

# Distribution, conservation status and proposed measures for preservation of *Radiodiscus* microgastropods in Chile

Gonzalo A. Collado<sup>1,2</sup>, Rodrigo B. Salvador<sup>3,4,5</sup>, Marcela Vidal<sup>1,2</sup>, Fernanda Parra Aravena<sup>1</sup>, Vannia Delgado<sup>1</sup> and Cristian Torres-Díaz<sup>1,2</sup>

- <sup>1</sup> Departamento de Ciencias Básicas, Universidad del Bío-Bío, Chillán, Ñuble, Chile
- <sup>2</sup> Grupo de Investigación en Biodiversidad and Cambio Global, Universidad del Bío-Bío, Chillán, Chile
- <sup>3</sup> Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand
- <sup>4</sup> Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and Economics, UiT—The Arctic University of Norway, Tromsø, Norway
- <sup>5</sup> The Arctic University Museum of Norway, UiT—The Arctic University of Norway, Tromsø, Norway

# **ABSTRACT**

The genus Radiodiscus includes minute terrestrial snails occurring throughout the American continent. We assessed the conservation status of eight poorly known Chilean Radiodiscus species using the International Union for Conservation of Nature (IUCN) and NatureServe categories and criteria. Under the IUCN guidelines the species were assessed using the Criterion B of geographic range, which considers the extent of occurrence (EOO) and area of occupancy (AOO) as subcriteria. For NatureServe we used these two parameters plus the number of occurrences, ecological viability, and threats. Considering species rarity and possible sampling bias, we also used ecological niche modeling to determine climate and environmental tolerances and predict potential species distributions analyzing bioclimatic and geographical layers. Radiodiscus australis, R. coarctatus and R. quillajicola were listed as Critically Endangered by IUCN and NatureServe standards; R. coppingeri, R. flammulatus, R. magellanicus and R. villarricensis as Endangered by both methods; while R. riochicoensis as Endangered by IUCN standards and Vulnerable by NatureServe standards. Niche modeling results indicated that Radiodiscus species respond to different environmental conditions and that the predicted distribution areas contain suitable habitats beyond the current ranges, which may be helpful for future management plans. Nature-based sport tourism, forestry activities, urbanization, roads, pollution, mining, forest fires, livestock, volcanism, tsunamis, soil erosion and introduced species are among the major threats affecting these snails. Based on the low number of occurrences and the threats identified, the most at-risk species are R. coarctatus and R. quillajicola (one record), R. australis (two records) and R. villarricensis (three records); the latter two lacking occurrences within protected areas. Compiling our findings, we propose a list of actions to preserve Chilean Radiodiscus species.

Subjects Conservation Biology, Ecology, Zoology

Keywords Conservation biology, Endangered species, IUCN Red List, Land snails,
Micromollusks, NatureServe

Submitted 5 May 2022 Accepted 16 August 2022 Published 10 January 2023

Corresponding author Gonzalo A. Collado, gcollado@ubiobio.cl, collado.gonzalo@gmail.com

Academic editor Alison Nazareno

Additional Information and Declarations can be found on page 15

DOI 10.7717/peerj.14027

© Copyright 2023 Collado et al.

Distributed under Creative Commons CC-BY 4.0

OPEN ACCESS

# INTRODUCTION

Habitat loss is considered the major threat to biodiversity (Rawat & Agarwal, 2015). However, other human-induced factors, such as the introduction of exotic species, environmental pollution and rapid climate change, can also lead species to extinction (Richards, 2002; Matthies et al., 2004; Thomas et al., 2004; Mason, 2015). The Mediterranean climate zone of central Chile harbors two of the 25 global biodiversity hotspots (Myers et al., 2000). However, like other important ecosystems around the world, these have been drastically affected by human activities (e.g., habitat loss, urbanization, poaching, overgrazing, pollution, mining, energy generation, roads, fires, introduced species), which impacts the local biota and the ecosystem services they provide (CONAMA, 2003; Soto et al., 2006; Valderrama, Contreras-Reyes & Carrasco, 2018; Carranza et al., 2020; Moat et al., 2021). According to the MMA (2021), over 33,000 native species have been described from Chile, of which around 22-25% are endemic. Thus, the totality of Chilean biota account for about 1.5% of the species described for the world (MMA, 2021). This relatively high biodiversity has been attributed to the country's biogeographical isolation due to the barriers surrounding the territory: the Andes to the east, the Pacific Ocean to the west, the Atacama Desert to the north, and the Antarctic Ocean to the south.

The genus Radiodiscus Pilsbry in Pilsbry & Ferriss, 1906 (Charopidae) comprises around 25 species of minute terrestrial snails distributed throughout the Americas from western USA to Tierra del Fuego (Smith, 1881; Hylton Scott, 1970; Schileyko, 2001; Rutherford, 2020). The taxonomic treatment of these micromollusks has been historically difficult due to their small size, since at an adult age, the individuals are generally less than 2 mm in shell length (Miquel & Bellosi, 2007; Rutherford, 2020). Furthermore, they live in the soil and leaf litter and are thus typically overlooked in collection efforts and underrepresented in natural history collections (Salvador et al., 2020). According to molecular phylogenetic studies, Charopidae is paraphyletic and so is the genus Radiodiscus: specimens of Radiodiscus from Chile and Brazil, for instance, form unrelated branches in the family's phylogenetic tree (Salvador et al., 2020). The placement of the type species of the genus, Radiodiscus millecostatus Pilsbry & Ferriss, 1906 (type locality in Arizona, USA; Pilsbry & Ferriss, 1906) in the tree remains unknown. In the few checklists that include Chilean Radiodiscus species, they were historically classified in the family Endodontidae (Stuardo & Vega, 1985; Valdovinos, 1999), but are currently placed in the family Charopidae following more recent taxonomic treatments based on morphological and molecular data (Aldea, Novoa & Rosenfeld, 2019; Schileyko, 2001; Salvador, 2021). As currently understood, Radiodiscus is potentially a wastebasket taxon that houses species whose protoconch sculpture pattern consists in numerous spiral cordlets (Zilch, 1959; Schileyko, 2001; Salvador, 2021). Despite these uncertainties, this genus remains a useful taxonomic umbrella for conservation purposes. In Chile, the degree of threat to which Radiodiscus species are exposed is not known.

A high degree of endemism has developed in the Chilean territory, with many species having one or few populations. Concordantly, few records may be a consequence of a restricted habitat, not necessarily sampling bias. *Hortal et al.* (2015) summarized the seven

main shortfalls that affect the knowledge of biodiversity in all taxonomic groups, covering taxonomy, distribution, abundance, phylogenetic relationships, adaptations, ecological niche and interactions, and Radiodiscus does not escape this situation. Although the Chilean species of this genus are poorly known in many aspects, the lack of "perfect" data should not impair conservation assessments (Pokharel, Ludwig & Storch, 2016). Thus, these limitations offer an opportunity to evaluate the conservation status of Chilean Radiodiscus species, appraise the threats they face, their known and potential geographic distribution, as well as the environmental and climatic variables influencing their habitats. A necessary step to prevent extinction of a species is making opportune assessments of the conservation status (Bernardos, Amado & Amich, 2006). The International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN, 2001) and the Natural Heritage Network Element Ranking System (NatureServe, 2006) are two international initiatives created for this purpose, and most countries have similar national-scale organizations. In Chile, the institution in charge of evaluating the conservation status of species is the Ministry of the Environment (MMA, 2021), based on the IUCN's guidelines (Squeo et al., 2010). On the other hand, environmental niche modeling, ecological niche modeling or species distribution modeling has achieved significant development in the last two decades, covering, in addition to the current and potential distribution of native and invasive species, aspects regarding climatic change, conservation biology, eco-restoration sites and eco-cultural reconstruction, species delimitation, estimate ancestral distribution, investigate speciation processes, discoveries of new species, subspecies, cryptic species and areas of endemism (Peterson & Holt, 2003; Graham et al., 2004; Wiens & Graham, 2005; Banks et al., 2006; Raxworthy et al., 2007; Hammerson et al., 2017; Carvajal-Hernández et al., 2020).

The aims of the present study were to (1) estimate the current distribution of the Chilean *Radiodiscus* species (*sensu lato*) and assess their conservation status according to categories and criteria implemented by the IUCN (*2001*, *2014*, *2019*) and *NatureServe* (*2006*) and (2) determine climate and environmental variables influencing the habitat of species and predict their potential distributions using ecological niche modeling. Finally, we propose measures to conserve the species based on occurrence records, geographic distribution, conservation status, habitat availability and threats.

#### **MATERIALS & METHODS**

### Chilean Radiodiscus species

We follow the currently accepted literature in assigning eight Chilean species to the genus Radiodiscus (Stuardo & Vega, 1985; Valdovinos, 1999; Aldea, Novoa & Rosenfeld, 2019). Three of those species are endemic to Chile, namely Radiodiscus coarctatus Hylton Scott, 1979, Radiodiscus quillajicola Vargas-Almonacid, 2000 and Radiodiscus villarricensis Miquel & Barker, 2009, while the remaining five species occur in Chile and Argentina: Radiodiscus australis Hylton Scott, 1970, Radiodiscus coppingeri (Smith, 1881), Radiodiscus flammulatus Hylton Scott, 1975, Radiodiscus magellanicus (Smith, 1881) and Radiodiscus riochicoensis Crawford, 1939.

