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

Maria Gabriela Cuezzo [Corresp., 1] , **Regina Gabriela Medina** [Corresp., 1] , **Carolina Nieto** [1]

[1] Instituto de Biodiversidad Neotropical, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET)-Universidad Nacional de Tucuman (UNT), Yerba Buena, Horco Molle, Tucumán, Argentina

Corresponding Authors: Maria Gabriela Cuezzo, Regina Gabriela Medina
Email address: gcuezzo@webmail.unt.edu.ar, regina.g.medina@gmail.com

Background: *Stephadiscus lyratus* (Couthouy *in* Gould, 1846), an endemic Charopidae from southern South America, was described from few dry shells. The distribution of this species is known on scattering 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 the National Parks of the Patagonian Forests. Snails were photographed, measured, and dissected for anatomical studies; shells were studied with scanning electron microscopy. 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 the Patagonian steppe. Seven bioclimatic variables of the 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 that distinguishes this species. *Stephadiscus lyratus* inhabit cold native forest areas, mainly living on or under humid logs in contact with the ground. The 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 turn *S. lyratus* into a potentially vulnerable species

1   **Geographic distribution modeling and taxonomy of *Stephadiscus lyratus* (Cothouny *in***

2   **Gould, 1846) (Charopidae) reveal potential distributional areas of the species along the**

3   **Patagonian Forests**

4

5   Maria Gabriela Cuezzo[1], Regina Gabriela Medina[1], Carolina Nieto[1]

6

7   [1]Instituto de Biodiversidad Neotropical, Consejo Nacional de Investigaciones Científicas y

8   Técnicas, Facultad de Ciencias Naturales, Universidad Nacional de Tucumán, Argentina

9

10

11   Corresponding authors:

12   MGC, Instituto de Biodiversidad Neotropical (IBN), Crisóstomo Álvarez 722, Tucumán,

13   Argentina. E-mail: gcuezzo@webmail.unt.edu.ar

14   RGM, Instituto de Biodiversidad Neotropical (IBN), Crisóstomo Álvarez 722, Tucumán,

15   Argentina. E-mail: regina.g.medina@gmail.com

16

17   **Abstract**

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

19   southern South America, was described from few dry shells. The distribution of this species is

20   known on scattering occurrences, mainly from material deposited in Museum collections. We

21   provide here new information on anatomy, habitat, and microhabitat preferences and estimate the

22   potential geographic distribution of the species to test if it is exclusively endemic to the Subpolar

23   Magellanic Forest. **Methods:** Fieldwork was carried out in the National Parks of the Patagonian

24   Forests. Snails were photographed, measured, and dissected for anatomical studies; shells were

25   studied with scanning electron microscopy. Estimation of the species geographical distribution

26   (EGD) was obtained through correlative ecological niche modeling (ENM). We designed a

27   calibration area a priori with known species points of occurrence in the Magellanic Subpolar

28   Forests and borders of the Patagonian steppe. Seven bioclimatic variables of the WorldClim

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

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

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

32   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 that distinguishes this species. *Stephadiscus lyratus*

42   inhabit cold native forest areas, mainly living on or under humid logs in contact with the ground.

43   The main constraining variables to explain *S. lyratus* distribution in the EGD were BIO3, BIO12,

44   BIO6, and BIO4. The potential area of distribution obtained almost duplicates their original

45   range (140,454 km^2) extending to the Valdivian Temperate forests mainly in Chile. Natural and

46   semi-natural terrestrial vegetation was predominant in the potential area of distribution of *S.*

47   *lyratus.* However, only 14.7% of this area occurs within current protected areas from Argentina

48   and Chile. The ectothermic physiological traits of this species, low dispersal capacity, and its

49   narrow habitat requirements turn *S. lyratus* into a potentially 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). The current distributional range of *Stephadiscus lyratus* (Couthouy *in*

74   Gould, 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 is restricted to southern areas.

83   Modern methodologies to estimate a species distributional area involve 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 (e.g., minimum convex polygon) (Marcer

90   et al., 2013; Syfert et al., 2014; Pena et al., 2014). These also allow avoiding the potential

91   subjective bias of experts (Fourcade et al., 2014). Furthermore, identifying the combination of

92   environmental conditions in the relevant scenopoetic variables offers the opportunity to discover

93   populations isolated (Wiens & Graham, 2005). On the other hand, modeling species potential

94   areas of distribution may also provide information on the geographic distribution of unknown

95   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 little 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 the 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, the dominant

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

137 low 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 + 2 cm of topsoil from moist microhabitats. Samples

167   were placed in plastic bags and posteriorly sieved through three decreasing mesh widths (3, 1.5,

168   and 0.5 mm) in the laboratory of the Centro Austral de Investigaciones Cientificas (CADIC-

169   CONICET, Tierra del Fuego) under a stereoscopic microscope. All snails collected were

170   photographed alive before relaxing them in water for 24 hours, posteriorly fixed in ethanol 96%,

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

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

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

174   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 the Patagonian steppe. To delineate abiotic

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

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

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

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

222   highly correlated variables ($r \geq 0.85$), we performed a correlation analysis through the "ntbox"

223   package (Osorio-Olvera et al., 2020). Thus, seven bioclimatic variables were selected for the

224   analyses: BIO1 = Annual mean temperature, BIO2 = Mean diurnal range (Mean of monthly

225   (max temp - min temp)), BIO3 = Isothermality (BIO2/BIO7) (* 100), BIO4 = Temperature

226   seasonality (standard deviation *100), BIO6 = Min temperature of coldest month, BIO12 =

227   Annual precipitation, and 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 their potential distribution in different categories of the land cover of the

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

259   (>15%) broadleaved evergreen or semi-deciduous forest (> 5m), Mosaic forest or shrubland (50-

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

261   (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 consists of 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. Uterus divided into two portions, proximal

318   short, cylindrical, continuous to albumen gland, distally expanded in a 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 the appearance of fork ending epiphallus.

330

Microhabitat characterization

331

332   Rainforests, including temperate forests, provide a variety of living spaces where snails can feed,

333   crawl, and live. Although micro snails are usually associated with leaf litter, *Stephadiscus lyratus*

334   was mainly found living on or under the bark of fallen trees or under humid logs in contact with

335   the ground (Figs. 1C, D). We found actively crawling snails only on tree barks or on moss logs.

336   This species is not considered to be arboreal or semi-arboreal. No specimens were found in

337   living trees, nor in their leaves or shrubs, the majority of alive snails were found under fallen

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

339   microhabitats in contact with soil can act as a buffer and help the species to survive during

340   extreme freezing conditions. Dry shells were recovered from soil samples, but in general, they

341   were worn out. Feeding habits in this species are not known. However, the diversity of fungi

342   from the decaying wood is an important food resource for snails (Solem, 1982; Barker, 2001).

343   Species of the genus *Radiodiscus* occur in sympatry with *S. lyratus*. In places outside protected

344   areas where the forest shows some degree of alteration, living snails were scarce or difficult to

345   find.

346

Species Remarks

347

348   The history of the species discovery as well as the problem of the species authorship is explained

349   in Supplementary Material (See Appendix).

350

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

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

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

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

355   *Stephadiscus lyratus* is also similar in shell sculpture and general shape to *S. stuardoi* (DM= 2.0-

356   2.02, H= 0.85), but differs from this species in its larger shell diameter and the absence of weak

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

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

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

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

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

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

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

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

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

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

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

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

369

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

385 subfamilies Semperdoninae, Trukcharopinae, and Rotadiscinae.

386

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

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

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

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

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

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

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

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

395   precipitation, BIO6 = Minimum temperature of the coldest month, and BIO4 = Temperature

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

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

398   under which the variable reaches its optimum suitability. The optimum suitability for

399   isothermality is around 43% to 55%, from here decreased abruptly to cero, which indicates that

400   day to night temperature oscillations are smaller than annual temperature fluctuations (Fig. 5A).

401   BIO4, BIO6, and BIO12 displayed a bell-shaped response of increased suitability as the variable

402   increases above a certain value (Fig. 5B-D). The optimum suitability of BIO4 is around 2750,

403   this is a measure of temperature change over the year, the larger the value (standard deviation of

404   mean monthly temperature x 100), the greater the variability of temperature (O'Donnell &

405   Ignizio, 2012). The optimum suitability of BIO6 is between -2 and 0 ºC (around -1°C, Fig. 5C),

406   this is a measure of minimum cold temperatures throughout the year. In the case of BIO12, the

407   species had its maximum suitability in the 500–600 mm within a narrow range that abruptly

408   decreased when the precipitation increased above this threshold (Fig. 5D).

