *Stephanoda* mainly in the sculpture of the protoconch, since the latter possesses a

378 reticulated pattern. Differences in anatomy are not possible to be established for the lack of

379 studies on these genera. Other South American charopid genera, such as

380 *Lilloiconcha* Weyrauch, 1965 and *Zylchogyra* Weyrauch, 1965 can reach similar shell sizes but

381 differ from *Stephadiscus* in general shell shape and in that their protoconch is smooth (Miquel &

382 Araya, 2013). *S. lyratus* shows a specialized vas deferens-epiphallus junction as other

383 Charopinae from the Pacific Islands described by Solem (1982), marking a difference with

384 subfamilies Semperdoninae, Trukcharopinae, and Rotadiscinae.

385

386 **Estimations of potential geographic distributions (EGDs)**

387 We obtained 24 candidate models statistically significantly better than null expectations (i.e.,

388 predictions from the models coincided with testing occurrence data more frequently than would

389 be expected by random association of points and a prediction of that areal extent) (Table S3).

390 From these, only one final model was selected that was statistically significant and met the AICc

391 criteria (two of three selection criteria) (Table S4). The chosen settings were linear, quadratic,

392 and product features and 0.1 of regularization multiplier. The bioclimatic variables that most

393 contribute to the model were BIO3 = Isothermality (BIO2/BIO7) (×100), BIO12 = Annual

394 Precipitation, BIO6 = Minimum Temperature of Coldest Month, and BIO4 = Temperature

395 Seasonality (standard deviation of mean month temperature * 100) (47%, 17%, 12% and 11.5%

396 percent of contribution, respectively). Response curves also gave an indication of the range

397 under which the variable reaches its optimum suitability. BIO3 quantifies how large the daily

398 temperature fluctuations are relative to annual oscillations. A value of 100 indicates that diurnal

399 temperature range is the same as the annual temperature range, while lower values indicate that

400 day to night temperature oscillations are smaller than annual temperature fluctuations

401 (O'Donnell & Ignizio, 2012). The optimum of suitability for isothermality is around 43% to

402 55%, from here decreased abruptly to cero (Fig. 5A). BIO4, BIO6 and BIO12 displayed a bell-

403 shaped response of increased suitability as the variable increases above a certain value (Fig. 5B-

404 D). The optimum suitability of BIO4 is around 2750, this is a measure of temperature change

405 over the course of the year, the larger the value (standard deviation of mean monthly temperature

406 x 100), the greater the variability of temperature (O'Donnell & Ignizio, 2012). The optimum

407 suitability of BIO6 is between -2 and 0 ºC (around -1°C, Fig. 5C), this is a measure of minimum

408 cold temperatures through the year. In the case of BIO12 the species had its maximum suitability

409 in the 500–600 mm within a narrow range that abruptly decreased when the precipitation

410 increased above this threshold (Fig. 5D).

411

412 **Spatial analysis**

413 The known area of distribution of *S. lyratus* was approximately 72,672 km², mainly coincident in

414 the southern portion of the Magellanic Subpolar Forest (below –51º of latitude), at both sides of

415 the Andes and marginally in the southern part of Patagonian steppe in Tierra del Fuego (Fig.

416 6A). The MOP analysis (Fig. S1) indicated that areas with the most dissimilar variables

417 conditions (i.e., where one or more environmental variables are outside the range present in the

418 training data) were found beyond the potential distributional areas predicted by the model in the

419 "G" area.

420 When the final model is transferred to region "G", we found that the potential area of distribution

421 almost duplicates their original range (140,454 Km^2). This new region extends mainly to the

422 Valdivian Temperate Forest between –40 and –46 latitude, mostly in Chile and a small portion of

423 the Argentina, while towards the Patagonian steppe increase marginally (Fig.6B).

424 Natural and semi-natural terrestrial vegetation was predominant in the occurrence points and in

425 the potential area of distribution of *S. lyratus*. The occurrences points overlap a 33% and the

426 EGD a 48% with woody trees (closed to open (>15%) broadleaved evergreen or semi-deciduous

427 forest (>5m)), while the overlap with shrub (closed to open (>15%) (broadleaved or needle-

428 leaved, evergreen or deciduous shrubland) was a 31% and 21%, respectively (Table 1).

429 The proportion of the potential distribution area in protected areas was 14.7%, occurring in 16

430 protected areas, from which six of them are located in Argentina while the remaining are from

431 Chile. The higher proportional area protected is due to National Parks "Alberto D'Agostini" and

432 "Yendegaia" (Chile), and Multiple Use Provincial Reserve "Corazon de la Isla Tierra del Fuego

433 (Argentina). Taking into account the category of management of IUCN, nine are category II

434 National Parks and Ib Wilderness Nature Reserve; the six remaining are category IV Forest

435 Reserve and VI Multiple Use Provincial Reserve (Table 2).

436

437 **Discussion**

438 *Taxonomy and Species Morphology*

439 Features of the gastropod shell have always been an essential and convenient source of

440 taxonomic information. However, it is well recognized that shell characters such as shape,

441 coiling patterns, and ribbing can be convergent and often mask crucial differences in anatomy

442 (Stanisic, 1990; Barker, 2001). Hylton Scott, understanding the value of anatomical information,

443 was the only researcher to provide anatomical descriptions of some South American charopids

444 such as *Stephacharopa testalba, Stephadiscus lyratus, S. mirabilis, Zilchogyra leptotera*

445 (Mabille, 1886). Recently, a study on Punctoidea phylogeny provided molecular information on

446 some charopid species (Salvador et al., 2020). *Stephadiscus lyratus*, as all the species of the

447 genus*,* has similar ornamentation in the shell protoconch and in the teleoconch, without a

448 marked limit between them. The type of ornamentation and similitude between protoconch and

449   teleoconch differences *Stephadiscus* from all other South American charopid genera (Miquel &

450   Cádiz Lorca, 2008; Miquel & Barker, 2009; Miquel & Araya, 2013). Anatomical information

451   provided proves to be an essential source of characters relevant for future taxonomic and

452   phylogenetic studies. The presence of a be-lobed kidney with the rectal side lobe bigger than the

453   pericardial portion, plus the presence of a close secondary ureter, clearly indicate that *S. lyratus*

454   belongs to Charopidae, differencing it from the Endodontidae. Solem (1982) raised these

455   characters as the main differences between both families. The terminal portion of the uterus

456   (spermoviduct), forming a compact glandular mass, is also a striking character that has only been

457   mentioned before for *Stephacharopa testalba*. Along with this, the insertion of the vas deferens

458   into the epiphallus through a dilatation constitutes unique structures of *S. lyratus*.