Information on the distribution and biology of these species was likewise obtained from the literature, through different sources including original descriptions, subsequent taxonomic contributions, distribution records and species checklists (*Smith*, 1881; *Pilsbry*, 1911; *Crawford*, 1939; *Hylton Scott*, 1957; *Hylton Scott*, 1963; *Hylton Scott*, 1970; *Hylton Scott*, 1979; *Stuardo & Vega*, 1985; *Fonseca & Thomé*, 1993; *Fonseca & Thomé*, 1994; *Valdovinos*, 1999; *Vargas-Almonacid*, 2000; *Sielfeld*, 2001; *Miquel & Bellosi*, 2007; *Tablado & Mantinian*, 2004; *Miquel & Bellosi*, 2007; *Miquel & Barker*, 2009; *Miquel & Aguirre*, 2011; *Aldea*, *Novoa & Rosenfeld*, 2019; *Salvador et al.*, 2021). In addition, we also include GBIF records provided by prominent malacologists or curators of mollusks collections (*Darrigran & Damborenea*, 2017; *Tablado & Rodríguez*, 2021; *Goud*, *van der Bijl & Creuwels*, 2022), as well as *Hylton Scott* (1970) and *Hylton Scott* (1979) (see Table S1 for links to these sources).

Six further species of micromollusks originally described by *Philippi* (1855) under the genus *Helix* Linnaeus, 1758 are considered of uncertain affinities (*Stuardo & Vega*, 1985) but have been recently listed as species of *Radiodiscus* in platforms such as *GBIF* (2021) and *MolluscaBase* (2021) without any explanation for the decision. Therefore, those six "*Helix*" species were not included in the present study.

#### **Conservation status**

Historical localities recovered from the literature for each species of *Radiodiscus* are available in Table S1. Those localities lacking geographic coordinates were georeferenced *via* the radio-point method. This procedure consists in establishing a central point within the area reported in the respective publication and to define a circumference around it that includes the most probable collection site and its associated uncertainty (*Wieczorek, Guo & Hijmans, 2004; Escobar et al., 2016*). Geographic coordinates and radius of uncertainty were obtained using the software Google Earth (v.7.3.3.7786; Google Inc., Mountain View, CA, USA).

The IUCN categorizes species according to five criteria: Criterion A refers to population size reduction, Criterion B to geographic range, Criterion C to small population size and decline, Criterion D to very small or restricted population, and Criterion E to quantitative analysis of the probability of extinction. We assessed the conservation status of the Chilean Radiodiscus species using Criterion B because no information is available for the application of criteria A, C, and E in this group. Criterion B considers geographic range of species, involving subcriterion B1, based on the extent of occurrence (EOO), and subcriterion B2, based on the area of occupancy (AOO). Basically, the EOO is the area covered by the polygon formed by a union line that encloses all occurrences of a species while the AOO is the sum of the estimated areas around each occurrence. In the latter case, a 2 km<sup>2</sup> grid cell was used (Bland et al., 2016; IUCN, 2019). To calculate the parameters EOO and AOO and to automatically obtain a preliminary conservation category, the geographic coordinates of each species were introduced into the GeoCAT program (Bachman et al., 2011). We also apply sub-criterion D2 (Criterion D), for species with few locations ( $\leq 5$ ), an AOO < 20 km<sup>2</sup> and at least one plausible threat. If a species meets these conditions it must be listed as Vulnerable: D2. The conservation categories that can be obtained using this

Table 1 Data used for conservation status assessment of Chilean species of <i>Radiodiscus</i> based on NatureServe standards.						
Species	О	EOO (km²)	AOO (km²)	Occurrences with good ecological viability	Threat impact	
Radiodiscus australis	1–5	<100	6–25	1–3	Very high	
Radiodiscus coarctatus	1–5	<100	3–5	1–3	Very high	
Radiodiscus coppingeri	21-80	200,000-2,500,000	126-500	13–40	Very high	
Radiodiscus flammulatus	6-20	20,000-200,000	26-125	4–12	High	
Radiodiscus magellanicus	6-20	200,000-2,500,000	26-125	13–40	Very high	
Radiodiscus quillajicola	1–5	<100	3–5	1–3	High	
Radiodiscus riochicoensis	6-20	200,000-2,500,000	26-125	13-40	High	
Radiodiscus villarricensis	1-5	1,000-5,000	6-25	1–3	High	

Notes.

Abbreviatures: O, occurrences; EOO, extent of occurrence; AOO, area of occupancy.

tool are Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN) and Critically Endangered (CR).

To assess the conservation status based on NatureServe's standards (Faber-Langendoen et al., 2012; Master et al., 2012) we used the Conservation Rank Calculator tool (NatureServe, 2021), which allows entering the data of the species to obtain a conservation category based on the range extent (equivalent to EOO), area of occupancy (AOO), numbers of occurrences, ecological viability, population trends and threats (Table 1). NatureServe also allows the researcher to specify the geographic level of the conservation assessment: Global (G), National (N), and Subnational (S) (Faber-Langendoen et al., 2012; Master et al., 2012). Under this methodology, the species may be assigned to one of the five categories: Critically Imperiled (G1/N1/S1), Imperiled (G2/N2/S2), Vulnerable (G3/N3/S3), Apparently Secure (G4/N4/S4) and Secure (G5/N5/S5). We determined ecological viability in the sense of habitat quality using satellite images on Google Earth exploring whether the occurrence records and surrounding areas of Radiodiscus species still have natural coverage thus providing a suitable environment to live ("Good" habitat in Table S1). The threats facing species were obtained merging species occurrence records with road, hydrographic and urban development vector layers available in the Library of the National Congress of Chile (https://www.bcn.cl/siit/mapas vectoriales), which were analyzed in QGIS v.3.22.7 software (QGIS Development Team, 2021), as well as information obtained from the literature, government organizations and the media. Operationally, in the Conservation Rank Calculator we first enter the threats identified previously in each species assigning the highest level of threat in the "Threats Assessment Worksheet" to then record in the "Calculator Form Worksheet" the data available per taxon regarding EOO, AOO, occurrence records, ecological viability and threats. The present study was carried out at the national level (N), without considering population trends due to lack of information.

# Mapping of occurrences over protected areas

The Chilean National System of Protected Areas (SNASPE, "Sistema Nacional de Áreas Silvestres Protegidas del Estado") has established 118 protected areas to preserve the country's natural heritage (*Root-Bernstein et al.*, 2013; Subsecretaría de Turismo, 2015). These areas include National Parks, National Reserves, Biosphere Reserves, Natural Monuments, Ramsar Sites, National Protected Goods, Marine Reserves and Coastal Marine Protected Areas. The total coverage of those areas is about 20% of the national territory (*Root-Bernstein et al.*, 2013; Subsecretaría de Turismo, 2015). To determine if any of the species occurs within any of the protected areas, we built maps in QGIS previously entering vector layers of the country's regions and protected areas available at the Library of National Congress of Chile (https://www.bcn.cl/siit/mapas\_vectoriales). At the same time, the EOO, AOO and occurrence records of the species were downloaded from GeoCAT in KML format to be used in QGIS.

# **Ecological niche modeling**

A total of 19 bioclimatic variables (Fick & Hijmans, 2017) were downloaded from the WorldClim database version 2.0 (http://www.worldclim.org) and used in conjunction with environmental variables obtained from the same platform (solar radiation, evaporation, elevation, wind) [resolution of  $\sim 1 \text{ km}^2(30 \text{ s})$ ]. Each variable was merged with a vector geographic layer of the Chilean territory available in the Library of the National Congress of Chile (https://www.bcn.cl/siit/mapas vectoriales) in a new raster variable (.ASCII) using ArcGIS v.10.8 software (Esri, Redlands, CA, USA). To estimate potential species distribution, we uploaded species occurrence records and the complete set of variables in the Maxent v.3.4.4 software (Phillips, Dudík & Schapire, 2004) to run four models per species computed using the logistic option. Model 1 was performed including all climatic and environmental variables and default settings. Model 2 included all variables with a setting of 25% of the occurrences for model testing. Model 3 included only the variables that most contributed to the model and that were obtained in Model 2, with default settings. Model 4 was the Model 3 but setting 25% for model testing. The performance of the model was validated with the AUC (area under the curve) based on the Receiver Operating Characteristic (ROC), which estimates values from 0.5 to 1.0, with values above 0.8 depicting a good fit of the model (Loo, Mac Nally & Lake, 2007). The importance of the variables that best explained the presence of Radiodiscus species was evaluated with the Jackknife test, which identifies the variable with highest gain regarding the other variables. The potential species distribution map resulting from the selected model was converted from ASCII to raster in ArcGIS for visualization.

## **RESULTS**

Considering historical records, the genus *Radiodiscus* is distributed in Chile from the country's central-south zone to the austral zone (Figs. 1A–1H; Table S1). The areas of occupancy still have natural coverage that can support species, even for those populations whose records in the literature are decades old (Table S1). The species with the largest geographic distributions are *R. flammulatus* and *R. riochicoensis*, which range from the

Table 2 Distributional data and conservation status based on IUCN Red List and NatureServe categories and criteria for Chilean species of *Radiodiscus*.

Species	O	OPA	EOO	AOO	IUCN			NS
			(km <sup>2</sup> )	(km <sup>2</sup> )	EOO	AOO	D	
R. australis	2	0	0.005*	8	CR B1ab(iii)	CR B2ab(iii)	D2	N1
R. coarctatus	1	1	$0.002^{*}$	4	CR B1ab(iii)	CR B2ab(iii)	D2	N1
R. coppingeri	34	21	361,932	128	LC	EN B2ab(iii)		N2
R. flammulatus	10	6	141,827	40	LC	EN B2ab(iii)		N2
R. magellanicus	19	13	461,888	76	LC	EN B2ab(iii)		N2
R. quillajicola	1	0	$0.003^{*}$	4	CR B1ab(iii)	CR B2ab(iii)	D2	N1
R. riochicoensis	15	9	335,700	56	LC	EN B2ab(iii)		N3
R. villarricensis	3	1	3,061	12	EN B2ab(iii)	EN B2ab(iii)	D2	N2

#### Notes.

Threatened IUCN categories: CR, Critically Endangered; EN, Endangered; LC, Least Concern; D2, Vulnerable. Threatened NatureServe categories: N1, Critically Imperiled; N2, Imperiled; N3, Vulnerable.