409

410   **Spatial analysis**

411   The known area of distribution of *S. lyratus* was approximately 72,672 km^2, mainly coincident in

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

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

414   6A). The MOP analysis (Fig. S1) indicated that areas with the most dissimilar variables

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

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

417   "G" area.

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

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

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

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

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

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

424   48% with woody trees (closed to open (>15%) broadleaved evergreen or semi-deciduous forest

425   (>5m)), while the overlap with shrub (closed to open (>15%) (broadleaved or needle-leaved,

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

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

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

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

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

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

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

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

434

435   **Discussion**

436   *Taxonomy and Species Morphology*

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

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

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

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

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

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

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

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

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

446   limit between them. The type of ornamentation and similitude between protoconch and

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

448   Cádiz Lorca, 2008; Miquel & Barker, 2009; Miquel & Araya, 2013). Inner anatomy information

449 proves to be an essential source of characters relevant for future taxonomic and phylogenetic
450 studies. The presence of a be-lobed kidney with the rectal side lobe bigger than the pericardial
451 portion, plus the presence of a close secondary ureter, clearly indicates that *S. lyratus* belongs to
452 Charopidae, differencing it from the Endodontidae. Solem (1982) raised these characters as the
453 main differences between both families. The terminal portion of the uterus (spermoviduct),
454 forming a compact glandular mass, is also a striking character that has only been mentioned
455 before for *Stephacharopa testalba.* Along with this, the insertion of the vas deferens into the
456 epiphallus through a dilatation constitutes unique structures of *S. lyratus*.
457
458 *Estimation of the potential geographical distribution (EGD) and spatial analysis.*
459 The new records obtained were associated with native areas of the Magellanic Subpolar Forest
460 sub-ecoregion in Argentina. The transferred model shows a potential distribution of *S. lyratus* to
461 the Valdivian Temperate Forest, spreading the known area to a new sub-ecoregion,
462 corresponding mainly to the area of this mentioned zone in Chile. Although no specimens of *S.*
463 *lyratus* have been found in the Valdivian forest areas in Argentina (Nahuel Huapi and Los
464 Alerces National Parks), these surveyed areas are outside to the east of the potential area
465 predicted by the model. Thus, the potential area of distribution of *S. lyratus* is coincident with the
466 Magellanic Subpolar Forest and the Valdivian Temperate Forest (more towards Chile) together
467 with its boundaries with the Patagonian Steppe ecoregion. The obtained hypothesis of the
468 potential distribution of *S. lyratus* will direct the next exploratory surveys with the expectation to
469 find new populations in the future.
470 The biogeographic Valdivian Forest province according to Kuschel (1960) and Morrone (2018)
471 has faunistic relationships with Magellanic Forests, probably because both regions have been
472 isolated from other South American forests since the Neogene (Axelrod, Kalin Arroyo & Raven,
473 1991). In addition, the cooling cycles followed by warmer periods in the Quaternary caused the
474 contractions and expansions of the temperate forests (Villagrán & Hinojosa, 1997), and some
475 areas in the coastal range remained free of ices and may have been the source for the recovery of
476 the forest biota (Smith, 2017). From the seven environmental variables used in the EGD analysis
477 of *S. lyratus,* the main constraining variables are the temperature (BIO3 = Isothermality, BIO6 =
478 Minimum temperature of coldest month, and BIO4 = Temperature seasonality) and Annual
479 precipitation (BIO12).

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

481   concerning their distribution are scarce e.g., the case of *Megalobulimus sanctipauli* (Ihering &

482   Pilsbry, 1900). This kind of study for native micro snails is virtually nonexistent. *Megalobulimus*

483   *sanctipauli,* known to inhabit the Atlantic Forest, showed temperature and rainfall as the

484   determinant factors of their geographic distribution (Beltramino et al., 2015). In the case of

485   *Achatina fulica* Bowdich, 1822, an exotic land gastropod in South America, Temperature

486   seasonality, and Mean temperature of the coldest quarter were the variables that contribute the

487   most to the model when they were used alone (Vogler et al., 2013). In the case of *S. lyratus*, the

488   bell-shape response of environmental suitability for the BIO4, BIO6, and BIO12 show that the

489   studied species try to avoid extreme temperature and precipitation oscillations. The BIO6

490   variable shows predicted suitable conditions at sub-zero temperatures. It suggests that this

491   climatic variable is relevant for its optimal growing conditions and in particular with the species'

492   winter survival. Indeed, *S. lyratus* is found in the Magellanic Subpolar Forest where winter

493   temperatures can drop below 0°C. Empirical data on the life history of small land snail species in

494   their natural habitat are hardly available worldwide. There is also very little data on gastropod

495   cold hardiness, especially on land snail species of small sizes. Ansart & Vernon (2003) sustained

496   that two alternatives exist for organisms living in areas that freeze in winter, such as the southern

497   forest in Patagonia: move to an unfrozen habitat or face freezing conditions. For this last

498   category, avoid freezing by extensive supercooling (freezing avoidance) or survive freezing of

499   the body fluids (freezing tolerance) are the only possibilities. Freezing avoidance involves the

500   choice of a hibernation site, which buffers the temperature differences, and which permits

501   avoidance of inoculative freezing (e.g., by contact with ice). During hibernation, the snails

502   rapidly suppress their metabolism and minimize water loss using a discontinuous gas exchange

503   pattern (Koštál et al., 2013). We sustain that *S. lyratus* find favorable overwintering microhabitat

504   in soil, under tree bark, or under fallen tree trunks in contact with soil, which is well buffered

505   from temperature and moisture fluctuations allowing the species to survive during winter

506   freezing.

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

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

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

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

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

512   snail species buried in the soil (Addison & Barber 1997). This can be a restrictive situation to

513   *Stephadiscus lyratus* occurrence as it is shown by the predicted environmental suitability in a

514   narrow range of annual precipitation not surpassing around 1500 mm per year. Also, this would

515   explain the occurrence of *S. lyratus* in humid areas of Magellanic subpolar forest, and the

516   projected potential environments in some regions of northern Valdivian Temperate Forest, which

517   featured by 1000 mm of precipitation per year

518   (https://www.worldwildlife.org/ecoregions/nt0404).

519

520   *Stephadiscus lyratus, a vulnerable species to protect*

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

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

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

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

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

526   gastropod food availability. Dead and decaying wood promotes a diversity of fungi, an important

527   food resource for many snails. Land gastropods are suffering habitat loss and competition from

528   introduced species (more numerous and prolific every year), although are regarded as non-

529   charismatic groups for conservation purposes (Régnier et al., 2009; 2015). In the case of

530   Orthalicoidean land snail in Argentina, only 3% of their average species distribution ranges are

531   safeguarded within current protected areas, showing that the existing protected areas system is

532   not effective at all for the protection of this invertebrate group (Ovando et al., 2019). In the

533   present study, we found that 14,5 % of the total current distributional area of 72,672 km^2 of *S.*

534   *lyratus* is inside the system of protected areas. However, it is important to emphasize that the

535   threats and pressures of land-use change such as tourism, logging, and frequent fires compromise

536   both, protected areas inside the southern National Parks, and the matrix that surrounds them. In

537   fact, 700–1000 ha are logged each year (from 1980 to 2003) in Argentina, Tierra del Fuego

538   (Gea-Izquierdo et al., 2004. Between 53.1 % and 68.1 % of the Chilean Magellanic forests are

539   influenced by human activity in some way (Inostroza, Zasada & König, 2016). In this context,

540   habitat loss for land gastropod conservation is very worrying. Moreover, the protected areas in