459

460   *Estimation of the potential geographical distribution (EGD) and spatial analysis.*

461   The new records obtained were associated with native areas of the Magellanic Subpolar Forest

462   sub-ecoregion in Argentina. The transferred model shows a potential distribution of *S. lyratus* to

463   the Valdivian Temperate Forest, spreading the known area to a new sub-ecoregion,

464   corresponding mainly to the area of this mentioned zone in Chile. Although, no specimens of *S.*

465   *lyratus* have been found in the Valdivian forest areas in Argentina (Nahuel Huapi and Los

466   Alerces National Parks), these surveyed areas are outside to the east of the potential area

467   predicted by the model. Thus, the potential area of distribution of *S. lyratus* is coincident with the

468   Magellanic Subpolar Forest and the Valdivian Temperate Forest (more towards Chile) together

469   with its boundaries with the Patagonian Steppe ecoregion. The obtained hypothesis of the

470   potential distribution of *S. lyratus* will direct the next exploratory surveys with the expectation to

471   find new populations in the future.

472   The biogeographic Valdivian Forest province according to Kuschel (1960) and Morrone (2018)

473   has faunistic relationships with Magellanic Forests, probably due to the fact that both regions

474   have been isolated from other South American forests since the Neogene (Axelrod, Kalin Arroyo

475   & Raven, 1991). In addition, the cooling cycles followed by warmer periods in the Quaternary

476   caused the contractions and expansions of the temperate forests (Villagrán & Hinojosa, 1997),

477   and some areas in the coastal range remained free of ices and may have been the source for the

478   recovery of the forest biota (Smith, 2017).

479   From the seven environmental variables used in the EGD analysis of *S. lyratus,* the main

480   constraining variables are the temperature (Isothermality, Minimum Temperature of Coldest

481   Month, and Temperature Seasonality) and Annual Precipitation.

482   Other studies using native snails in South America that analyzed the role of abiotic factors in

483   relation to their distribution are scarce e.g., the case of *Megalobulimus sanctipauli* (Ihering &

484   Pilsbry, 1900). This kind of studies for native micro snails are virtually nonexistent.

485   *Megalobulimus sanctipauli,* known to inhabit the Atlantic Forest, showed temperature and

486   rainfall as the determinant factors of their geographic distribution (Beltramino et al., 2015). In

487   the case of *Achatina fulica* Bowdich, 1822, an exotic land gastropod in South America,

488   Temperature Seasonality, and Mean Temperature of the coldest quarter were the variables that

489   contribute the most to the model when they were used alone (Vogler et al., 2013). In the case of

490   *S. lyratus*, the bell shape of environmental suitability for the Minimum Temperature of Coldest

491   Month, Seasonality Temperature and Annual Precipitation apparently show that the studied

492   species try to avoid extreme temperature and precipitations oscillations. The minimum

493   temperature of the coldest month shows predicted suitable conditions at sub-zero temperatures. It

494   suggests that this climatic variable is relevant for its optimal growing conditions and in particular

495   in relation to the species winter survival. Indeed, *S. lyratus* is found in the Magellanic Subpolar

496   Forest where winter temperatures can drop below 0°C. Empirical data on the life history of small

497   land snail species in their natural habitat are hardly available worldwide. There are also very few

498   data on gastropod cold hardiness, especially on land snail species of small sizes. Ansart &

499   Vernon (2003) sustained that two alternatives exist for organisms living in areas that freeze in

500   winter, such as the southern forest in Patagonia: move to an unfrozen habitat or face freezing

501   conditions. For this last category, avoid freezing by extensive supercooling (freezing avoidance)

502   or survive freezing of the body fluids (freezing tolerance) are the only possibilities. Freezing

503   avoidance, involves the choice of a hibernation site, which buffers the temperature differences,

504   and which permits avoidance of inoculative freezing (e.g., by contact with ice). During

505   hibernation, the snails rapidly suppress their metabolism and minimize water loss using a

506   discontinuous gas-exchange pattern (Koštál et al., 2013). We sustain that *S. lyratus* find

507   favorable overwintering microhabitat in soil, under tree bark or under fallen tree trunks in

508   contact with soil, which is well buffered from temperature and moisture fluctuations allowing the

509   species to survive during winter freezing.

510   Decaying wood can absorb and retain water for several weeks during periods of low

511   precipitation, providing a buffer from microclimate extremes (Jordan & Hoffman Black, 2012).

512   Land gastropods require moisture for respiration and locomotion, and humid microenvironments

513   are known to be a prerequisite for the occurrence of many land mollusk species. However,

514   excessive wet extremes that lead to flooded soils for long periods are not tolerated by most micro

515   snail species that buried in the soil. This can be a restrictive situation to *Stephadiscus lyratus*

516   occurrence as it is showed by the predicted environmental suitability in a narrow range of annual

517   precipitation not surpassing around 1500 mm per year. Also, this would explain the occurrence

518   of *S. lyratus* in humid areas of Magellanic subpolar forest, and the projected potential

519   environments in some regions of northern Valdivian Temperate Forest, which featured by 1000

520   mm of precipitation per year (https://www.worldwildlife.org/ecoregions/nt0404).