Other abbreviatures: NS, NatureServe; O, occurrences; OPA, occurrences in protected areas; EOO, extent of occurrence; AOO, area of occupancy.

Bío-Bío Region to the Magallanes y Antártica Chilena Region. *Radiodiscus quillajicola* is the northernmost species of the genus in Chile. Four species have less than four occurrences at national level and four others have between 10 and 34 occurrences, and only *R. coppingeri* has over 20 occurrences (Table 2). The species restricted to a single locality are *R. coarctatus* (Magallanes y Antártica Chilena Region in southern Patagonia) and *R. quillajicola* (Maule Region in the central area of the country). Six species have at least one occurrence within protected areas, namely: *R. coarctatus*, *R. coppingeri*, *R. flammulatus*, *R. magellanicus*, *R. riochicoensis* and *R. villarricensis* (Table 2).

Based on IUCN standards, GeoCAT outputs showed EOO values ranging between 0.002 km<sup>2</sup> (R. coarctatus) and 461,888 km<sup>2</sup> (R. magellanicus), and AOO values between 4 km<sup>2</sup> (R. coarctatus and R. quillajicola) and 128 km² (R. coppingeri). Since EOO is greater than AOO, empirical values of EOO lower than AOO should be changed to make them equal to AOO (IUCN, 2014; IUCN, 2019). According to EOO, three species were classified as Critically Endangered (CR), four as Least Concern (LC) and one Endangered (EN); conversely, by using AOO, three species were classified as CR and five as EN (Table 2). Radiodiscus australis is listed as Critically Endangered CR B1ab(iii)+2ab(iii) since the EOO < 100 km<sup>2</sup> (B1), AOO < 10 km<sup>2</sup> (B2), number of locations =2 (a) and decline in habitat quality due to human activities and invasive species [b(iii)]. Radiodiscus coarctatus and R. quillajicola are listed as CR B1ab(iii)+2ab(iii) since the EOO  $< 100 \text{ km}^2 \text{ (B1)}$ , AOO  $< 10 \text{ km}^2 \text{ (B2)}$ , number of locations = 1 (a) and decline in habitat quality due to human activities and natural disasters [b(iii)]. Radiodiscus villarricensis is listed as EN B1ab(iii)+2ab(iii) since the EOO < 5000 km<sup>2</sup> (B1), AOO < 500 km<sup>2</sup> (B2), number of locations = 3 (a) and decline in habitat quality due to human activities and natural disasters [b(iii)]. Radiodiscus coppingeri, R. flammulatus, R. magellanicus and R. riochicoensis are listed as EN B2ab(iii) since the AOO < 500 km<sup>2</sup> (B2), AOO severely fragmented assumed from the great distance between the known populations and low vagility of species (a), and decline in habitat quality due to

<sup>\*</sup>Values of EOO should be changed to make them equal to AOO (IUCN, 2019).

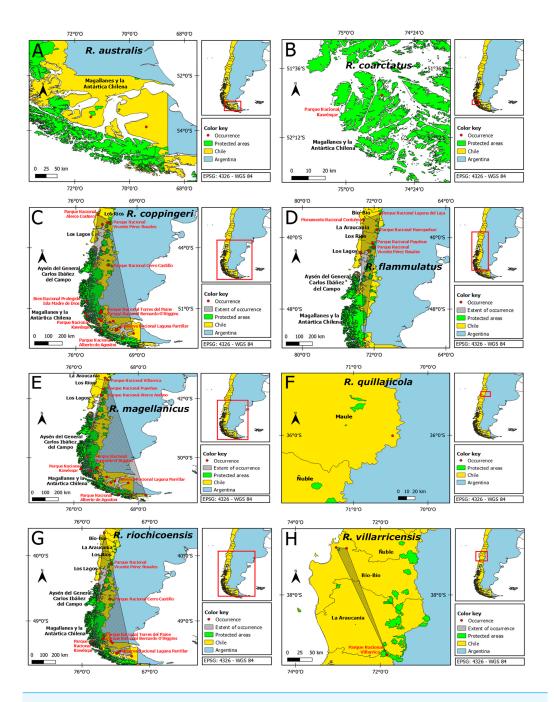


Figure 1 Mapping of occurrences Radiodiscus spp. in Chile, highlighting protected areas. (A) Radiodiscus australis, (B) Radiodiscus coarctatus, (C) Radiodiscus coppingeri, (D) Radiodiscus flammulatus, (E) Radiodiscus magellanicus, (F) Radiodiscus quillajicola, (G) Radiodiscus riochicoensis, (H) Radiodiscus villaricensis. The maps were created using GeoCAT (http://geocat.kew.org/) and QGIS (http://www.arcgis.com/index.html) software. (Maps: F Parra, V Delgado and GA Collado).

Full-size DOI: 10.7717/peerj.14027/fig-1

human activities and natural disasters [b(iii)]. Using the D2 subcriterion, four species were also listed as Vulnerable (D2) (Table 2). Based on NatureServe standards, the threats impact obtained using the Conservation Rank Calculator was "High" for four species and

"Very high" for four others (Table 1). Under this system, three species were classified as Critically Imperiled (N1), four as Imperiled (N2) and one as Vulnerable (N3) (Table 2).

We did not find reports in the scientific literature of any specific threats affecting Chilean *Radiodiscus* species. However, we detected at least 17 potential threats with the other methods proposed, which are applicable to most terrestrial snails in the country: nature and sports tourism, forestry activities, illegal logging of native forests, livestock, heavy rainfall events, introduced species, activities associated with artisanal fishing, soil erosion, pollution, forest fires, urbanization, volcanism, tsunamis, mining, highways and roads, hydroelectric plants, and droughts (Table S2). The most common threats affecting all species are tourism and geological events (volcanism).

We performed niche modeling in six of the eight species in which the conservation status was evaluated given that R. coarctatus and R. quillajicola had only one occurrence record and for this reason they were not modeled. Niche modeling results showed that Radiodiscus species may occupy potential habitats beyond their current range (Fig. 2), especially R. riochicoensis and R. magellanicus, whose potential distribution could extend to northern Chile, and R. flammulatus to Chiloé Island. Modeling also indicated that different climate and environmental variables influencing the habitat of Chilean Radiodiscus species (Table 3). Among all variables, MaxEnt selected the solar radiation as the most influential in the probability of occurrence of R. australis, R. magellanicus and R. riochicoensis, contributing with 29.7%, 43.5% and 65.1% to the model, respectively. For R. magellanicus, however, the Minimum temperature of coldest month (Bio6) was also important, accounting for 35.9%. For R. villarricensis, the most influential variable was Precipitation of wettest month (Bio13), contributing with 42.7%, while for R. flammulatus it was Precipitation of the coldest quarter (Bio19) (87.3%), and for R. coppingeri Precipitation of driest quarter (Bio17) (40.7%). The contribution of the other variables to the model in each species is shown in Table 3. The AUC values ranged from 0.79 to 0.97 among species, indicating a good fit of the model (Table 3).

#### DISCUSSION

The conservation status assessment estimated in the present study shows that *R. australis*, *R. coarctatus* and *R. quillajicola* should be listed as Critically Endangered (CR) by the IUCN Red List and Critically Imperiled (N1) by NatureServe, two equivalent categories that represent the highest threats. Of these three species, the most threatened are *R. coarctatus* and *R. quillajicola* since their distribution is restricted to only one locality (Figs. 1B and 1F). These species, which have few records, were not considered as Data Deficient (DD) due to their endemism, so they were treated as being circumscribed to one or a few localities, as recommended by the *IUCN* (2014). In addition, this organization also recommends that taxa listed as Data Deficient (DD) should not be treated as if they were not threatened, considering the number of threats species face. Of all species, it can be argued that *R. quillajicola* is the most at-risk species since it inhabits only one locality that does not fall within a protected area. Based on the AOO, *R. coppingeri*, *R. flammulatus*, *R. magellanicus*, *R. villarricensis* and *R. riochicoensis* were listed as Endangered (EN) by the IUCN criteria,

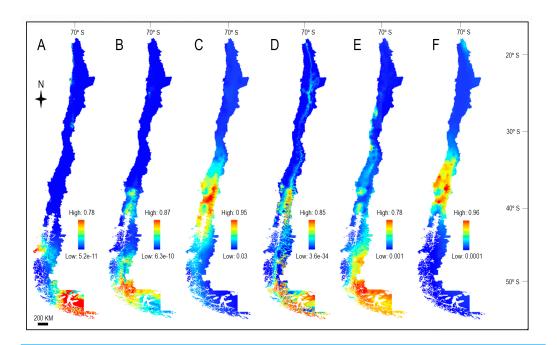


Figure 2 Ecological niche modeling for Chilean Radiodiscus spp. generated using MaxEnt. (A) Radiodiscus australis, (B) Radiodiscus coppingeri, (C) Radiodiscus flammulatus, (D) Radiodiscus magellanicus, (E) Radiodiscus riochicoensis, (F) Radiodiscus villarricensis. The maps were created using ArcGIS software (http://www.arcgis.com/index.html). (Maps: GA Collado).

Full-size DOI: 10.7717/peerj.14027/fig-2

which is consistent with the classification of these species as Imperiled (N2) according to NatureServe (except *R. riochicoensis*).