541   Argentina were created for the protection of plants (Ortega-Baes et al., 2012) and/or vertebrates

542 (Tabeni, Bender & Ojeda, 2004; Arzamendia & Giraudo, 2004; Corbalán et al., 2011; Tognelli et
543 al., 2011), ignoring the invertebrates, even when their importance has been proven (Chehébar et
544 al., 2013). This situation is a worldwide problem since there are more than a million invertebrate
545 described species but only 3,500 are protected (Baillie, Hilton-Taylor & Stuart, 2004; Brooks et
546 al., 2004, 2006; Nieto et al., 2017). We sustain that *S. lyratus* find favorable overwintering
547 microhabitat in soil or under stones in contact with soil, which is well buffered from temperature
548 and moisture fluctuations allowing them to survive during winter freezing. The combination of
549 the ectothermic traits of this species, low dispersal capacity, probable low fecundity producing
550 only a few eggs, and its narrow habitat requirements (forest specialist) turns *S. lyratus* into a
551 potentially vulnerable species. Along with habitat loss through human land use, climate change
552 is a major contributor to biodiversity loss in the 21st century (Lee et al., 2015). The climate is
553 changing rapidly, and terrestrial ectotherms are expected to be particularly vulnerable to an
554 increase in extreme weather events in temperate regions (Nicolai & Ansart, 2017). They will be
555 affected seasonally by more frequent hot temperature extremes and fewer cold temperature
556 extremes over most land areas (IPCC, 2014). Meanwhile, the projected precipitation changes
557 show reductions for the dry area in the central-western region and the whole of Patagonia
558 (Barros et al., 2015). In the Magellanean region, there have been reported extreme events that
559 could be increased in frequency and intensity in the context of climate change. Examples of these
560 events were severe droughts (1920–1926, 1928, 1966), heavy rainfall events with floods (1983,
561 1990, 2012, 2015), and devastating snowfall storms. Thus, the quality and availability of habitat
562 for *S. lyratus* could be compromised by the effect of both land uses changes and global warming.
563 In this context, these regional changes in climate and land use put *S. lyratus* populations at
564 serious risk of extinction that must be taken into consideration for future conservation actions.
565

566 **Conclusions**

567 1. Here we confirm that the shell ultrastructure of *S. lyratus* has a protoconch and teleoconch
568 with similar ornamentation, not showing a marked limit between them. We provide new
569 anatomical information highlighting the presence of a be-lobed kidney, a close secondary ureter,
570 and the terminal portion of the uterus (spermoviduct) forming a compact glandular mass, the vas
571 deferens inserting into the epiphallus through a dilatation as the most notable anatomical
572 characters of *S. lyratus*.

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

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

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

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

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

578   coldest month, and Temperature seasonality) and Annual precipitation.

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

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

581   overwintering, buffered from temperature and moisture fluctuations, and survive during winter,

582   probably as a strategy to avoid freezing.

583   5. The combination of its narrow habitat requirements (forest specialist), the ectothermic traits of

584   this species, and its low dispersal capacity turn *S. lyratus* into a potentially vulnerable species, to

585   current land-use change, and future climate change scenarios.

586

602   Meyer, T. Escalante, and an anonymous reviewer for providing valuable comments on the

603   manuscript.

References

Addison, J.A. and K.N. Barber. 1997. Response of soil invertebrates to clearcutting and partial cutting in a boreal mixedwood forest in Northern Ontario. Natural Resources Canada, Canadian Forest Service, Great Lakes Forestry Centre. Information Report GLC-X-1. 23 pp. Available at http://cfs.nrcan.gc.ca/pubwarehouse/pdfs/9135.pdf

Ansart A, Vernon P. 2003. Cold hardiness in molluscs. *Acta Oecologica* 24:95–102 DOI: 10.1016/S1146-609X(03)00045-6.

Arino O, Ramos Perez JJ, Kalogirou V, Bontemps S, Defourny P, Van Bogaert E. 2012. Global Land Cover Map for 2009 (GlobCover 2009). *European Space Agency (ESA) & Universit Catholique de Louvain (UCL)* DOI: 10.1594/PANGAEA.787668.

Armesto JJ, Rozzi R and Caspersen J. 2001. Temperate forests of North and South America. In: Chapin F.S., Sala O.E. and Huber-Sannwald E. (eds), Global Biodiversity in a Changing Environment. Scenarios for the 21st Century. Springer, New York, pp. 223–249.

Arzamendia V, Giraudo AR. 2004. Usando patrones de biodiversidad para la evaluación y diseño de áreas protegidas: Las serpientes de la provincia de Santa Fe (Argentina) como ejemplo. *Revista Chilena de Historia Natural* 77: 335–348 DOI: 10.4067/s0716-078x2004000200011.

Axelrod DI, Kalin Arroyo MT, Raven PH. 1991. Historical development of temperate vegetation in the Americas. *Revista Chilena de Historia Natural* 64:413–446

Baillie JE, Hilton-Taylor C, Stuart SN. 2004. *2004 IUCN red list of threatened species: A global species assessment*. Gland, Switzerland and Cambridge, UK: IUCN

Barahona-Segovia R, Riveros-Díaz AL, Zaror S, Catalán R, Araya JF. 2019. Shelter, ecophysiology and conservation status of Plectostylus araucanus (Pulmonata: Bothriembryontidae) in the fragmented Maulino Forest, central Chile. *Revista Mexicana de Biodiversidad* 90: e902703.

Barker GM. 2001. Gastropods on land: phylogeny, diversity and adaptive morphology. In: *The biology of terrestrial molluscs*. CABI, 1–146 DOI: 10.1079/9780851993188.0001.

Barros VR, Boninsegna JA, Camilloni IA, Chidiak M, Magrín GO, Rusticucci M. 2015. Climate change in Argentina: Trends, projections, impacts, and adaptation. *Wiley Interdisciplinary Reviews: Climate Change* 6:151–169 DOI: 10.1002/wcc.316.

Barve N, Barve V, Jiménez-Valverde A, Lira-Noriega A, Maher SP, Peterson AT, Soberón J,

635   Villalobos F. 2011. The crucial role of the accessible area in ecological niche modeling and

636   species distribution modeling. *Ecological Modelling* 222:1810–1819 DOI:

637   10.1016/j.ecolmodel.2011.02.011.

638 Barve N, Barve V. 2019. Package ENMGadgets: pre and post-processing in ENM workflow.

639   Available at https://github.com/narayanibarve/ENMGadgets.

640 Beltramino AA, Vogler RE, Gutiérrez Gregoric DE, Rumi A. 2015. Impact of climate change on

641   the distribution of a giant land snail from South America: predicting future trends for setting

642   conservation priorities on native malacofauna. *Climatic Change* 131:621–633 DOI:

643   10.1007/s10584-015-1405-3.

644 Brooks TM, Bakarr MI, Boucher T, Da Fonseca GAB, Hilton-Taylor C, Hoekstra JM, Moritz T,

645   Olivieri S, Parrish J, Pressey RL, Rodrigues ASL, Sechrest W, Stattersfield A, Strahm W,

646   Stuart SN. 2004. Coverage provided by the global protected-area system: Is it enough?

647   *BioScience* 54:1081–1091 DOI: 10.1641/0006-3568(2004)054[1081:CPBTGP]2.0.CO;2.

648 Brooks TM, Mittermeier RA, Da Fonseca GAB, Gerlach J, Hoffmann M, Lamoreux JF,

649   Mittermeier CG, Pilgrim JD, Rodrigues ASL. 2006. Global biodiversity conservation

650   priorities. *Science* 313:58–61 DOI: 10.1126/science.1127609.

651 Chehébar C, Novaro A, Iglesias G, Walker S, Funes M, Tammone M, Didier K. 2013.

652   *Identificación de áreas de importancia para la biodiversidad en la estepa y el monte de*

653   *Patagonia: Valoración en base a distribución de especies y ecosistemas.* Buenos Aires,

654   Argentina: APN, WCS, TNC.

655 Christensen JH, Hewitson B, Busuioc A, Chen A, Gao X, Held I, Jones R, Kolli RK, Kwon W-T,

656   Laprise R, Magan~a Rueda V, Mearns L, Menendez CG, Ra¨isa¨nen J, Rinke A, Sarr A,

657   Whetton P. 2007. Regional climate projections. In: Solomon S, Qin D, Manning M, Chen Z,

658   Marquis M, Averyt KB, Tignor M, Miller L, eds. *Climate Change 2007: The Physical*

659   *Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the*

660   *Intergovernmental Panel on Climate Change.* Cambridge: University Press, 847–940.

661 Cobos ME, Peterson T, Barve N, Osorio-Olvera L. 2019. Kuenm: An R package for detailed

662   development of ecological niche models using Maxent. *PeerJ* 2019:1–15 DOI:

663   10.7717/peerj.6281.

664 Cobos ME, Osorio-Olvera L, Soberón J, Peterson T, Barve V, Barve N. 2020. ellipsenm: an R

665   package for ecological niche's characterization using ellipsoids. Available at

666   https://github.com/marlonecobos/ellipsenm.