521

522   *Stephadiscus lyratus, a vulnerable species to protect*

523   *Stephadiscus lyratus* inhabit mostly woody areas of native forests. The preferred microhabitats of

524   the species are sites on or under the bark of fallen trees or under humid logs in contact with the

525   soil. These microhabitats are less frequent in disturbed forest areas with high human pressure

526   located in Tierra del Fuego outside the National Park, where specimens were difficult to find

527   alive. In addition to microclimate effects, coarse woody debris has a significant influence on

528   gastropod food availability. Dead and decaying wood promote a diversity of fungi, an important

529   food resource for many snails

530   Land gastropods are suffering habitat loss and competition from introduced species (more

531   numerous and prolific every year), although are regarded as non-charismatic groups for

532   conservation purposes (Régnier et al., 2009; 2015). In the case of Orthalicoidean land snail in

533   Argentina, only 3% of their average species distribution ranges are safeguarded within current

534   protected areas, showing that the existing protected areas system is not effective at all for the

535   protection of this invertebrate group (Ovando et al., 2019). In the present study, we found that

536   14,5 % from a total current distributional area of 72,672 km^2 of *S. lyratus* is inside the system of

537   protected areas. However, it is important to emphasize the threats and pressures of land-use

538   change such as tourism, logging and frequent fires that compromise not only areas inside the

539   southern National Parks but also the matrix that surrounds them. In fact, 700–1000 ha are logged

540   each year (from 1980 to 2003) in Argentina, Tierra del Fuego (Gea-Izquierdo et al., 2004). In

541   addition, extensive livestock holdings, aquaculture, and tourism are advancing into formerly
542   undisturbed areas. In the Chilean Magellanic forests between 53.1 % and 68.1 % of this land is
543   influenced by human activity in some way (Inostroza, Zasada & König, 2016). In this context,
544   habitat loss for land gastropod conservation is very worrying. Moreover, the protected areas in
545   Argentina were created for the protection of plants (Ortega-Baes et al., 2012) and/or vertebrates
546   (Tabeni, Bender & Ojeda, 2004; Arzamendia & Giraudo, 2004; Corbalán et al., 2011; Tognelli et
547   al., 2011), ignoring the invertebrates even when their importance has been proven (Chehébar et
548   al., 2013). This situation is a worldwide problem since there are more than a million invertebrate
549   described species but only 3,500 are protected (Baillie, Hilton-Taylor & Stuart, 2004; Brooks et
550   al., 2004, 2006; Nieto et al., 2017). We sustain that *S. lyratus* find favorable overwintering
551   microhabitat in soil or under stones in contact with soil, which is well buffered from temperature
552   and moisture fluctuations allowing them to survive during winter freezing.
553   The combination of the ectothermic traits of this species, low dispersal capacity, probable low
554   fecundity producing only few eggs, and its narrow habitat requirements (forest specialist) turns
555   *S. lyratus* into a vulnerable species. Along with habitat loss through human land use, climate
556   change is a major contributor to biodiversity loss in the 21st century (Lee et al., 2015). However,
557   terrestrial gastropods have so far received little attention regarding the potential impact of current
558   rapid climate change on their distribution, compared with other taxa (Lee et al., 2015).
559   The climate is changing rapidly, and terrestrial ectotherms are expected to be particularly
560   vulnerable to an increase in extreme weather events in temperate regions (Nicolai & Ansart,
561   2017). They will be affected seasonality by more frequent hot temperature extremes and fewer
562   cold temperature extremes over most land areas (IPCC, 2014). Meanwhile, the projected
563   precipitation changes show reductions for the dry area in the central-western region and for the
564   whole of Patagonia (Barros et al., 2015). In the Magellanean region, there have been reported
565   extreme events that could be increase in frequency and intensity in the context of climate change.
566   Examples of these events were severe droughts (1920–1926, 1928, 1966), heavy rainfall events
567   with floods (1983, 1990, 2012, 2015), and devastating snowfall storms. Thus, the quality and
568   availability of habitat for *S. lyratus* could be compromised by the effect of both land uses
569   changes and global warming. In this context, these regional changes in climate and land use put
570   *S. lyratus* populations at serious risk of extinction that must be taken into consideration for future
571   conservation actions.

572

Conclusions

574   1. Here we confirm that the shell ultrastructure of *S. lyratus* has a protoconch and teleoconch

575   with similar ornamentation, not showing a marked limit between them. We provide new

576   anatomical information highlighting the presence of a be-lobed kidney, a close secondary ureter,

577   and the terminal portion of the uterus (spermoviduct) forming a compact glandular mass, the vas

578   deferens inserting into the epiphallus through a dilatation as the most notable anatomical

579   characters of *S. lyratus.*

580   2. The potential distribution obtained shows that *S. lyratus* could be found beyond the

581   Magellanic Subpolar Forests into the Valdivian Temperate Forest, which would increase its

582   known distribution area to a new sub-ecoregion, mainly within Chile.

583   3. From seven environmental abiotic variables used, the main constraining ones to explain *S.*

584   *lyratus* occurrence in the EGD are the temperature (Isothermality, Minimum Temperature of

585   Coldest Month, and Tempearture Seasonality) and Annual Precipitation.

586   4. *Stephadiscus lyratus* inhabits cold native forest areas where it is found mainly on or under the

587   bark of fallen trees or under damp trunks in contact with the ground. This microhabitat allows

588   them overwintering, buffered from temperature and moisture fluctuations, and survive during

589   winter, probably as a strategy to avoid freezing.

590   5. The combination of the ectothermic physiological traits of this species, low dispersal capacity,

591   and its narrow habitat requirements (forest specialist) turns *S. lyratus* into a vulnerable species,

592   not only because of current land-use change but also to climate change.

593

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609

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Figure 1

Study area and collection points of *Stephadiscus lyratus*.