While *Mansur* (1996a) listed *R. coppingeri* (as *Radiodiscus coppingers* [sic]) as Data Deficient (DD) following IUCN criteria, our national scale evaluation of this species as Least Concern (LC) (EOO) or Endangered (EN) (AOO) is more informative and useful for conservation efforts in Chile. Besides *R. coppingeri*, only three *Radiodiscus* species have been assessed by the IUCN: *Radiodiscus amoenus* Thiele, 1927 and *Radiodiscus compactus* Suter, 1980 from Brazil, listed as Endangered (EN) and Vulnerable (VU), respectively (*Mansur*, 1996b; *Mansur*, 1996c), and *Radiodiscus iheringi Smith*, 1881 from Argentina, Brazil, and Uruguay, listed as Data Deficient (DD) (*Mansur*, 1996d). Under NatureServe, *Turgeon et al.* (1998) listed *R. millecostatus* as Vulnerable (G3) and *Radiodiscus abietum* (Barker, 1930) as Apparently Secure (G4). No species of *Radiodiscus* has so far been evaluated by the *MMA* (2021) in Chile.

While the potential distribution models of species are not considered as a parameter to evaluate their conservation status of species through IUCN or NatureServe guidelines, they can be used to determine potential suitable habitats, in addition to knowing the environmental factors that species tolerate (*Carvajal-Hernández et al.*, 2020). *Radiodiscus flammulatus* and *R. villarricensis* inhabit the central-south area of Chile, while *R. australis*, *R. coppingeri*, *R. magellanicus* and *R. riochicoensis* occur in the south-austral zone of the country. Although the distribution patterns of these species appear as highly disjunct, in

Table 3 Ecological niche modeling results with respect to the relative contributions (in percentage) of the climate and environmental variables in species of *Radiodiscus* and model validation.

Variable/model performance	Radiodiscus spp.						
	Australis	Coppingeri	Flammulatus	Magellanicus	Riochicoensis	Villarricencis	
Climatic							
bio1							
Bio2	15.6	15.6			3.5		
Bio3		3.6	3.5	6.3	1.7		
Bio4							
Bio5							
Bio6				35.9			
Bio7							
Bio8	3.5						
Bio9							
bio10							
bio11		0.1					
bio12		0.7					
bio13		0.9				42.7	
bio14		8.6		4.3		39.3	
bio15	14.1	0.9		1.5			
bio16	6.7			6.4			
bio17		40.7					
bio18			9.2				
bio19	19.5	6.5	87.3		23.1	18	
Environmental							
Elevation	10.9	8.5		2.1	6.6		
Evaporation		1.5					
Solar Radiation	29.7	1.9		43.5	65.1		
Wind		10.5					
Performance							
AUC training data	0.97	0.95	0.84	0.92	0.89	0.974	
AUC test data	_	0.85	0.92	0.91	0.79	_	

#### Notes.

Variables used: Bio1, Annual mean temperature; bio2, Mean diurnal range (monthly mean: T° max–T° min); bio3, Isothermality; bio4, Temperature seasonality; bio5, Maximum temperature of warmest month; bio6, Minimum temperature of coldest month; bio7, Temperature annual range (bio5–bio6); bio8, Mean temperature of wettest quarter; bio9, Mean temperature of driest quarter; bio10, Mean temperature of the warmest quarter; bio11, Mean temperature of coldest quarter; bio12, Annual precipitation; bio13, Precipitation of wettest month; bio14, Precipitation of driest month; bio15, Precipitation seasonality; bio16, Precipitation of wettest quarter; bio17, Precipitation of driest quarter; bio18, Precipitation of the warmest quarter; bio19, Precipitation of the coldest quarter.

some cases being separated by hundreds of kilometers, MaxEnt modeling inferred that their distribution areas contain suitable habitats beyond the currently known occurrences and range. However, considering that for *R. australis* and *R. villarricensis* two and three records were used in the modeling, respectively, the derived results should be interpreted as identifying regions that have similar environmental conditions to those present in the occurrence sites of the species (*Pearson et al.*, 2007), *i.e.*, not predicting realized niches. Modeling also indicated that the Chilean *Radiodiscus* species respond to different

environmental conditions. These overpredicted areas have been identified as potential habitats that may contain new species, as well as discovering previously unknown ranges (*Raxworthy et al.*, 2003; *Menon et al.*, 2010).

#### **Recommended conservation measures**

To date, there are no studies addressing the genetic diversity of any of the species of *Radiodiscus* in Chile, so it is still unknown whether there is gene flow between populations of more widespread species. Even their basic biology, such as life cycle, reproduction, development, vagility and population sizes, remains to be investigated. Considering these gaps in knowledge, and according to the degree of risk reported here, our first recommendation is to carry out basic studies on the biology of these species, prioritizing the most threatened ones.

Several in situ and ex situ conservation measures have been proposed in conservation biology (Berkmüller & Savasdiasara, 1981; Bloxam, Tonge & Horton, 1984; Tonge & Bloxam, 1991; CBD, 1992; Pearce-Kelly et al., 1997; Balmford, Leader-Williams & Green, 1995; Mace, Pearce-Kelly & Clarke, 1998; IUCN, 2002; Hadfield, Holland & Olival, 2004; Anonymous, 2005; Kadis, Thanos & Laguna Lumbreras, 2013; Trias-Blasi, Gücel & Özden, 2017). Article 8 of the CBD (1992) proposes 13 in situ conservation measures, including the establishment of protected areas, along with its management and protection, to promote the preservation of ecosystems and natural habitats, as well as to prevent the introduction of (or facilitate control or eradication) of exotic species. In accordance with these recommendations, ideally, we propose to enlarge the area of some national parks, create reserves, micro-reserves and environmental interpretive trails to preserve species of Radiodiscus in Chile (Berkmüller & Savasdiasara, 1981; Balmford, Leader-Williams & Green, 1995; Laguna et al., 2004). Although the beneficial results of interpretive trails have been questioned (Navrátil, Knotek & Pícha, 2015), the creation of this type of infrastructure remains common in conservation biology as it focuses on the education of the public rather than in all-out preservation of the area and its biota (Berkmüller & Savasdiasara, 1981; Munro, Morrison-Saunders & Hughes, 2008). On the other hand, micro-reserves have proven effective in conservation, where small plots of land of a few hectares are established (Kadis, Thanos & Laguna Lumbreras, 2013; Trias-Blasi, Gücel & Özden, 2017). Micro-reserves are easier to create and can benefit the area and its species, although they need to be established as a network of reserves to succeed (Lumbreras, 2001). Their success for plant species (Laguna et al., 2016) might be a good sign for micromollusks with supposed reduced mobility.

Article 9 of the *CBD* (1992) also proposes five *ex situ* measures that may be implemented for species conservation. Some *ex situ* conservation efforts have been developed through captive breeding programs to preserve tree snails of the families Achatinellidae and Partulidae (*Bloxam*, *Tonge & Horton*, 1984; *Tonge & Bloxam*, 1991; *Pearce-Kelly et al.*, 1997; *Mace*, *Pearce-Kelly & Clarke*, 1998; *Hadfield*, *Holland & Olival*, 2004), endemic to Hawaii and islands of the south-western tropical Pacific Ocean, respectively, which face extinction. However, up to our knowledge there are no reports of successful breeding of

minute Charopidae snails such as *Radiodiscus* spp., so the feasibility of this approach is uncertain.

Some *in situ* and *ex situ* conservation measures are proposed below for Chilean *Radiodiscus* species. The benefits and drawbacks of each approach must be assessed and weighted against costs and immediate and potential benefits. Realistically, not all of these measures will be feasible in all concerned areas in Chile and, as such, they should be assessed on a case-by-case basis alongside policy makers.

Radiodiscus australis (Fig. 1A) presents only two occurrences in Chile, none of them within a protected area. It is exposed to a high level of nature and sports tourism, and forestry activities (exploitation of native forests for wood, firewood and paper and livestock disturbance) (Magallanes, 2012; Arredondo et al., 2019). Furthermore, the area is inhabited by beavers (Castor canadensis Kuhl, 1820), an invasive species that drastically modifies the habitat (Graells, Corcoran & Aravena, 2015), although its net impact on the terrestrial snail fauna remains unstudied. Moreover, the Brunswik Peninsula has coal reservoirs (Magallanes, 2012), the exploitation of which could become a threat to the species in the near future. Today, ex situ conservation actions such as captive breeding should be trialed as a priority to preserve the species. We also recommend the implementation of in situ conservation actions such as environmental interpretive trails and beaver eradication where R. australis populations occur. The implementation of micro-reserves would also be an appropriate conservation measure.

Radiodiscus coarctatus (Fig. 1B) faces threats associated to tsunamis, tourism, artisanal fishing and soil erosion due to heavy rainfalls and strong winds (*DAPMA*, 2009), although adverse weather conditions in turn reduce tourism (*CONAF*, 2021). Although the species was described from Caleta Nantuel, Vidal Gormaz Island, within the Kawésqar National Park (Fig. 1B), we recommend the implementation of an environmental interpretation trail and implement *ex situ* conservation programs as mentioned above.