667 Corbalán V, Tognelli MF, Scolaro JA, Roig-Juñent SA. 2011. Lizards as conservation targets in

668   Argentinean Patagonia. *Journal for Nature Conservation* 19:60–67 DOI:

669   10.1016/j.jnc.2010.05.004.

670 Cuezzo MG. 2006. Systematic revision and cladistic analysis of Epiphragmophora Doering from

671   Argentina and southern Bolivia (Gastropoda: Stylommatophora: Xanthonychidae).

672   *Malacologia* 49:121–188 DOI: 10.4002/1543-8120-49.1.121.

673 Cuezzo MG, Miranda MJ, Vogler RE, Beltramino AA. 2018. From morphology to molecules: a

674   combined source approach to untangle the taxonomy of *Clessinia* (Gastropoda,

675   Odontostomidae), endemic land snails from the Dry Chaco ecoregion. *PeerJ* 6:e5986 DOI:

676   10.7717/peerj.5986.

677 Di Gregorio A. 2005. *Land cover classification system. Classification concepts and user manual*

678   *for software version 2*. Rome: Food and Agriculture Organization of the United Nations.

679 Dos Santos D, Domínguez E, Miranda MJ, Gutiérrez Gregoric D, Cuezzo MG. 2020. The

680   relevance of ecoregions and mountainous environments in the diversity and endemism of

681   land gastropods. *Progress in Physical Geography: Earth and Environment* 1–25 DOI:

682   10.1177/0309133320948839.

683 Dudley N. 2008. *Guidelines for applying protected area management categories* Website:

684   www.iucn.org/themes/wcpa.

685 Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ. 2011. A statistical explanation of

686   MaxEnt for ecologists. *Diversity and Distributions* 17:43–57 DOI: 10.1111/j.1472-

687   4642.2010.00725.x.

688 Escobar LE, Lira-Noriega A, Medina-Vogel G, Townsend Peterson A. 2014. Potential for spread

689   of the white-nose fungus (*Pseudogymnoascus destructans*) in the Americas: Use of Maxent

690   and NicheA to assure strict model transference. *Geospatial Health* 9:221–229 DOI:

691   10.4081/gh.2014.19.

692 Fourcade Y, Engler JO, Rödder D, Secondi J. 2014. Mapping species distributions with

693   MAXENT using a geographically biased sample of presence data: A performance

694   assessment of methods for correcting sampling bias. *PLoS ONE* 9:1–13 DOI:

695   10.1371/journal.pone.0097122.

696 Frangi JL, Barrera MD, Puigdefábregas J, Yapura PF, Arambarri AM, Richter LL. 2004.

697   Ecología de los bosques de Tierra del Fuego. In: Goya JF, Frangi JL, Arturi MF eds.

698   *Ecología y manejo de los bosques de Argentina: Investigación en bosques nativos de*

699   *Argentina*. La Plata, Buenos Aires: Editorial de la Universidad Nacional de La Plata

700   (EDULP).

701   Gea-Izquierdo G, Pastur GM, Cellini JM, Lencinas MV. 2004. Forty years of silvicultural

702   management in southern Nothofagus pumilio primary forests. *Forest Ecology and*

703   *Management* 201: 335–347 DOI: 10.1016/j.foreco.2004.07.015.

704   Gould AA. 1845-1848. Dr. Gould described the following species of *Helix* from the shells of the

705   Exploring Expedition. *Proceedings of the Boston Society of Natural History* II: 165–170.

706   Gould AA. 1852. The *United States Exploring Expedition 1838-1842 under the command of*

707   *Charles Wilkes*. Boston: Mollusks & Shells.

708   Guevara L, Gerstner BE, Kass JM, Anderson RP. 2018. Toward ecologically realistic predictions

709   of species distributions: A cross-time example from tropical montane cloud forests. *Global*

710   *Change Biology* 24:1511–1522 DOI: https://doi.org/10.1111/gcb.13992.

711   Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated

712   climate surfaces for global land areas. *International Journal of Climatology* 25:1965–1978

713   DOI: 10.1002/joc.1276.

714   Hylton Scott MI. 1964. *Helix costellata* d´Orbigny, a la luz de su anatomía. *Neotropica* 10:15–

715   19.

716   Hylton Scott MI. 1968. Endodontidos Neotropicales III. *Neotropica* 14:99–102.

717   Hylton Scott MI 1970. Endodontidos de la Región Austral Americana. *Revista del Museo*

718   *Argentino de Ciencias Naturales "Bernardino Rivadavia"* X: 267–296.

719   Hylton Scott MI. 1972. Lista de Gastropoda terrestres, principalmente Endodontidos de Tierra

720   del Fuego, Isla de los Estados e islotes vecinos. *Neotropica* 18:67–72.

721   Hylton Scott MI. 1973. Endodontidos Neotropicales V. *Neotropica* 19:126–131.

722   Hylton Scott MI. 1981. Referencias al género *Stephanoda* Albers, 1860 y la creación del género

723   *Stephadiscus* gen. nov. (Mollusca, Endodontidae). *Neotropica* 27:123–126.

724   Inostroza L, Zasada I, König HJ. 2016. Last of the wild revisited: assessing spatial patterns of

725   human impact on landscapes in Southern Patagonia, Chile. *Regional Environmental Change*

726   16:2071–2085 DOI: 10.1007/s10113-016-0935-1.

727   IPCC. 2014. Climate Change 2014: Synthesis Report. In: Core Writing Team, Pachauri RK,
728   Meyer LA, eds. *Contribution of Working Groups I, II, and III to the Fifth Assessment*
729   *Report of the Intergovernmental Panel on Climate Change*. Geneva, Switzerland: IPCC,
730   151.

731   IUCN, UNEP-WCMC. 2020. The World Database on Protected Areas (WDPA), Cambridge,
732   UK: UNEP-WCMC. *Available at: www.protectedplanet.net*.

733   Johnson RL. 1964. *The Recent Mollusca of Augustus Addison Gould. Museum of Natural*
734   *History*. Washington DC: Smithsonian Institution.

735   Jordan SF, Hoffman Black S. 2012. *Effects of Forest Land Management on Terrestrial*
736   *Mollusks: A Literature Review*. The Xerces Society for Invertebrate Conservation
737   Portland, Oregon. Interagency Special Status and Sensitive Species Program USDA
738   Forest Service, Region 6 and USDI Oregon/Washington Bureau of Land Management.

739   Kerney MP, Cameron RAD. 1979. *Field guide to the land snails of Britain and northwest*
740   *Europe*. London, Europe: Collins.

741   Koštál V, Rozsypal J., Pech P., Zahradníčková H., Šimek P. 2013. Physiological and
742   biochemical responses to cold and drought in the rock-dwelling pulmonate snail, *Chondrina*
743   *avenacea*. *Journal of Comparative Physiology B: Biochemical, Systemic, and*
744   *Environmental Physiology* 183:749–761. DOI: 10.1007/s00360-013-0749-0.

745   Kuschel G. 1960. Terrestrial zoology in southern Chile. *Proceedings of the Royal Society of*
746   *London, Series B* 152: 540–550.

747   Lee JR, Maggini R, Taylor MFJ, Fuller RA. 2015. Mapping the Drivers of Climate Change
748   Vulnerability for Australia's Threatened Species. *PLoS ONE* 10:e0124766 DOI:
749   10.1371/journal.pone.0124766.

750   Marcer A, Sáez L, Molowny-Horas R, Pons X, Pino J. 2013. Using species distribution modeling
751   to disentangle realized versus potential distributions for rare species conservation.
752   *Biological Conservation* 166:221–230 DOI: 10.1016/j.biocon.2013.07.001.

753   McGlone MS, Lusk CH and Armesto JJ. 2016. Biogeography and ecology of south-temperate
754   forests. *New Zealand Journal of Botany* 54(2): 94-99. doi:10.1080/0028825x.2016.1162819

755   Medina RG, Ponssa ML, Aráoz E. 2016. Environmental, land cover, and land use constraints on
756   the distributional patterns of anurans: *Leptodacylus* species (Anura, Leptodactylidae) from
757   Dry Chaco. *PeerJ* 2016 DOI: 10.7717/peerj.2605.

758   Merow C, Smith MJ, Edwards TC, Guisan A, McMahon SM, Normand S, Thuiller W, Wüest
759   RO, Zimmermann NE, Elith J. 2014. Back to the basics of species distribution modeling:
760   what do we gain from complex versus simple models? *Ecography* in review:1267–1281
761   DOI: 10.1111/ecog.00845.