(A) Magellanic Subpolar Forest, Valdivian Temperate Forest and Patagonian steppe sub ecoregions showing historic records of occurrence. **(B)** Southern portion of Tierra del Fuego with new records of occurrences. **(C) (D)** Aspect of the Magellanic subpolar forest trees, mainly corresponding to the genus *Nothofagus*, where the studied species was collected.

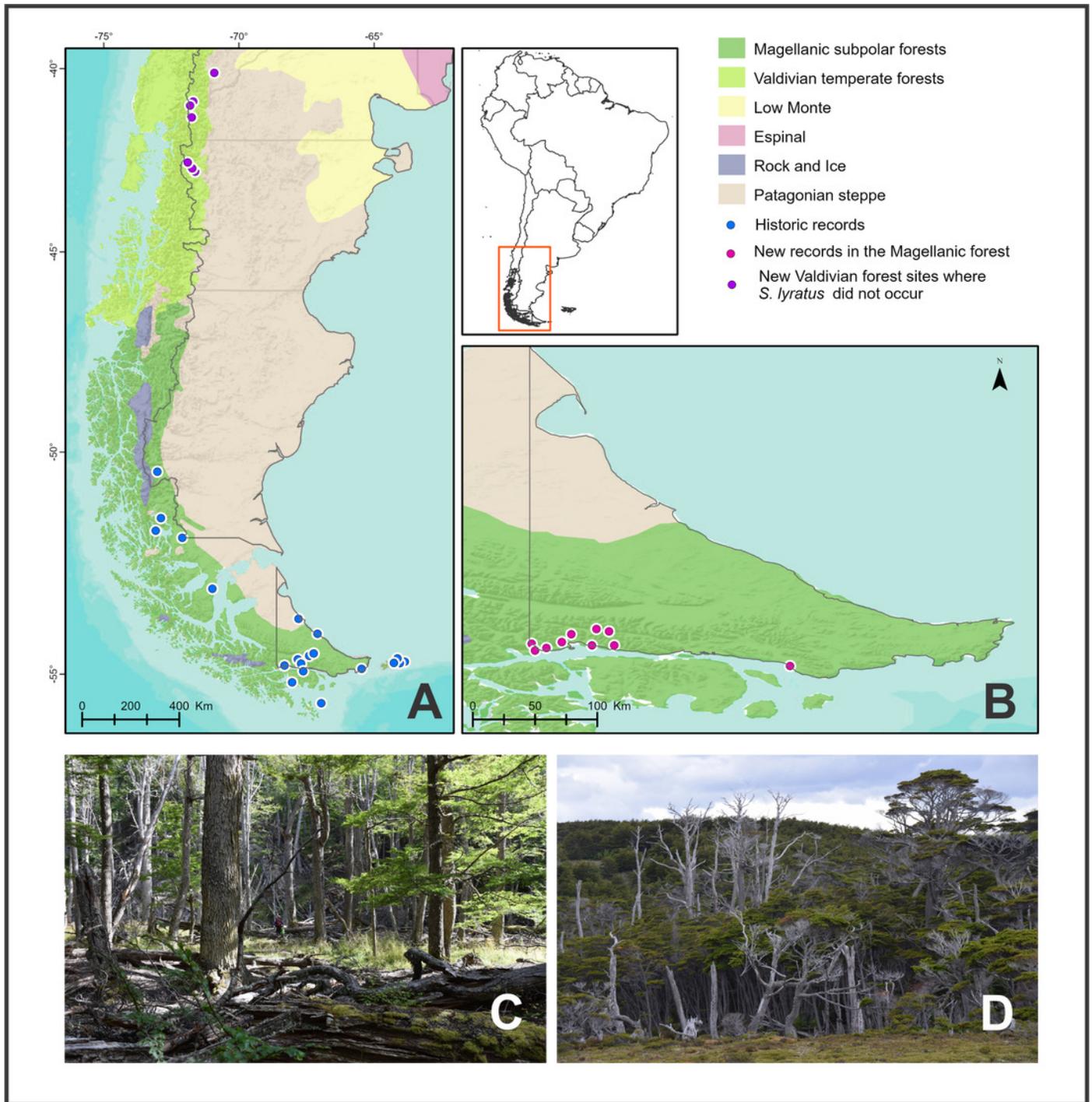



Figure 2

External morphology of *Stephadiscus lyratus* shell and live animal.

(A) (B) Live animal from Tierra del Fuego National Park showing natural shell coloration and by transparency, the irregular spots of the lung. Note black animal body with lighter basal foot and mantle collar. (C) Dorsal, (D) ventral and (E) lateral views of shell, scale bar= 1mm (IBN 951). Photo credit: MG Cuezzo.