Radiodiscus coppingeri (Fig. 1C) faces threats in many fronts, such as tourism, soil erosion due to rainfall (storms), activities associated to artisanal fishing (*DAPMA*, 2009), solid contamination caused by the influx of tourists (*El Heraldo Austral*, 2019), illegal logging of native forest (*Magallanes*, 2012; *Mardones*, 2020), risk of forest fires (*CONAF*, 2020), and change in land use due to livestock (*Arredondo et al.*, 2019), as well as the presence of beavers in austral Patagonia (*Graells*, *Corcoran & Aravena*, 2015; *GEF*, 2019). In addition, several populations are close to urban areas, volcanoes, hydrocarbon mines (*SONAMI*, 2021) and coal reserves (*Martinic*, 2004; *Magallanes*, 2012). Even though *R. coppingeri* is the species with the highest number of occurrences, the conservation category resulting from this study was Endangered (EN) according to IUCN criteria (AOO) and Imperiled (N2) under NatureServe criteria (Table 2). We recommend enlarging the Bernardo O'Higgins National Park since there are five occurrences located on the eastern margin of the Serrano River. We also recommend the creation of environmental interpretive trails in different localities where this species occurs, as well as beaver eradication.

Radiodiscus flammulatus (Fig. 1D) is threatened by tourism and recreational activity, such as camping, that causes solid contamination (*El Heraldo Austral, 2019; Robles, 2021*). On the other hand, the Laguna del Laja National Park borders on infrastructure associated

with the El Toro hydroelectric plant, causing droughts in the area (*Arnaboldi*, 2016; *Díaz*, *Jaque & Ojeda*, 2018). Because *R. flammulatus* is Endangered (EN) or Imperiled (N2) according to our assessment, we suggest enlarging the Alerce Andino National Park since there is one occurrence approximately 0.1 km outside the park towards the V-657 highway. Similarly, we also suggest enlarging the Bernardo O'Higgins National Park (as for *R. coppingeri* above) because there is another occurrence located approximately 1.6 km from the park towards Lake Brush. We also recommend the creation of environmental interpretive trails since some of the threats mentioned above affect even the interior of protected areas.

Radiodiscus magellanicus (Fig. 1E) faces various threats such as monoculture forestry and exploitation of native trees (Magallanes, 2012), livestock activities for consumption and export (Arredondo et al., 2019), heavy rainfall (storms), high tourist activity and presence of the invasive beaver (Graells, Corcoran & Aravena, 2015; GEF, 2019). In addition, several populations of the species are located near volcanoes, highways/roads, urban areas and hydrocarbon mines. We recommend the creation of environmental interpretive trails in addition to enlarging the Bernardo O'Higgins National Park (as for R. coppingeri and R. flammulatus above), since there is one occurrence approximately 1 km from the park towards Lake Brush. We also recommend beaver eradication.

Radiodiscus quillajicola (Fig. 1F) inhabits a single locality near a busy highway with potential for landslides (Cooperativa, 2016; Arenas, 2017). In addition, this locality is not a protected area and is close to the Laguna del Maule volcanic complex, which currently has a yellow alert level (SERNAGEOMIN, 2021). Thus, the severity of the threats to this species is high. The trialing and implementation of ex situ conservation actions such as captive breeding should be considered a priority to preserve the species. We also recommend the creation of a micro-reserve to protect both the species and its habitat, in addition to implementing an environmental interpretation trail and surveying the neighboring area for eventual occurrences of the species.

Radiodiscus riochicoensis (Fig. 1G) faces serious threats such as the presence of the invasive beaver (*Graells, Corcoran & Aravena, 2015*; *GEF, 2019*), forestry activities for the exploitation of native forests (*Magallanes, 2012*), livestock activity focused on export (*Arredondo et al., 2019*), activities associated with artisanal fishing (*DAPMA, 2009*), pollution (*El Heraldo Austral, 2019*), risk of forest fires (*Vidal et al., 2015*), heavy rainfall (storms), and a high degree of tourism and recreational activities. In addition, some populations are located close to volcanoes, highways, urban areas, coal reservoirs (*Magallanes, 2012*) and hydrocarbon mines (*SONAMI, 2021*). We recommend the creation of environmental interpretive trails and micro-reserves for the protection of the species, as well as beaver eradication.

The three localities where *R. villarricensis* inhabits (Fig. 1H) face a large amount of tourism and recreational activities (*Subsecretaría de Turismo*, 2017; *Morales Flores*, 2019) and the risk of forest fires (*Villavicencio*, 2015; *Morales Flores*, 2019; *Enríquez*, 2021). In addition, two of the three occurrences are close to urban areas and one to volcanoes. We recommend the trialing and implementation of *ex situ* conservation programs, the creation of environmental interpretive trails, and the creation of a micro-reserve in Fundo

El Manzano, Bío-Bío Region. The feasibility of creating a national reserve in Cerro Caracol, Concepción city, should also be taken into consideration.

Identifying threatened species is one of the main tasks of conservation biology, following with an assessment of the threats and the development of strategies to remediate the situation (*Purvis et al.*, 2000; *Barbini et al.*, 2020). In the present study, we proposed *in situ* and *ex situ* conservation measures to preserve eight species of *Radiodiscus* in Chile, most of which are highly threatened. However, although these types of actions are not exempt from difficulties, such as the cost of the land, its management, territorial custody, associated facilities, staff and the type of feed and appropriate abiotic environmental conditions in the case of artificial rearing systems (*Hadfield, Holland & Olival, 2004*; *O'Rorke et al., 2016*; *Kadis, Thanos & Laguna Lumbreras, 2013*; *Laguna et al., 2004*; *Carranza et al., 2020*), they have been rather promising and therefore applicable to preserve species, including small snails.

## **CONCLUSIONS**

This study assesses for the first time the conservation status of *Radiodiscus* species using IUCN and NatureServe standards in parallel. Both systems categorized the eight Chilean species evaluated in categories of serious threat. The distribution of each of the species was also updated and the potential threats affecting them were identified. It is strongly recommended to carry out studies of the basic biology of the species and to implement conservation measures in the short term, especially for those that present a high risk of extinction.

#### **ACKNOWLEDGEMENTS**

We thank the referees for their helpful comments to improve the manuscript.

# **ADDITIONAL INFORMATION AND DECLARATIONS**

# **Funding**

The authors received no funding for this work.

# **Competing Interests**

The authors declare there are no competing interests.

#### **Author Contributions**

- Gonzalo A. Collado conceived and designed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- Rodrigo B. Salvador analyzed the data, authored or reviewed drafts of the article, and approved the final draft.
- Marcela Vidal performed the experiments, authored or reviewed drafts of the article, and approved the final draft.

- Fernanda Parra Aravena performed the experiments, analyzed the data, prepared figures and/or tables, and approved the final draft.
- Vannia Delgado performed the experiments, analyzed the data, prepared figures and/or tables, and approved the final draft.
- Cristian Torres-Díaz performed the experiments, authored or reviewed drafts of the article, and approved the final draft.

# **Data Availability**

The following information was supplied regarding data availability: The raw data is available in the Supplemental Files.

# **Supplemental Information**

Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.14027#supplemental-information.

# **REFERENCES**

- **Anonymous. 2005.** Environmental interpretation manual for protected areas in the mesoamerican Barrier Reef system region. Technical Document No. 25. Belize City, Belize.
- Aldea C, Novoa L, Rosenfeld S. 2019. Lista sistemática actualizada de los Moluscos de Chile. v1.4. Universidad de Magallanes. *Available at http://gbif-chile.mma.gob.cl/ipt/resource?r=moluscos-chile* (accessed on 30 April 2022).
- **Arenas J. 2017.** Derrumbe en paso internacional Pehuenche. TVMaulinos. *Available at http://tvmaulinos.com/derrumbe-en-paso-internacional-pehuenche/* (accessed on 30 April 2022).
- **Arnaboldi T. 2016.** ¿Qué le hemos hecho al Laja? Outdoors. *Available at https://outdoors.cl/que-le-hemos-hecho-al-laja/* (accessed on 30 April 2022).
- Arredondo C, Eisenman E, Püschel N, Teneb E, Kusch A, Dougnac C, Vila A. 2019.

  Diagnóstico de la relación entre la ganadería y los carnívoros en la Isla Grande de Tierra del Fuego. Chile, Providencia: Wildlife Conservation Society.
- **Bachman S, Moat J, Hill AW, Scott B. 2011.** Supporting Red List threat assessments with GeoCat: geospatial conservation assessment tool. *ZooKeys* **150**:117–126 DOI 10.3897/zookeys.150.2109.
- Balmford A, Leader-Williams N, Green MJB. 1995. Parks or arks: where to conserve threatened mammals? *Biodiversity and Conservation* 4:595–607 DOI 10.1007/BF00222516.
- Banks WE, d'Errico F, Dibble HL, Krishtalka L, West D, Olszewski D, Peterson AT, Anderson D, Gillam JC, Montet-White A, Crucifix M, Marean CW, Goñi MFSanchez, Wohlfarth B, Vanhaeran M. 2006. Eco-cultural niche modeling: new tools for reconstructing the geography and ecology of past human populations. *Paleoanthropology* 2006:68–83.