762   Miquel SE, Araya JF. 2013. A new Charopidae from Chile and Argentina, *Stephacharopa*
763   *calderaensis* n. gen. and n. sp., with remarks on the taxonomy of the genus *Stephadiscus*
764   Hylton Scott 1981 (Mollusca: Gastropoda Pulmonata). *Archiv fur Molluskenkunde*
765   142:227–235 DOI: 10.1127/arch.moll/1869-0963/142/227-235.

766   Miquel SE, Barker GM. 2009. New Charopidae from Chilean — Argentine Patagonia:
767   (Mollusca: Gastropoda: Stylommatophora). *Archiv für Molluskenkunde: International*
768   *Journal of Malacology* 138:53–61 DOI: 10.1127/arch.moll/0003-9284/138/053-061.

769   Miquel SE, Cádiz Lorca FJ. 2008. *Araucocharopa gallardoi* gen. et sp. n. of Charopidae
770   (Gastropoda: Stylommatophora: Punctoidea) from Southern Chile. *Revista del Museo*
771   *Argentino de Ciencias Naturales, Nueva Serie* 10:329–339 DOI: 10.22179/revmacn.10.287.

772   Morello J, Matteucci SD, Rodriguez AF, Silva ME. 2012. *Ecorregiones y complejos*
773   *ecosistémicos argentinos*. Buenos Aires: Facultad de Arquitectura, Diseño y Urbanismo.

774   Morrone JJ. 2015. Biogeographical regionalization of the Andean region. *Zootaxa* 3936:207–236
775   DOI: 10.11646/zootaxa.3936.2.3.

776   Morrone JJ. 2018. *Evolutionary Biogeography of the Andean Region*. Boca Raton: CRC Press
777   DOI: 10.1201/9780429486081.

778   Nicolai A, Ansart A. 2017. Conservation at a slow pace: Terrestrial gastropods facing fast-
779   changing climate. *Conservation Physiology* 5 DOI: 10.1093/conphys/cox007.

780   Niemelä, J., 1997. Invertebrates and boreal forest management. Conservation Biology 11: 601–
781   610.

782   Nieto C, Ovando XMC, Loyola R, Izquierdo A, Romero F, Molineri C, Rodríguez J, Rueda
783   Martín P, Fernández H, Manzo V, Miranda MJ. 2017. The role of macroinvertebrates for
784   conservation of freshwater systems. *Ecology and Evolution* 7:5502–5513 DOI:
785   10.1002/ece3.3101.

786   Olson DM, Dinerstein E. 1998. The global 200: A representation approach to conserving the
787   earth's most biologically valuable ecoregions. *Conservation Biology* 12:502–515 DOI:
788   10.1046/j.1523-1739.1998.012003502.x.

789 Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC,
790   D'Amico JA, Itoua I, Strand HE, Morrison JC, Loucks CJ, Allnutt TF, Ricketts TH,
791   Kura Y, Lamoreux JF, Wettengel WW, Hedao P, Kassem KR. 2001. Terrestrial
792   ecoregions of the world: A new map of life on Earth. *BioScience* 51:933–938 DOI:
793   10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2.

794 Ortega-Baes P, Bravo S, Sajama J, Sühring S, Arrueta J, Sotola E, Alonso-Pedano M, Godoy-
795   Bürki AC, Frizza NR, Galíndez G, Gorostiague P, Barrionuevo A, Scopel A. 2012.
796   Intensive field surveys in conservation planning: Priorities for cactus diversity in the
797   Saltenian Calchaquíes Valleys (Argentina). *Journal of Arid Environments* 82:91–97 DOI:
798   10.1016/j.jaridenv.2012.02.005.

799 Osorio-Olvera L, Lira-Noriega A, Soberón J, Peterson AT, Falconi M, Contreras-Díaz RG,
800   Martínez-Meyer E, Barve V, Barve N. 2020. ntbox: An r package with graphical user
801   interface for modeling and evaluating multidimensional ecological niches. *Methods in*
802   *Ecology and Evolution* 11:1199–1206 DOI: 10.1111/2041-210X.13452.

803 Ovando XMC, Miranda MJ, Loyola R, Cuezzo MG. 2019. Identifying priority areas for
804   invertebrate conservation using land snails as models. *Journal for Nature Conservation*
805   50:125707 DOI: 10.1016/j.jnc.2019.04.004.

806 Owens HL, Campbell LP, Dornak LL, Saupe EE, Barve N, Soberón J, Ingenloff K, Lira-Noriega
807   A, Hensz CM, Myers CE, Peterson AT. 2013. Constraints on interpretation of ecological
808   niche models by limited environmental ranges on calibration areas. *Ecological Modelling*
809   263:10–18 DOI: 10.1016/j.ecolmodel.2013.04.011.

810 Pena JC de Castro, Kamino LHY, Rodrigues M, Mariano-Neto E, de Siqueira MF. 2014.
811   Assessing the conservation status of species with limited available data and disjunct
812   distribution. *Biological Conservation* 170:130–136 DOI: 10.1016/j.biocon.2013.12.015.

813 Peterson AT, Papeş M, Eaton M. 2007. Transferability and model evaluation in ecological niche
814   modeling: A comparison of GARP and Maxent. *Ecography* 30:550–560 DOI:
815   10.1111/j.2007.0906-7590.05102.x.

816 Peterson AT, Soberón J, Pearson RG, Anderson RP, Martínez-Meyer E, Nakamura M, Araújo
817   MB. 2011. *Ecological Niches and Geographic Distributions (MPB-49)*. Princeton and
818   Oxford: Princeton University Press DOI: 10.1515/9781400840670.

819 Phillips SJ, Anderson RP, Schapire RE. 2006. Maximum entropy modeling of species

820   geographic distributions. *Ecological Modelling* 190:231–259 DOI:

821   10.1016/j.ecolmodel.2005.03.026.

822   Phillips SJ, Dudík M. 2008. Modeling of species distributions with Maxent: new extensions and

823   a comprehensive evaluation. *Ecography* 31:161–175 DOI: 10.1111/j.0906-

824   7590.2008.5203.x.

825   Régnier C, Fontaine B, Bouchet P. 2009. Not knowing, not recording, not listing: numerous

826   unnoticed mollusk extinctions. *Conservation Biology* 23: 1214–1221.

827   Régnier C, Achaz G, Lambert A, Cowie RH, Bouchet P, Fontaine B. 2015. Mass extinction in

828   poorly known taxa. *Proceeding of Natural Academy of Sciences* 112: 7761–7766.

829   Salvador RB, Brook FJ, Shepherd LD, Kennedy M. 2020. Molecular phylogenetic analysis of

830   Punctoidea (Gastropoda, Stylommatophora). *Zoosystematics and Evolution* 96:397–410

831   DOI: 10.3897/zse.96.53660.

832   Schneider CA, Rasband WS, Eliceiri KW. 2012. NIH Image to ImageJ: 25 years of image

833   analysis. *Nature Methods* 9:671–675. DOI: 10.1038/nmeth.2089.

834   Smith C. 2017. Southern South America: Chile and Argentina. In: Terrestrial Ecoregions of

835   Latin America and the Caribbean, World Wildlife Fund. WWF NT0404. *Available at*

836   *https://www.worldwildlife.org/ecoregions/nt0404.* (accessed 20 November 2017).

837   Soberón J, Peterson AT. 2005. Interpretation of Models of Fundamental Ecological Niches and

838   Species ' Distributional Areas. *Biodiversity Informatics* 2:1–10 DOI: 10.1093/wber/lhm022.

839   Solem A. 1982. *Endodontoid land snails from Pacific Islands (Mollusca : Pulmonata :*

840   *Sigmurethra).* Chicago: Field Museum of Natural History DOI: 10.5962/bhl.title.2553.

841   Stanisic J. 1990. Systematics and biogeography of eastern Australian Charopidae (Mollusca,

842   Pulmonata) from subtropical rainforests. *Memoirs of the Queensland Museum* 30:1–241.

843   Syfert MM, Joppa L, Smith MJ, Coomes DA, Bachman SP, Brummitt NA. 2014. Using species

844   distribution models to inform IUCN Red List assessments. *Biological Conservation*

845   177:174–184 DOI: 10.1016/j.biocon.2014.06.012.