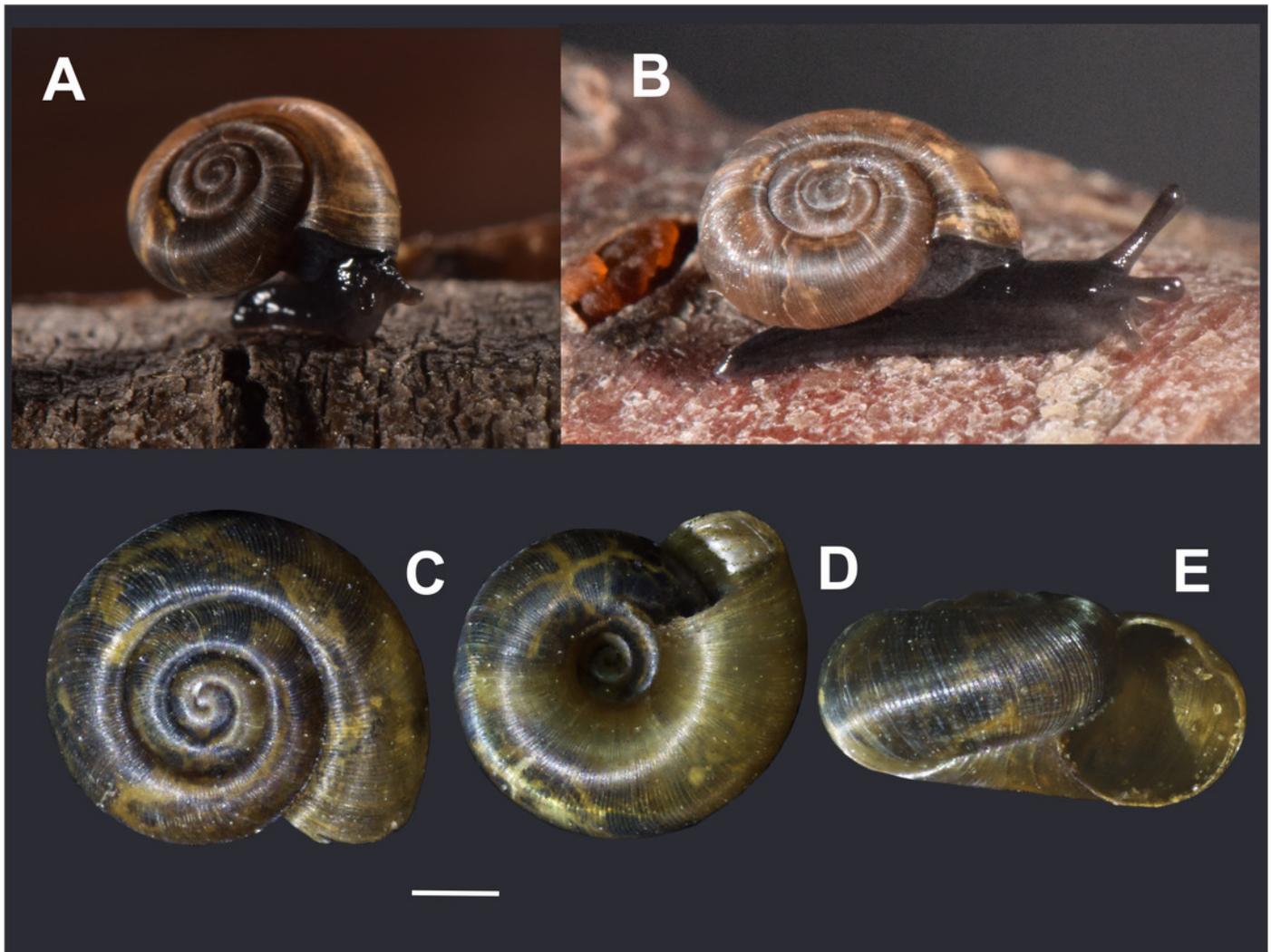



Figure 3

Shell ultrastructure of *Stephadiscus lyratus*.

(A) Ultrastructure of protoconch showing the radial disposition of major ribs, scale bar= 100 µm. (B) (C) details of the body whorl sculpture with major ribs separated at regular spaces, and micro radial ribs. Note nodules supporting ribs, scale bar= 10 µm. (D) Deep suture between body whorls and penultimate whorl, scale bar= 10 µm. (E) Shell umbilicus with sculpture, scale bar=20 µm. Photo credit: MG Cuezzo.