- **Barbini SA, Lucifora LO, Sabadin DE, Figueroa DE. 2020.** Ecological specialization is associated with high conservation concern in skates (Chondrichthyes, Rajiformes). *Animal Conservation* **23**:222–228 DOI 10.1111/acv.12531.
- **Berkmüller K, Savasdiasara T. 1981.** *Guidelines and techniques for environmental interpretation.* Ann Arbor: University of Michigan.
- **Bernardos S, Amado A, Amich F. 2006.** The narrow endemic *Scrophularia valdesii* Ortega-Olivencia and Devesa (Scrophulariaceae) in the Iberian Peninsula: an evaluation of its conservation status. *Biodiversity and Conservation* **15**:4027–4043 DOI 10.1007/s10531-005-3017-0.
- **Bland LM, Keith DA, Miller RM, Murray NJ, Rodríguez JP. 2016.** Directrices para la aplicación de las categorías y criterios de la Lista Roja de Ecosistemas de UICN, Versión 1.0. Gland, Suiza 1–7. *Available at https://portals.iucn.org/library/sites/library/files/documents/2016-010-Es.pdf*.
- **Bloxam QMC, Tonge SJ, Horton R. 1984.** A preliminary account of the history and management of populations of endangered Moorean tree snail *Partula* spp at the Jersey Wildlife Preservation Trust. *The Dodo: Journal of the Jersey Wildlife Preservation Trust* **20**:73–79.
- Carranza D, Varas-Belemmi K, Veer D, Iglesias-Müller C, Coral-Santacruz D, Méndez F, Torres-Lagos E, Squeo F, Gaymer C. 2020. Socio-environmental conflicts: an underestimated threat to biodiversity conservation in Chile. *Environmental Science* & Policy 110:46–59 DOI 10.1016/j.envsci.2020.04.006.
- Carvajal-Hernández CI, Juárez-Fragoso MA, Armenta-Montero S, Demeneghi-Calatayud AP, Vázquez-Torres M. 2020. Different criteria for evaluation of the conservation status of *Ceratozamia miqueliana* (Zamiaceae). *Tropical Conservation Science* 13:1–12 DOI 10.1177/1940082920952682.
- **CONAMA. 2003.** Estrategia nacional de biodiversidad. Santiago: Comisión Nacional del Medio Ambiente. Available at https://biodiversidad.mma.gob.cl/enb-2003/.
- **Convention on Biological Diversity (CBD). 1992.** Secretariat of the Convention on Biological Diversity. United Nations, Montreal, Canada *Available at http://wbbb.wb.gov.in/pdf/ConventiononBiologicalDiversity1992.pdf*.
- **Cooperativa. 2016.** Paso internacional Pehuenche se encuentra cerrado por derrumbe de rocas. Cooperativa. *Available at https://www.cooperativa.cl/noticias/pais/region-del-maule/paso-internacional-pehuenche-se-encuentra-cerrado-por-derrumbe-de-rocas/2016-07-30/132817.html* (accessed on 30 April 2022).
- Corporación Nacional Forestal (CONAF). 2020. Corporación Nacional Forestal. Conmemoran el 10.0 aniversario del Parque Nacional Alerce Costero. *Available at https://www.conaf.cl/conmemoran-10-o-aniversario-del-parque-nacional-alerce-costero/* (accessed on 30 April 2022).
- **Corporación Nacional Forestal (CONAF). 2021.** Reserva Nacional Alacalufes. *Available at https://www.conaf.cl/parques/reserva-nacional-alacalufes/* (accessed on 30 April 2022).
- **Crawford GI. 1939.** Notes on *Stephanoda patagonica* (Suter) and the genus *Radiodiscus*, with a new name for *R. patagonicus* Pilsbry. *The Nautilus* **52**:115–117.

- **Darrigran G, Damborenea C. 2017.** Zoología Invertebrados Malacología. Version 1.1. *Museo de La Plata. Occurrence dataset. Available at https://www.gbif.org/occurrence/1500052161* (accessed on 30 April 2022).
- Departamento Áreas Protegidas y Medio Ambiente (DAPMA). 2009. Plan de manejo Reserva Nacional Alacalufe (No. 536). Gobierno de Chile, Ministerio de Agricultura, CONAF *Available at http://areasprotegidas.mma.gob.cl/areas-protegidas/* (accessed on 30 April 2022).
- **Díaz P, Jaque E, Ojeda C. 2018.** Presión hídrica en ambientes lacustres de alta montaña: entre el cambio climático y el desarrollo energético. Laguna del Laja, Chile. *Diálogo andino* 55:143–158.
- Enríquez J. 2021. Extinguen incendios forestales en el Parque Nacional Villarrica. biobiochile.cl. *Available at https://www.biobiochile.cl/noticias/nacional/region-de-la-araucania/2021/02/14/extinguen-incendios-forestales-en-el-parque-nacional-villarrica.shtml* (accessed on 30 April 2022).
- El Heraldo Austral. 2019. Guardaparques del Parque Nacional Vicente Pérez Rosales realizan Limpieza en Petrohué. Available at https://www.eha.cl/noticia/local/guardaparques-del-parque-nacional-vicente-perez-rosales-realizan-limpieza-en-petrohue-3876 (accessed on 30 April 2022).
- Escobar D, Jojoa LM, Díaz SR, Rudas E, Albarracín RD, Ramírez C, Gómez JY, López CR, Saavedra J, Ortiz R. 2016. *Georreferenciación de localidades: Una guía de referencia para colecciones biológicas, versión 4.0.* Bogotá: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt y Instituto de Ciencias Naturales, Universidad Nacional de Colombia.144. *Available at https://hdl.handle.net/20.500.11761/35180* (accessed on 30 April 2022).
- Faber-Langendoen D, Nichols J, Master L, Snow K, Tomaino A, Bittman R, Hammerson G, Heidel B, Ramsay L, Teucher A, Young B. 2012. *NatureServe conservation status assessments: methodology for assigning ranks*. Arlington: NatureServe..
- **Fick SE, Hijmans RJ. 2017.** WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* **37(12)**:4302–4315 DOI 10.1002/joc.5086.
- **Fonseca ALM da, Thomé JW. 1993.** Descrição de *Glabrogyra* subgen. n. recaracterização de *Austrodiscus twomeyi* (Parodiz, 1954) e reclassificação das espécies sulamericanas dos géneros *Austrodiscus* Parodiz 1957, Radioconus Baker, 1927, Radiodomus Baker, 1930 e *Trochogyra* Weyrauch 1965 (Charopidae) e *Zilchogyra* Weyrauch 1965 (Helicodiscidae) (Gastropoda, Stylommatophora, Endodontoidea). Iheringia. *Série Zoologia* **75**:97–105.
- **Fonseca ALM da, Thomé JW. 1994.** Descrição de *Radiodiscus vazi*, sp. n. de São Paulo, Brasil, com proposição de recombinação de duas outras espécies sob este gênero e *R. bolachaensis*, nom. n. e sinonimização de uma espécie de *Radioconus* (Gastropoda, Stylommatophora, Charopidae). *Revista Brasileira de Zoologia* 11:265–275 DOI 10.1590/S0101-81751994000200010.
- **Global Biodiversity Information Facility (GBIF). 2021.** Radiodiscus Pilsbry, 1906. *Available at https://www.gbif.org/species/181387988* (accessed on 30 April 2022).

- Global Environment Facility (GEF). 2019. Proyecto GEF Castor confirma presencia de la especie invasora en todos los ríos de la Reserva Laguna Parrillar. Conservando los ecosistemas de la Patagonia chilena manejo, prevención y control del castor. Available at https://gefcastor.mma.gob.cl/proyecto-gef-castor-confirma-presencia-de-la-especie-invasora-en-todos-los-rios-de-la-reserva-laguna-parrillar/ (accessed on 30 April 2022).
- **Goud J, van der Bijl B, Creuwels J. 2022.** Naturalis Biodiversity Center (NL) Mollusca. *Naturalis Biodiversity Center. Occurrence dataset. Available at https://www.gbif.org/occurrence/2444569071* (accessed on 30 April 2022).
- **Graells G, Corcoran D, Aravena JC. 2015.** Prospección y datación de la fecha de colonización del área del Río Hollemberg, provincia de Última Esperanza, el punto más septentrional de presencia de Castor canadensis (Castoridae) en Sudamérica. *Anales del Instituto de la Patagonia* **43**:61–67 DOI 10.4067/S0718-686X2015000200004.
- **Graham CH, Ron SR, Santos JC, Schneider CJ, Moritz C. 2004.** Integrating phylogenies and environmental niche models to explore speciation mechanisms in dendrobatid frogs. *Evolution* **58**:1781–1793 DOI 10.1554/03-274.
- **Hadfield MG, Holland BS, Olival KJ. 2004.** Contributions of ex-situ propagation and molecular genetics to conservation of Hawaiian trees snails. In: Gordon MG, Bartol SM, eds. *Experimental approaches to conservation biology*. Berkeley: University of California Press, 16–34.
- Hammerson GA, Kling M, Harkness M, Ormes M. Young BE. 2017. Strong geographic and temporal patterns in conservation status of North American bats. *Biological Conservation* 212:144–152 DOI 10.1016/j.biocon.2017.05.025.
- Hortal J, de Bello F, Diniz-Filho J, Lewinsohn TM, Lobo JM, Ladle RJ. 2015. Seven Shortfalls that Beset Large-Scale Knowledge of Biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 46:523–549 DOI 10.1146/annurev-ecolsys-112414-054400.
- Hylton Scott MI. 1957. Endodóntidos neotropicales I (Moll. Pulm.). Neotropica 3:7–16.
- **Hylton Scott MI. 1963.** Tres nuevos Endodóntidos de Tucumán. *Neotropica* **9**:45–54.
- **Hylton Scott MI. 1970.** Endodóntidos de la región austral americana (Gastropoda-Pulm.). *Revista del Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Zoologia* **10(18)**:267–296.
- **Hylton Scott MI. 1975.** Endodóntidos neotropicales VII (Gastropoda Pulmonata). *Neotropica* **21**:119–121.
- **Hylton Scott MI. 1979.** Información malacológica de la Campaña de la Transecta de Botánica de Patagonia Austral. *Neotropica* **25**:3–8.
- **IUCN. 2001.** *IUCN red list categories and criteria: version 3.1.* Switzerland and Cambridge: IUCN Species Survival Commission, IUCN.
- **IUCN. 2002.** Technical Guidelines on the Management of *Ex-situ* populations for Conservation. Gland: International Union for the Conservation of Nature. *Available at https://www.iucnredlist.org/resources/redlistguidelines*.
- **IUCN. 2014.** Guidelines for using the IUCN red list categories and criteria (Version 11). Prepared by the Standards and Petitions Subcommittee. *Available at https://www.iucnredlist.org/resources/redlistguidelines*.