846   Tabeni S, Bender BJ, Ojeda RA. 2004. Estudio de los puntos calientes para la conservación de

847   mamíferos en la Provincia de Tucumán. *Mastozoología Neotropical* 11:55–67.

848   Tognelli MF, Abba AM, Bender JB, Seitz VP. 2011. Assessing conservation priorities of

849   xenarthrans in Argentina. *Biodiversity and Conservation* 20:141–151 DOI: 10.1007/s10531-

850   010-9951-5.

851   Villagrán C, Hinojosa LF. 1997. Historia de los bosques del sur de Sudamérica, II: Análisis

852   fitogeográfico. *Revista Chilena de Historia Natural* 70:241–267.

853   Vogler RE, Beltramino AA, Sede MM, Gutierres Gregoric DE, Núñez V, Rumi A. 2013. The

854   Giant African Snail, *Achatina fulica* (Gastropoda: Achatinidae): Using Bioclimatic Models

855   to Identify South American Areas Susceptible to Invasion. *American Malacological*

856   *Bulletin* 31:39–50 DOI: 10.4003/006.031.0115.

857   Weaver KF, Anderson T, Guralnick R. 2006. Combining phylogenetic and ecological niche

858   modeling approaches to determine the distribution and historical biogeography of Black

859   Hills mountain snails (Oreohelicidae). *Diversity and Distributions* 12: 756–766.

860   Wiens JJ, Graham CH. 2005. Niche Conservatism: Integrating Evolution, Ecology, and

861   Conservation Biology. *Annual Review of Ecology, Evolution, and Systematics* 36:519–539

862   DOI: 10.1146/annurev.ecolsys.36.102803.095431.

863   Wyman J. 1903. Biographical memoir of Augustus Addison Gould. *National Academy of*

864   *Sciences* 91–113.

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.
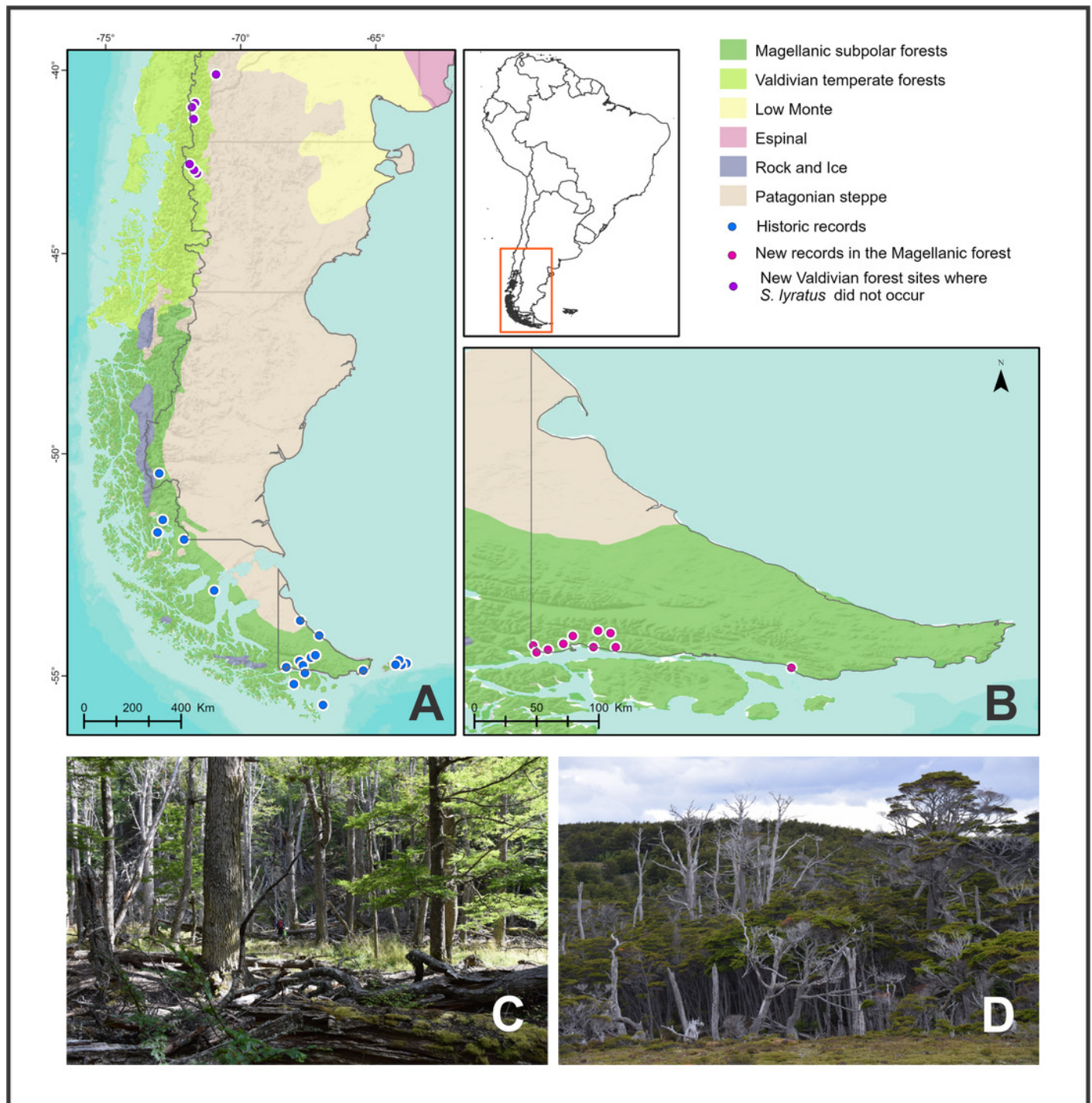
Figure 2

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.
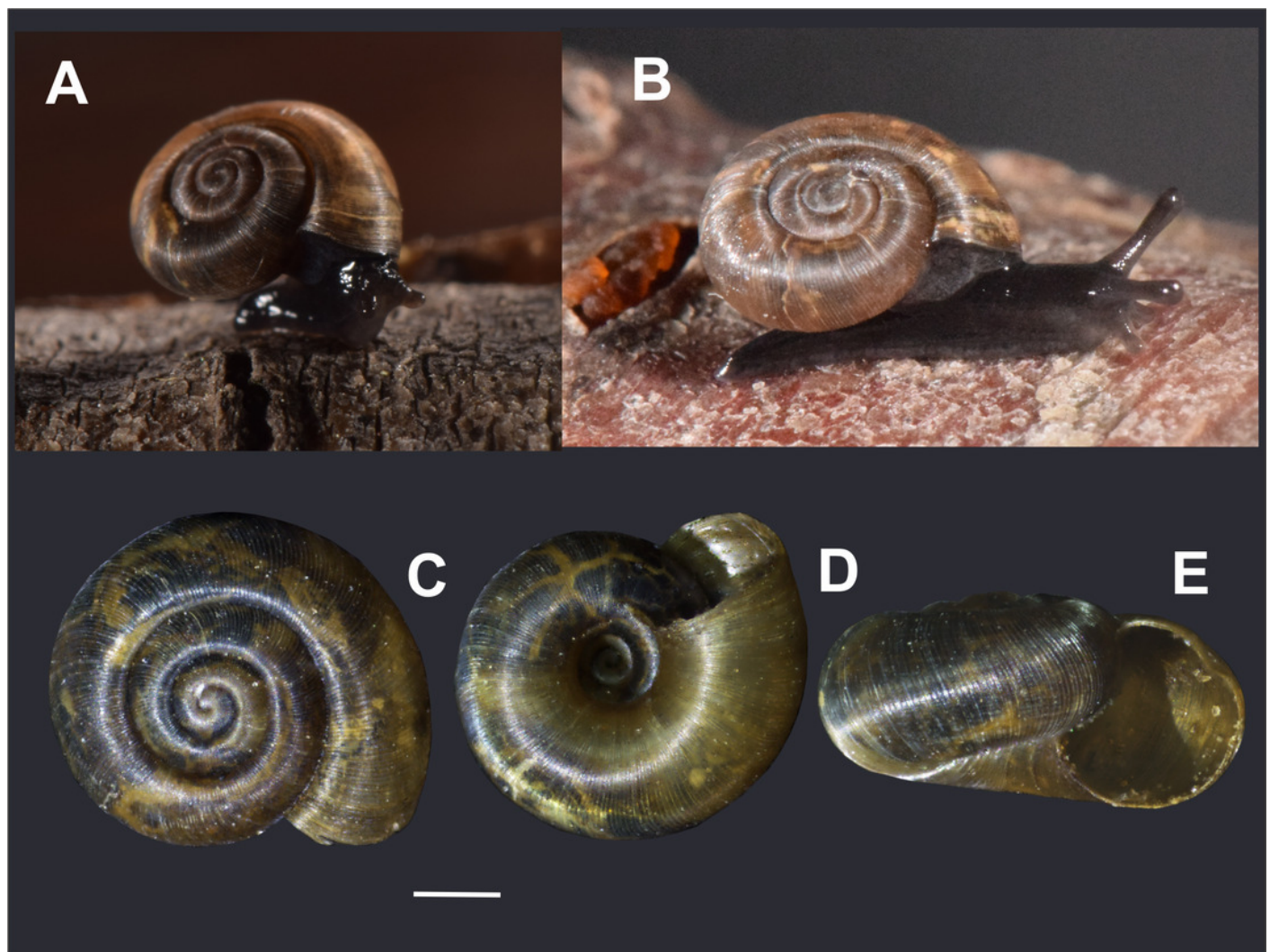
Figure 3