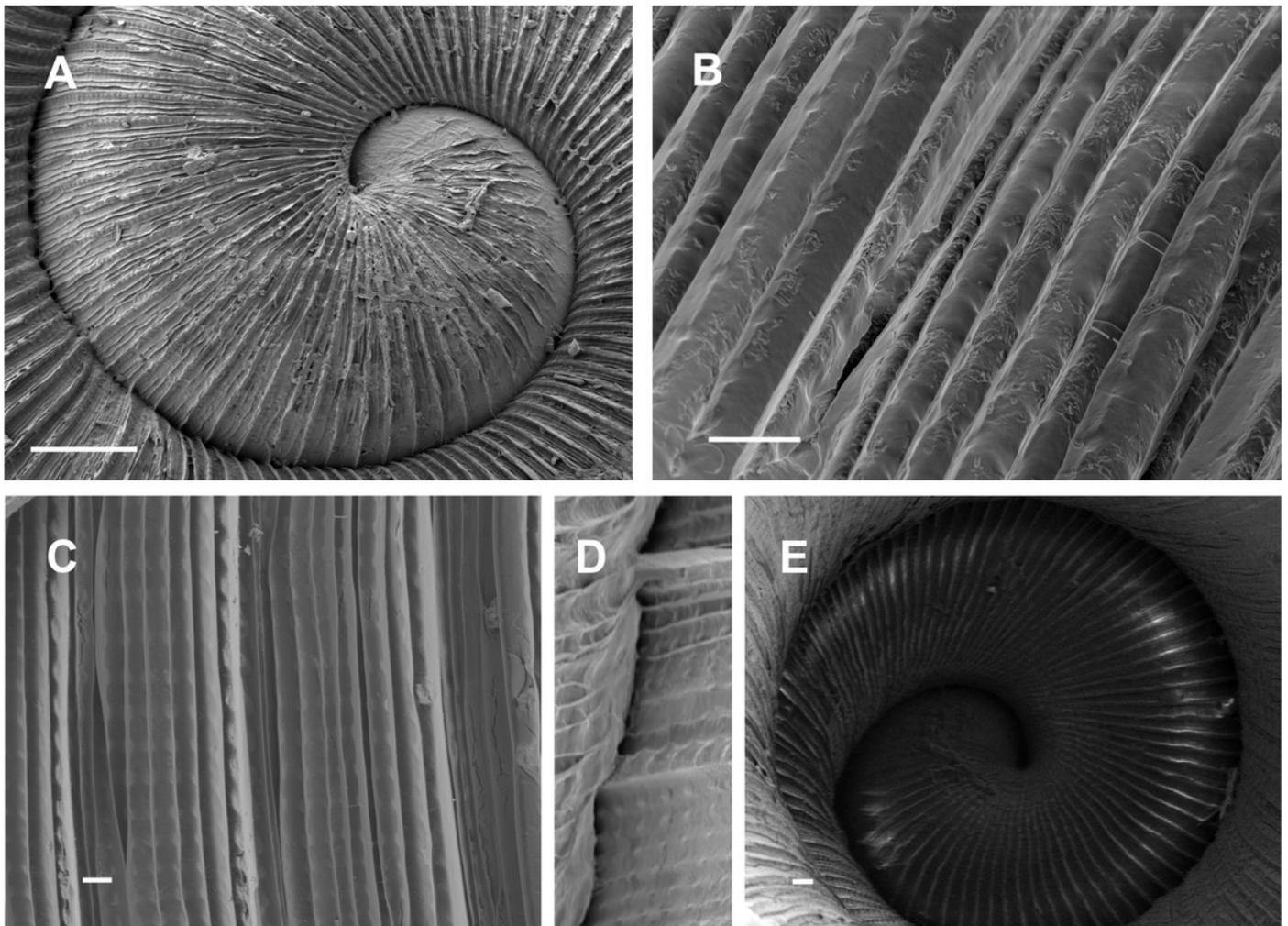



Figure 4

Morphology of pallial and reproductive systems *of Stephadiscus lyratus.*

(A) Pallial system with pulmonary and pericardial cavity. Note the beloved kidney overlapping the pericardium. Small whitish concretion are scatter along the pulmonary roof. (B) General shape of reproductive system showing large, rounded albumen gland and spermoviduct divided in two portions, proximal short, cylindrical, continuous to albumen gland, distal expanded in rounded glandular chamber, scale bar= two mm. (C) Detail of the uterus chamber in distal spermoviduct, free oviduct cylindrical, short, scale bar= two mm. (D) Duct of bursa copulatrix with basal widening, sac rounded. (E) Detail of the penial complex showing penis with a sac-like appendix. The epiphallus reflected over penis, is continuous with a short finger-like flagellum. Note that the vas deference is delated before inserting into epiphallus and that the dilatation is as long as the flagellum, giving appearance of fork ending epiphallus, scale bar= two mm. Abbreviations: ag, albumen gland; bc, bursa copulatrix; dbc, bursa copulatrix duct; e, epiphallus; f, flagellum; fo, free oviduct; hd, hermaphroditic duct; kl1, pericardial side kidney lobe; kl2, rectal side kidney lobe; mc, mantle collar; p, penis, pr, penial retractor; r, rectum; s, Spermoviduct; su, secondary ureter; u, uterus; v, vagina; vd, vas deferens.

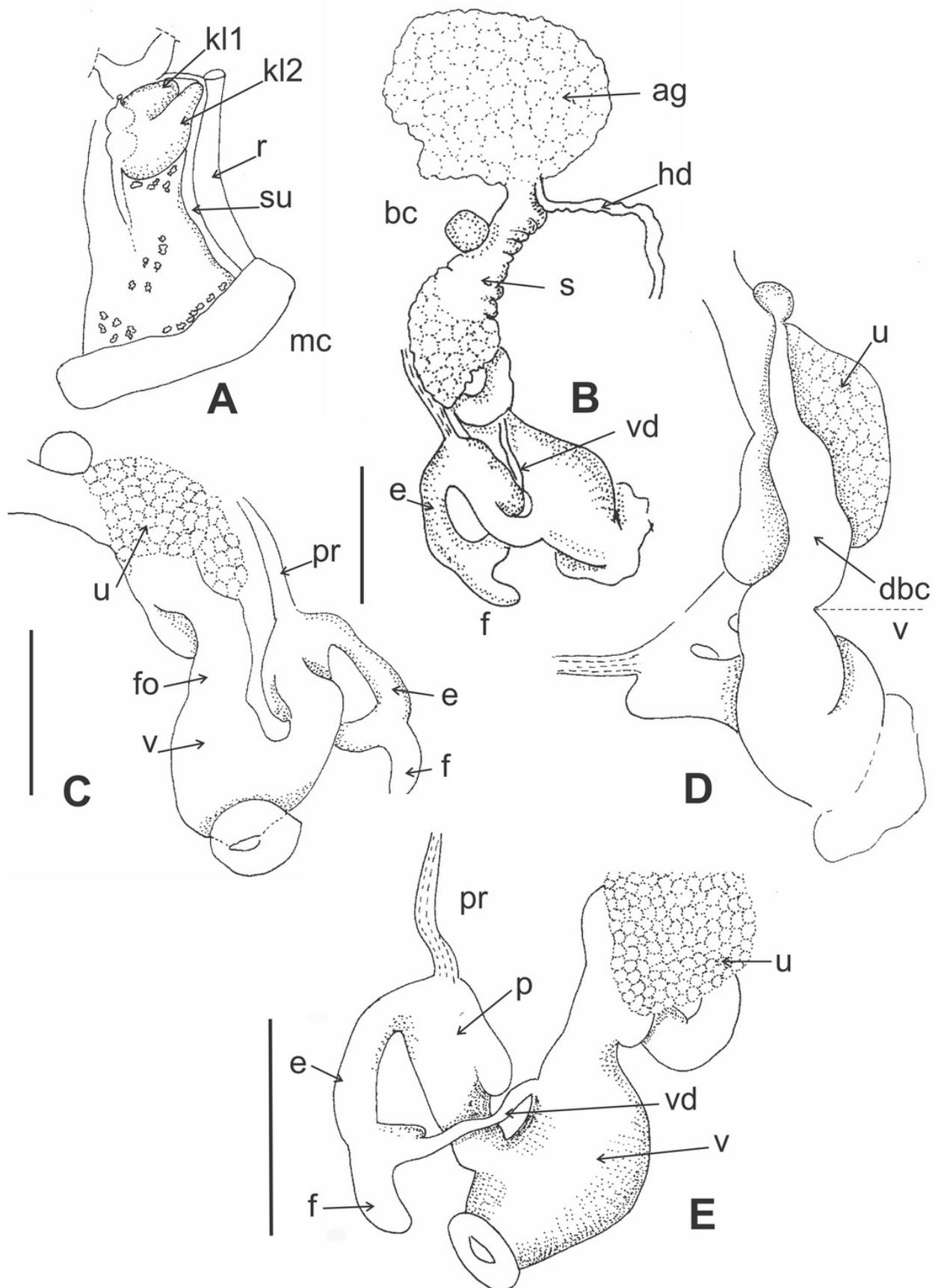



Figure 5

Response curves for the most important variables in the Maxent model for the environmental suitability of *Stephadiscus lyratus.*