- **IUCN. 2019.** Guidelines for Using the IUCN Red List Categories and Criteria. Version 14. Prepared by the Standards and Petitions Committee. *Available at https://www.iucnredlist.org/resources/redlistguidelines*.
- **Kadis C, Thanos CA, Laguna Lumbreras E. 2013.** *Plant micro-reserves: from theory to practice.* Athens, Greece: Utopia Publishing.
- Laguna E, Deltoro VI, Pèrez-Botella J, Pèrez-Rovira P, Serra L, Olivares A, Fabregat C. **2004.** The role of small reserves in plant conservation in a region of high diversity in eastern Spain. *Biological Conservation* **119**:421–426 DOI 10.1016/j.biocon.2004.01.001.
- **Laguna E, Fos S, Jiménez J, Volis S. 2016.** Role of micro-reserves in conservation of endemic, rare and endangered plants of the Valencian region (Eastern Spain). *Israel Journal of Plant Sciences* **63(4)**:320–332 DOI 10.1080/07929978.2016.1256131.
- **Loo SE, Mac Nally R, Lake PS. 2007.** Forecasting New Zealand mudsnail invasion range: Model comparisons using native and invaded ranges. *Ecological Applications* **17**:181–189 DOI 10.1890/1051-0761(2007)017[0181:FNZMIR]2.0.CO;2.
- **Lumbreras EL. 2001.** The micro-reserves as a tool for conservation of threatened plants in Europe. Nature and Environment Series no 121. Strasbourg: Council of Europe.
- Mace GM, Pearce-Kelly P, Clarke D. 1998. An integrated conservation programme for the tree snails (Partulidae) of Polynesia: a review of captive and wild elements. *Memoirs of Museum Victoria* 56:431–433 DOI 10.24199/j.mmv.1997.56.34.
- **Magallanes G. 2012.** Estrategia Regional de Desarrollo Magallanes y Antártica chilena 2012–2020. Chile: Gobierno Regional de Magallanes y Antártica Chilena. Available at https://www.goremagallanes.cl/sitioweb/documentos/ERD%20Magallanes2020.pdf.
- Mansur MCD. 1996a. Radiodiscus coppingers. *The IUCN Red List of Threatened Species* 1996:e.T19068A8804380 DOI 10.2305/IUCN.UK.1996.RLTS.T19068A8804380.en (accessed on 30 April 2022).
- Mansur MCD. 1996b. Radiodiscus amdenus. *The IUCN Red List of Threatened Species* 1996:e.T19066A8803387 DOI 10.2305/IUCN.UK.1996.RLTS.T19066A8803387.en (accessed on 30 April 2022).
- Mansur MCD. 1996c. Radiodiscus compactus. *The IUCN Red List of Threatened Species* 1996:e.T19067A8803418 DOI 10.2305/IUCN.UK.1996.RLTS.T19067A8803418.en (accessed on 30 April 2022).
- Mansur MCD. 1996d. Radiodiscus iheringi. *The IUCN Red List of Threatened Species* 1996:e.T19069A8806464 DOI 10.2305/IUCN.UK.1996.RLTS.T19069A8806464.en (accessed on 30 April 2022).
- Mardones J. 2020. Investigan tala ilegal en Parque Nacional Alerce Costero. Diario Futrono. *Available at https://www.diariofutrono.cl/noticia/actualidad/2020/05/investigan-tala-ilegal-en-parque-nacional-alerce-costero* (accessed on 30 April 2022).
- **Martinic M. 2004.** La minería del carbón en Magallanes entre 1868-2003. *Historia* **37**:129–167.
- **Mason RA. 2015.** The sixth mass extinction and chemicals in the environment: our environmental deficit is now beyond nature's ability to regenerate. *Journal of Biological Physics and Chemistry* **15**:160–176 DOI 10.4024/10MA15F.jbpc.15.03.

- Master L, Faber-Langendoen D, Bittman R, Hammerson G, Heidel B, Nichols J, Ramsay L, Tomaino A. 2012. *Natureserve conservation status assessments: factors for assessing extinction risk*. Arlington: NatureServe.
- Matthies D, Brauer I, Maibom W, Tscharntke T. 2004. Population size and the risk of local extinction: empirical evidence from rare plants. *Oikos* 105:481–488 DOI 10.1111/j.0030-1299.2004.12800.x.
- Menon S, Choudhury BI, Khan ML, Peterson AT. 2010. Ecological niche modeling and local knowledge predict new populations of *Gymnocladus assamicus* a critically endangered tree species. *Endangered Species Research* 11(2):175–181 DOI 10.3354/esr00275.
- Ministerio del Medio Ambiente, Chile (MMA). 2021. Inventario nacional de especies de Chile. Ministerio del Medio Ambiente de Chile. Available at http://especies.mma.gob. cl/CNMWeb/Web/WebCiudadana/especies.aspx (accessed on 30 April 2022).
- Miquel SE, Aguirre ML. 2011. Taxonomía de los gasterópodos terrestres del Cuaternario de Argentina. *Revista española de paleontología* 26:101–133 DOI 10.7203/sjp.26.2.18535.
- **Miquel SE, Barker GM. 2009.** New charopidae from chilean-argentine patagonia: (Mollusca: Gastropoda: Stylommatophora). *Archiv für Molluskenkunde* **138**:53–61 DOI 10.1127/arch.moll/0003-9284/138/053-061.
- **Miquel SE, Bellosi ES. 2007.** Microgasterópodos terrestres (Charopidae) del Eoceno medio de Gran Barranca (Patagonia Central, Argentina). *Ameghiniana* **44**:121–131.
- Moat J, Orellana-Garcia A, Tovar C, Arakaki M, Arana C, Cano A, Faundez L, Gardner M, Hechenleitner P, Hepp J, Lewis G, Mamani JM, Miyasiro M, Whaley OQ. 2021. Seeing through the clouds—mapping desert fog oasis ecosystems using 20 years of MODIS imagery over Peru and Chile. *International Journal of Applied Earth Observation and Geoinformation* 103:102468 DOI 10.1016/j.jag.2021.102468.
- **MolluscaBase. 2021.** Radiodiscus Pilsbry, 1906. *Available at http://www.molluscabase.org/aphia.php?p=taxdetailsandid=996004* (accessed on 30 April 2022).
- **Morales Flores A. 2019.** Concepción Cota 50: interfaz urbano-forestal como proyecto de paisaje. MSc thesis, Pontificia Universidad Católica de Chile.
- **Munro JK, Morrison-Saunders A, Hughes M. 2008.** Environmental interpretation evaluation in natural areas. *Journal of Ecotourism* **7**(1):1–14 DOI 10.2167/joe137.0.
- Myers N, Mittermeir CG, Da Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:218–222 DOI 10.1038/35002501.
- NatureServe. 2006. *NatureServe explorer: an online encyclopedia of life. Version 6.1.*Arlington: NatureServe. *Available at https://explorer.natureserve.org/* (accessed on 30 April 2022).
- **NatureServe. 2021.** Products. Conservation Rank Calculator. Accessed *via* nature-serve.org on 2021-07-20. *Available at https://www.natureserve.org/products/conservation-rank-calculator* (accessed on 30 April 2022).
- Navrátil J, Knotek J, Pícha K. 2015. The significance of self-guided interpretive trails in protected areas for the environmental education of visitors. *Socijalna Ekologija* 24:5–21 DOI 10.17234/SocEkol.24.1.3.

- O'Rorke R, Holland BS, Cobian GM, Gaughen K, Amend AS. 2016. Dietary preferences of Hawaiian tree snails to inform culture for conservation. *Biological Conservation* 198:177–182 DOI 10.1016/j.biocon.2016.03.022.
- Pearce-Kelly P, Clarke D, Walker C, Atkin P. 1997. A conservation programme for the partulid tree snails of the Pacific region. *Memoirs of Museum Victoria* **56**:431–433 DOI 10.24199/j.mmv.1997.56.34.
- **Pearson R, Raxworthy C, Nakamura M, Peterson A. 2007.** Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography* **34**:102–117 DOI 10.1111/j.1365-2699.2006.01594.x.
- **Peterson AT, Holt RD. 2003.** Niche differentiation in Mexican birds: using point occurrences to detect ecological innovation. *Ecology Letters* **6**:774–782 DOI 10.1046/j.1461-0248.2003.00502.x.
- **Philippi R. 1855.** Observaciones sobre las especies del jénero *Helix*. *Anales de la Universidad de Chile* **Serie** 1:213–217.
- **Phillips SJ, Dudík M, Schapire RE. 2004.** MaxEnt software for modeling species niches and distributions (version 3.4.1). *Available at http://biodiversityinformatics.amnh.org/open\_source/maxent/* (accessed on 10 June 2022).
- **Pilsbry HA. 1911.** Non-marine Mollusca of Patagonia. In: Scott WB, ed. *Reports of the Princeton University expeditions to Patagonia*, 1896–1899. Princeton: Princeton University, 513–633.
- **Pilsbry HA, Ferriss JH. 1906.** Mollusca of the Southwestern States. II. *Proceedings of the Academy of Natural Sciences of Philadelphia* **58**:123–175.
- **Pokharel KP, Ludwig T, Storch I. 2016.** Predicting potential distribution of poorly known species with small database: the case of four-horned antelope *Tetracerus quadricornis* on the Indian subcontinent. *Ecology and Evolution* **6(8)**:2297–2307 DOI 10.1002/ece3.2037.
- **Purvis A, Gittleman JL, Cowlishaw G, Mace GM. 2000.** Predicting extinction risk in declining species. *Proceedings of the Royal Society B: Biological Sciences* **267**:1947–1952 DOI 10.1098/rspb.2000.1234.
- **QGIS Development Team. 2021.** QGIS Geographic Information System. Open Source Geospatial Foundation Project. *Available at http://qgis.osgeo.org* (accessed on 30 April 2022).
- **Rawat US, Agarwal NK. 2015.** Biodiversity: concept, threats and conservation. *Environment Conservation* **16**:19–28 DOI 10.36953/ECJ.2015.16303.
- Raxworthy CJ, Ingram CM, Rabibisoa N, Pearson RG. 2007. Applications of ecological niche modeling for species delimitation: a review and empirical evaluation using day geckos (*Phelsuma*) from Madagascar. *Systematic Biology* **56(6)**:907–923 DOI 10.1080/10635150701775111.
- Raxworthy CJ, Martínez-Meyer E, Horning N, Nussbaum RA, Schneider GE, Ortega-Huerta MA, Peterson AT. 2003. Predicting distributions of known and unknown reptile species in Madagascar. *Nature* 426:837–841 DOI 10.1038/nature02205.