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.
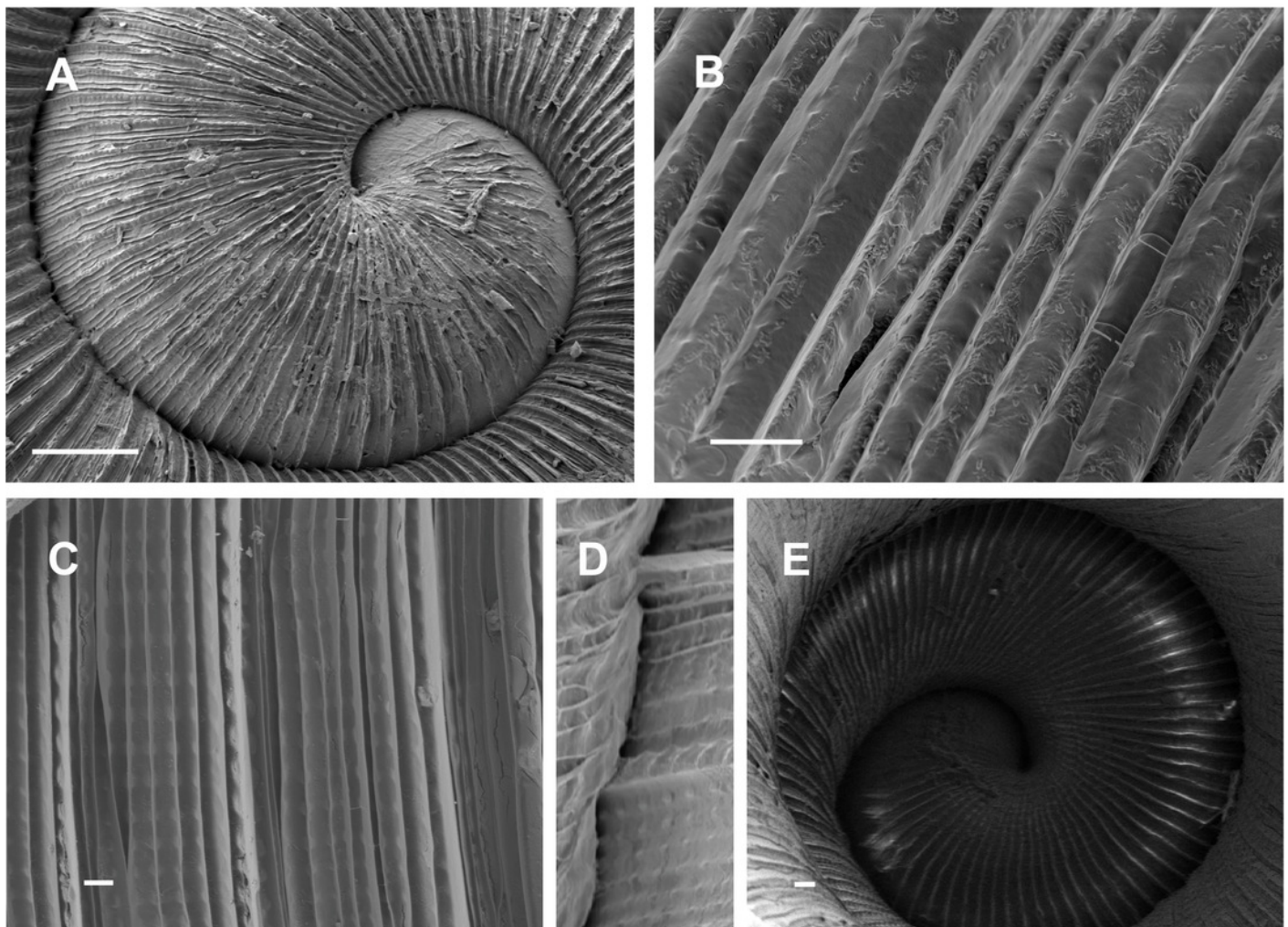
Figure 4

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.
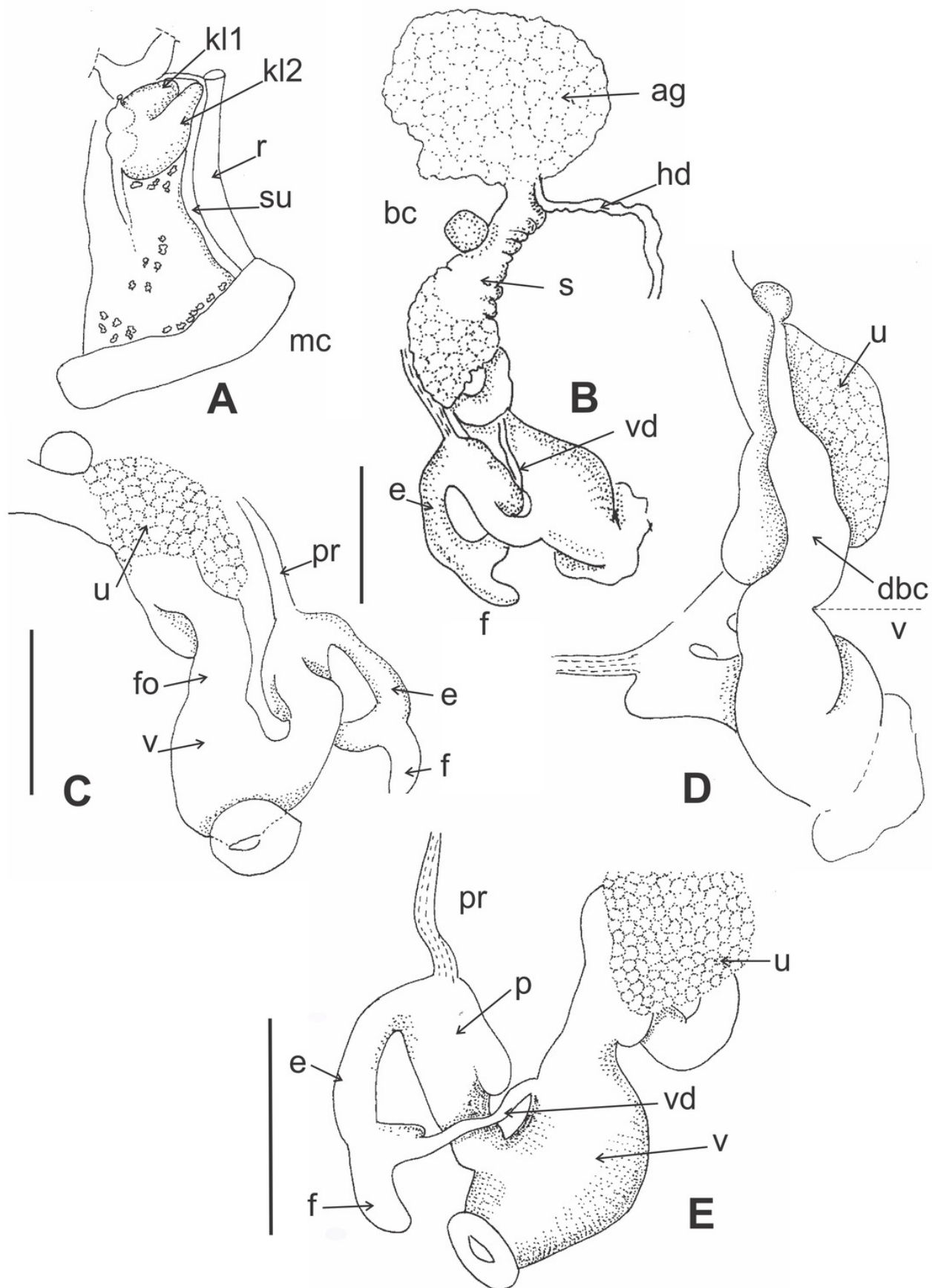
Figure 5