(A) BIO3:Isothermality, (B) BIO4: Seasonality, (C) BIO6: Minimum temperature of the coldest month, and (D) BIO12: Annual precipitation. The red lines indicate the mean values, while blue areas denote 1 standard deviation limits, resulting from bootstrap replicates in model runs.

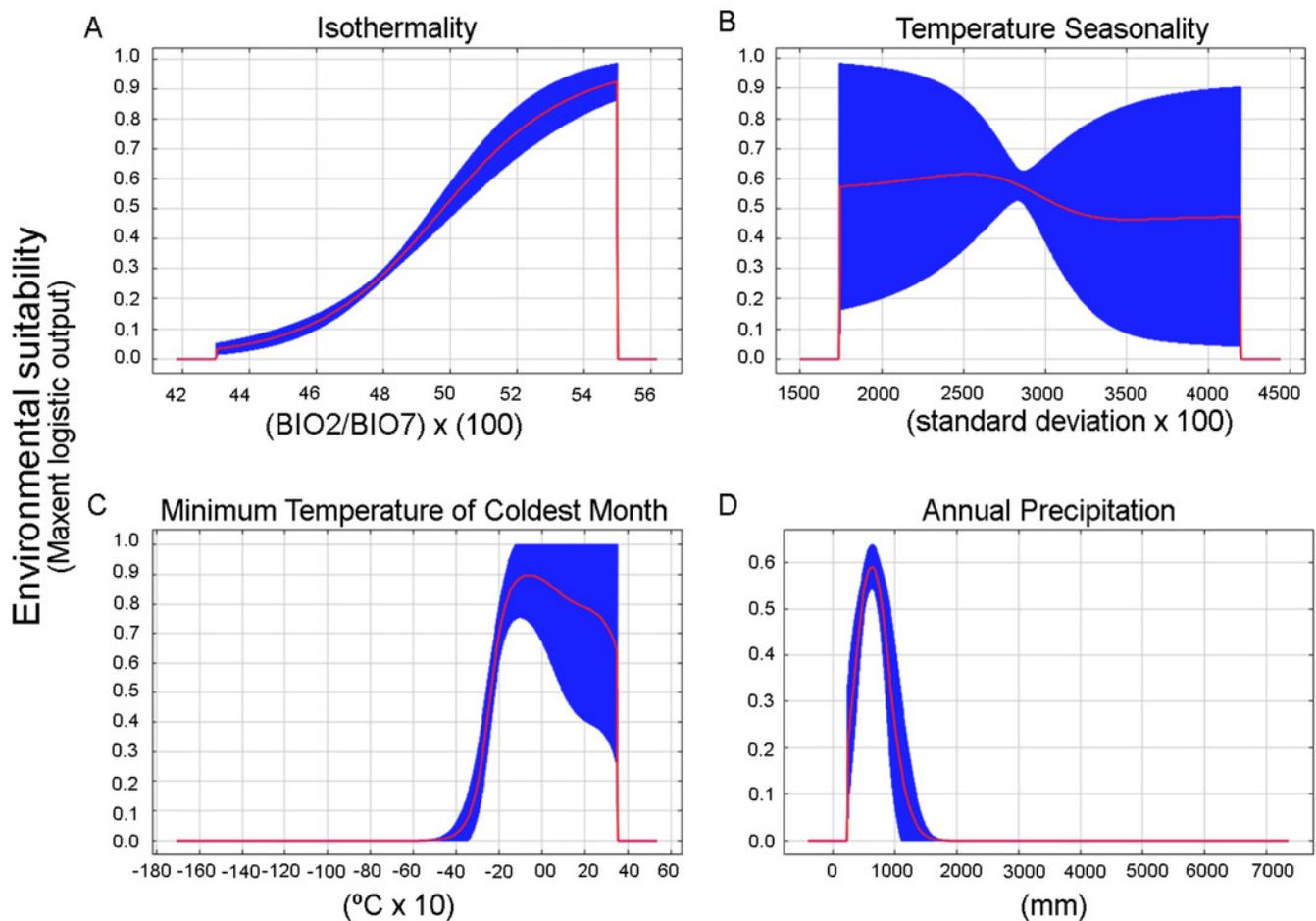
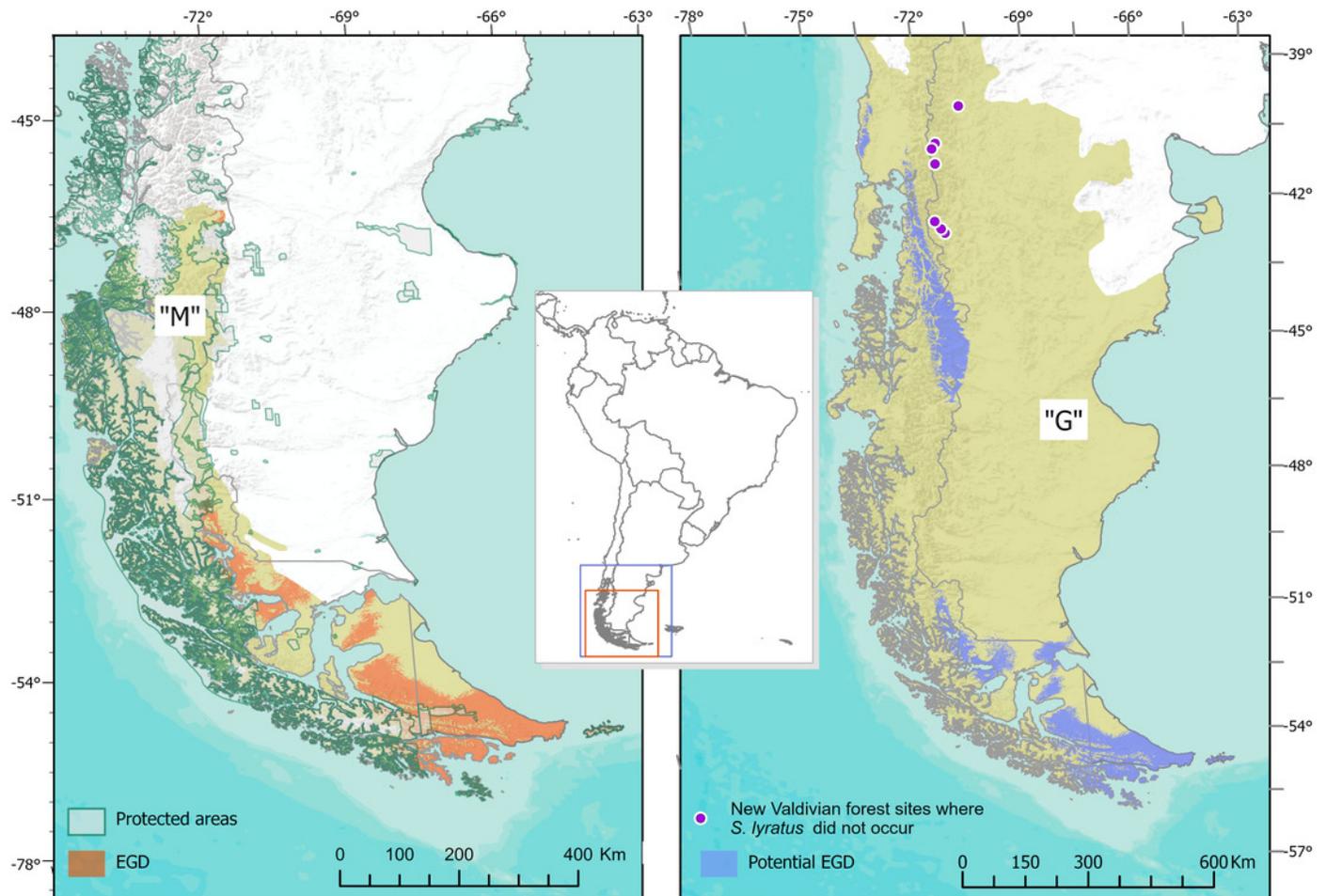