- **Richards DC. 2002.** The New Zealand mudsnail invades the Western United States. *Aquatic Nuisance Species* **4**:42–44.
- Robles C. 2021. Retiran más de 3 mil kilos de basura desde el Parque Nacional Laguna del Laja. La Tribuna. *Available at https://www.latribuna.cl/noticias/2021/08/14/retiran-mas-de-3-mil-kilos-de-basura-desde-el-parque-nacional-laguna-del-laja.html* (accessed on 30 April 2022).
- Root-Bernstein M, Carvajal YMontecinos, Ladle R, Jepson P, Jaksic F. 2013. Conservation easements and mining: the case of Chile. *Earth's Future* 1:33–38 DOI 10.1002/2013EF000136.
- **Rutherford MG. 2020.** A new species of *Radiodiscus* (Gastropoda: Eupulmonata: Charopidae) from Trinidad and Tobago. *Archiv für Molluskenkunde* **149**:67–74 DOI 10.1127/arch.moll/149/067-074.
- **Salvador RB. 2021.** Type specimens of the South American terrestrial gastropods described by Henry Suter. *Integrative Systematics* **3**:61–68 DOI 10.18476/insy.v03.a4.
- Salvador RB, Brook FJ, Shepherd LD, Kennedy M. 2020. Molecular phylogenetic analysis of Punctoidea (Gastropoda, Stylommatophora). *Zoosystematics and Evolution* **96(2)**:397–410 DOI 10.3897/zse.96.53660.
- **Salvador RB, Wahab A, Phillips NE, Breure ASH. 2021.** South American and Trinidadian terrestrial Gastropoda in the collection of the Museum of New Zealand Te Papa Tongarewa. *Tuhinga* **32**:64–80.
- **Schileyko AA. 2001.** Treatise on Recent terrestrial pulmonate molluscs. Part 7. Endodontidae, Thyrophorellidae, Charopidae. *Ruthenica Supplement* **2**:881–1034.
- Servicio Nacional de Geología y Minería (SERNAGEOMIN). 2021. Complejo Volcánico Laguna del Maule. *Available at https://rnvv.sernageomin.cl/complejo-volcanico-laguna-del-maule/* (accessed on 30 April 2022).
- **Sielfeld W. 2001.** *Phylum Mollusca. Guías de Identificación y Biodiversidad Fauna Chilena.* Iquique, Chile: Apuntes de Zoología, Universidad Arturo Prat.
- Smith EA. 1881. Account of the zoological collections made during the survey of the H.M.S. 'Alert' in the Straits of Magellan and on the coast of Patagonia. IV. Mollusca and Molluscoidea. *Proceedings of the Zoological Society of London* 22–44.
- **Sociedad Nacional de Minería (SONAMI). 2021.** Mapa minero impreso. *Available at https://www.sonami.cl/v2/centro-de-documentacion/mapa-minero-impreso/* (accessed on 30 April 2022).
- Soto D, Arismendi I, González J, Sanzana J, Jara F, Jara C, Guzmán E, Lara A. 2006. Southern Chile, trout and salmon country: invasion patterns and threats for native species. *Revista Chilena de Historia Natural* **79**:97–117 DOI 10.4067/S0716-078X2006000100009.
- Squeo FA, Estades C, Bahamonde N, Cavieres L, Rojas G, Benoit I, Parada E, Fuentes A, Avilés R, Palma A, Solís R, Guerrero S, Montenegro G, Torres-Mura JC. 2010. Revisión de la clasificación de especies en categorías de amenaza en Chile. *Revista Chilena de Historia Natural* 83:511–529 DOI 10.4067/S0716-078X2010000400006.

- **Stuardo JR, Vega R. 1985.** Synopsis of the land Mollusca of Chile. With remarks on distribution. *Studies on Neotropical Fauna and Environment* **20**:125–146 DOI 10.1080/01650528509360682.
- **Subsecretaría de Turismo. 2015.** *Plan de Acción de Turismo Sustentable en Áreas Protegidas del Estado 2014–2018.* Santiago: Subsecretaría de Turismo.
- Subsecretaría de Turismo. 2017. Proyecto puesta en valor Parque Nacional Villarrica, Región de la Araucanía. Gobierno de Chile, SERNATUR: CONAF. Available at http://www.subturismo.gob.cl/wp-content/uploads/2015/11/FICHA-VILLARRICA\_13032017.pdf.
- **Tablado A, Mantinian J. 2004.** Catálogo de ejemplares tipo de la División Invertebrados del Museo Argentino de Ciencias Naturales. II. Mollusca. *Revista del Museo Argentino de Ciencias Naturales, Nueva Serie* **6**:363–384 DOI 10.22179/REVMACN.6.95.
- **Tablado A, Rodríguez D. 2021.** Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN). Invertebrates National Collection (MACNIn). *Invertebrates National Collection (MACNIn). Museo Argentino de Ciencias Naturales. Occurrence dataset. Available at https://www.gbif.org/occurrence/730553866* (accessed on 30 April 2022).
- Thomas CD, Cameron A, Green RE, Bakkenes B, Beaumont LJ, Collingham YC, Erasmus BFN, Ferriera de Siqueira M, Grainger A, Hannah L, Hughes L, Huntley B, Van Jaarsveld AS, Midgley GF, Miles L, Ortega-Huerta MA, Peterson AT, Phillips OL, Williams SE. 2004. Extinction risk from climate change. *Nature* 427:145–148 DOI 10.1038/nature02121.
- **Tonge S, Bloxam Q. 1991.** A review of the captive-breeding programme for Polynesian tree snails *Partula* spp. *International Zoo Yearbook* **30**:51–59 DOI 10.1111/j.1748-1090.1991.tb03465.x.
- **Trias-Blasi A, Gücel S, Özden Ö. 2017.** Current distribution and conservation status reassessment of the Cyprus Tulip (*Tulipa cypria*: Liliaceae), new data from Northern Cyprus. *Plant Biosystems* **151**:394–402 DOI 10.1080/11263504.2016.1174177.
- Turgeon DD, Quinn JF, Bogan AE, Coan EV, Hochberg FG, Lyons WG, Mikkelsen PM, Neves RJ, Roper CFE, Rosenberg G, Roth B, Scheltema A, Thompson FG, Vecchione M, Williams JD. 1998. Common and scientific names of aquatic invertebrates from the United States and Canada: Mollusks. Second Edition. Bethesda: Maryland American Fisheries Society Special Publication, 26.
- **Valderrama L, Contreras-Reyes JE, Carrasco R. 2018.** Ecological impact of forest fires and subsequent restoration in Chile. *Resources* 7:26 DOI 10.3390/resources7020026.
- **Valdovinos C. 1999.** Biodiversidad de moluscos chilenos: Base de datos taxonómica y distribucional. *Gayana* **63**:111–164.
- **Vargas-Almonacid P. 2000.** Nueva especie de microgastrópodo humícola para Chile, Radiodiscus quillajicola spec. nov. (Stylommatophora: Charopidae). *Gayana* **64**:61–66.
- **Villavicencio C. 2015.** Incendio amenaza casa en el sector quebradas Las Ulloas en la comuna de Florida. *Available at https://www.biobiochile.cl/noticias/2015/02/18/*

- incendio-amenaza-casas-en-el-sector-quebrada-las-ulloa-en-la-comuna-de-floridaen-bio-bio.shtml.
- Vidal OJ, Aguayo M, Niculcar R, Bahamonde N, Radic S, San Martín C, Kusch A, Latorre J, Félez J. 2015. Plantas invasoras en el Parque Nacional Torres del Paine (Magallanes, Chile): estado del arte, distribución post-fuego e implicancias en restauración ecológica. *Anales del Instituto de la Patagonia* 43(1):75–96 DOI 10.4067/S0718-686X2015000100006.
- Wieczorek J, Guo Q, Hijmans R. 2004. The point-radius method for georeferencing locality descriptions and calculating associated uncertainty. *International Journal of Geographical Information Science* 18:745–767 DOI 10.1080/13658810412331280211.
- Wiens JJ, Graham CH. 2005. Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution and Systematics* 36:519–539 DOI 10.1146/annurev.ecolsys.36.102803.095431.
- **Zilch A. 1959–1960.** Gastropoda von Wilhelm Wenz. Teil 2. Euthyneura. In: Schindewolf OH, ed. *Handbuch der Paläozoologie, Band 6, Teil 2*. Berlin: Gebrüder Borntrager, 1–835.