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.
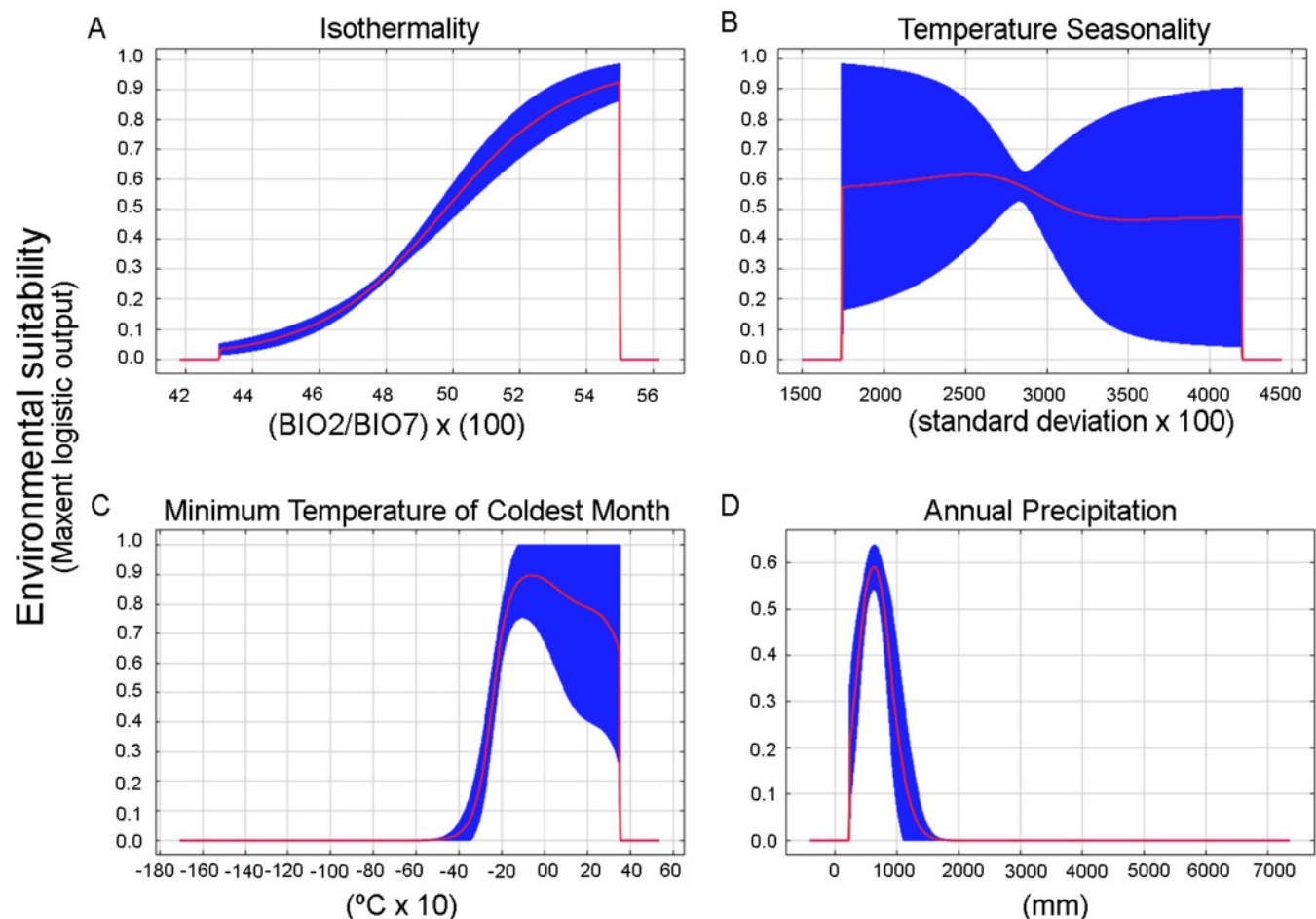
Figure 6

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.
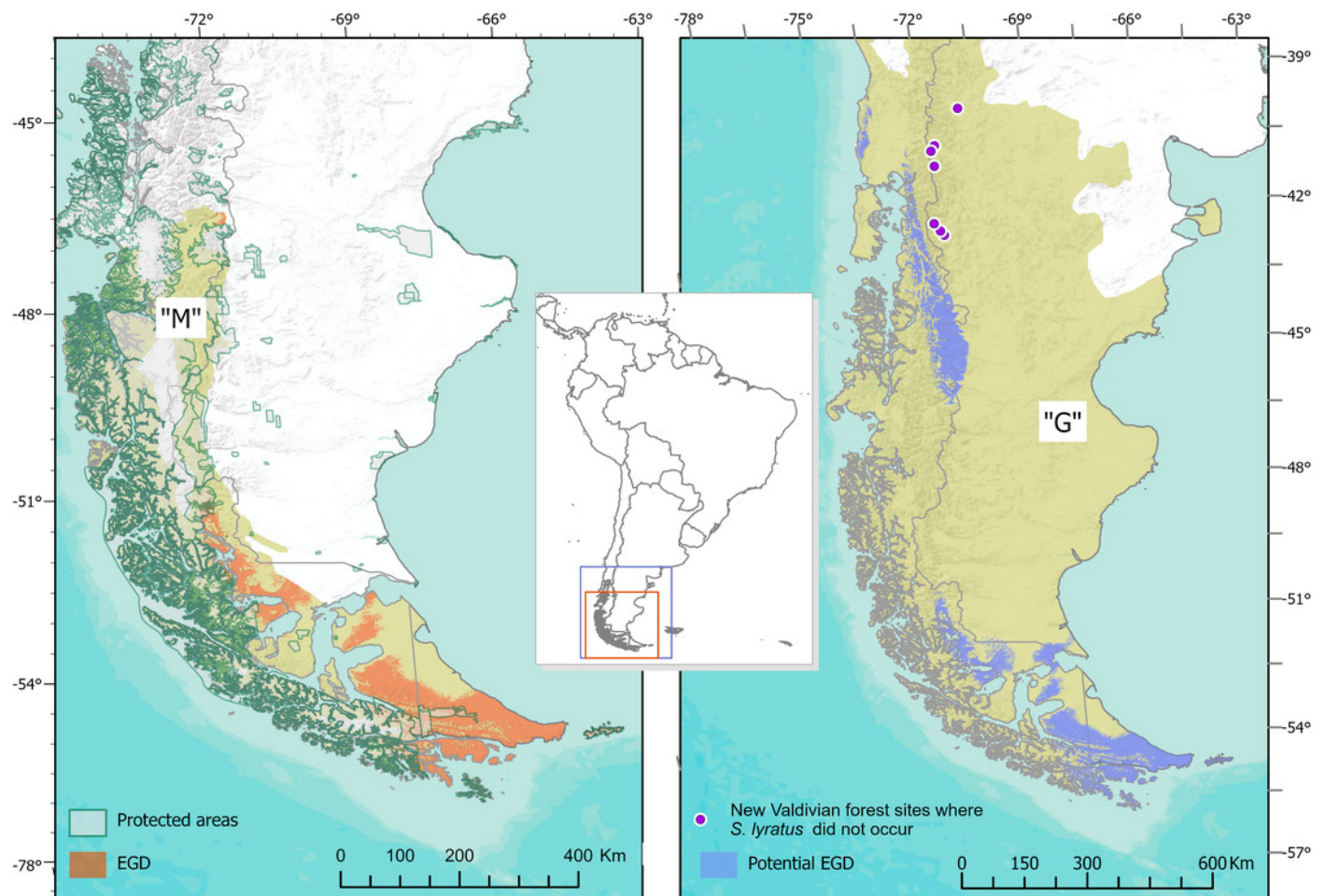
PeerJ

Table 1(on next page)

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

1

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

2

Table 2(on next page)

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

1