Figure 6

Estimated and Potential areas of occurrence of *Stephadiscus lyratus*

(A) Valdivian Temperate Forest and Magellanic Subpolar Forest sub ecoregions, showing "M" area and the estimated geographic distribution (EGD). (B) Final model transferred to region "G", with the potential area of distribution of *Stephadiscus lyratus*. Note that areas of the model coincident with the Valdivian Temperate Forest mostly occur in the Chilean portion of the sub ecoregion.

Percentages of overlap of the distribution model of *Stephadiscus lyratus* and occurrence points with land cover categories from Globcover 2009 dataset (UCLouvain & ESA Team).

Landcover	Overlapping (%)	
	EGD	**Ocurrences**
Closed to open (>15%) broadleaved evergreen or semi-deciduous forest (>5m)	48.67	33.33
Closed to open (>15%) (broadleaved or needleleaved, evergreen or deciduous) shrubland (<5m)	21.04	30.77
Closed (>40%) broadleaved deciduous forest (>5m)	5.77	0.00
Closed to open (>15%) herbaceous vegetation (grassland, savannas or lichens/mosses)	4.41	12.82
Mosaic cropland (50-70%) / vegetation (grassland/shrubland/forest) (20-50%)	2.66	0.00
Mosaic vegetation (grassland/shrubland/forest) (50-70%) / cropland (20-50%)	2.02	5.13
Rainfed croplands	1.95	0.00
Open (15-40%) broadleaved deciduous forest/woodland (>5m)	1.75	2.56
Water bodies and Others	11.72	15.38

Protected areas overlapped with distribution model of *S. lyratu*s. Names, IUCN categories, country of origin and number of *S. lyratus* EGD pixels within protected areas.

NAME OF PROTECTED AREA	DESIGN TYPE	IUCN CATEGORY	COUNTRY	PIXELS (Nº)
Alberto D'Agostini	National Park	II	Chile	3065
Bernardo O'Higgins	National Park	II	Chile	56
Cabo de Hornos	National Park	II	Chile	694
Corazón de la Isla	Multiple Use Provincial Reserve	VI	Argentina	1599
Isla de los Estados y Archipiélago de Año Nuevo	Wilderness Nature Reserve	Ib	Argentina	703
Kawésqar	National Park, National Reserve	II, IV	Chile	868
Laguna Negra	Multiple Use Provincial Reserve	VI	Argentina	27
Laguna Parrillar	Forest Reserve	IV	Chile	9
Los Glaciares	National Park, National reserve and World Heritage Site	II, VI, Not Applicable*	Argentina	41
Magallanes	Forest Reserve	IV	Chile	16
Patagonia	National Park	II	Chile	11
Rio Valdez	Multiple Use Provincial Reserve	VI	Argentina	57
Seno Almirantazgo	Marine and Coastal Protected Area	IV	Chile	102
Tierra del Fuego	National Park	II	Argentina	932
Torres del Paine	National Park	II	Chile	836
Yendegaia	National Park	II	Chile	1687