Gayana Bot. 72(1): 58-69, 2015 ISSN 0016-5301

Latitudinal patterns in Pteridophyte distribution of Continental Chile

Patrones latitudinales de distribución de las Pteridófitas en Chile continental

María José Parra[1], Roberto Rodríguez[2], Lohengrin Cavieres[2], Laureana Muñoz-Tapia[3] & Cristian Atala[3*]

[1]Universidad San Sebastián, Facultad de Ciencia, Departamento de Ciencias Biológicas y Químicas, Cruz 1577, Concepción, Chile.
[2]Universidad de Concepción, Facultad de Ciencias Naturales y Oceanográficas, Departamento de Botánica, Casilla 160-C, Concepción, Chile.
[3]Pontificia Universidad Católica de Valparaíso, Campus Curauma, Facultad de Ciencias, Instituto de Biología, Laboratorio de Anatomía y Ecología Funcional de Plantas, Curauma, Chile.
*cristian.atala@ucv.cl

ABSTRACT

Chilean vegetation has been described based on dominant trees and shrubs, giving little attention to less conspicuous plants such as pteridophytes *sensu lato* (ferns and lycophytes). These plants have different ecological demands and reproductive strategies than woody plants and are excellent tools to recognize vegetation zones. In the present study we analyze the distributional patterns of the 124 pteridophyte taxa occurring in continental Chile, regarding species richness and habitat preferences distribution. Using Jaccard's similarity index and grouping analysis, we obtained 5 pteridophyte zones that are significantly different from each other. Species richness distribution showed unimodal pattern with latitude, increasing from 17º S toward south up to a maximal value at 40º S and abruptly decreasing southward. These patterns are coincident with the habitat preference where the xerophytic species tend to decrease with latitude. In contrast, epiphytic pteridophytes increased with latitude, as temperate forests appear. Terrestrial hygrophytic species were present in all areas, but showed a southward increase. These distributions suggest an important role of the precipitation patterns, which is considered a limiting resource for pteridophytes' life cycle.

Keywords: Pteridophytes, geographic distribution, species richness, habitat preferences, Jaccard's index.

RESUMEN

La vegetación de Chile se ha descrito basada en los árboles y arbustos dominantes, prestando poca atención a plantas menos conspicuas como las pteridófitas *sensu lato* (helechos y licófitas). Estas plantas tienen diferentes demandas ecológicas y estrategias reproductivas que las plantas leñosas y son excelentes herramientas para reconocer zonas vegetacionales. En este estudio, analizamos los patrones de distribución de 124 taxa de pteridófitos de Chile continental, en particular, la distribución de la riqueza de especies y las preferencias de hábitat de las mismas. Usando el índice de similitud de Jaccard y análisis de agrupamiento se obtuvieron 5 zonas pteridofíticas significativamente diferentes entre sí. La distribución de la riqueza específica mostró una tendencia unimodal con la latitud, aumentando desde los 17º S hasta llegar a un valor máximo a los 40º S, declinando abruptamente hacia el sur. Estos patrones coinciden con el tipo de hábitat, donde las especies xerofíticas tienden a disminuir con la latitud. En contraste, los pteridófitos epífitos incrementan con la latitud, al aparecer los bosques templados. Las especies higrofíticas terrestres se encuentran presentes en todas las áreas, pero aumentan hacia el sur. Estas distribuciones sugieren un importante rol de los patrones de precipitación, factor considerado como limitante para el ciclo de vida de las pteridofitas.

Palabras clave: Pteridófitas, distribución geográfica, riqueza de especies, preferencias de hábitat, índice de Jaccard.

INTRODUCTION

Continental Chile extends from 17º30'S to 56º S, corresponding to approximately 4,300 km of latitudinal distance. In Chile, temperature decreases and precipitation increases with increasing latitude, producing a succession of climatic zones from extremely dry and warm in the northern-most extreme, to cold and moist in the south (Di Castri & Hajek 1976). The resulting vegetation is heterogeneous and characteristic of each climatic zone (Grau 1995).

Extant Chilean vegetation has been described mainly from a phytosociological perspective (Gajardo 1994, Oberdorfer 1960, Schmithüsen 1956). Gajardo (1994) defined eight regions in Chile: desert, high-elevation (Andean) grassland, shrubland and sclerophyllous forest, deciduous forest, laurifolium forest (also called Valdivian forest), Andean-Patagonian forest, evergreen forest and peat bogs, and Patagonian shrubland and grassland. These studies, however, are based mainly on dominant woody species (i.e. trees and shrubs), excluding less conspicuous elements of the flora such as mosses, and pteridophytes which have different dispersion strategies and habitat requirements than woody plants, and depend on free water for their sexual reproduction (Castán & Vetaas 2005, Pausas & Sáez 2000). Thus, their distribution is closely associated with water availability and precipitation (Karst *et al.* 2005). Therefore they are excellent tools for recognizing ecologically meaningful vegetation zones (Frahm & Gradstein 1991, Hemp 2002).

The first studies of fern distribution in Chile were conducted by Looser (1932), who divided Chile in five pteridophytic zones. These divisions corresponded to three continental zones (roughly north, central and south), and two island zones. One zone included the Juan Fernández archipelago, and the other one corresponded to Easter Island (Pascua or Rapa Nui). Rodríguez (1989), following Cabrera & Willink (1973), proposed five biogeographic regions for continental ferns: High-elevation Andean province, Puneña province, desert province, central province, and subantartic province. Godoy & Figueroa (1989) used a similarity analysis to recognize six pteridophyte zones, resulting in a division similar to Looser (1932), but adding Mocha Island as a new pteridophytic zone. These studies proposed different ways of subdividing Chilean territory, but generally agreed that continental Chile has three main zones -northern, central, and southern- with diffuse boundaries. The present study quantitatively addresses the existence of these pteridophytic zones in continental Chile. To achieve this, we analyzed the distribution patterns of pteridophytes along continental Chile. We also conducted a latitudinal analysis of pteridophytes species richness, and habitat requirements, information seldom find in the literature for Chilean pteridophyte species. For the present study we consider informally pteridophytes in broad sense, including ferns and lycophytes. This was done mainly because their share some biological and ecological traits.

MATERIALS AND METHODS

The country was divided into 38 latitudinal strips called operational geographic units (OGUs) of 1º of latitude each. Using the Universidad de Concepción Herbarium (CONC) database we established presence/absence of each of the 124 pteridophyte taxa reported in Chile (Rodríguez 1995) in each of the 38 OGUs. We revised the database and checked the herbarium samples for possible errors in identifications and distribution. Though we used these data for practical purposes, more recent studies indicate that continental Chile could include more pteridophyte taxa (Zuloaga *et al*. 2008).

For taxonomic considerations we followed Rodríguez (1995) and other more recent studies (Macluf & Hikey 2007, Rodríguez & Ponce 2008, Arana & Ollgaard 2012, Larsen *et al*. 2013). We then mapped the distribution of each species in order to detect incomplete or questionable distributions. With these data we elaborated a matrix of presence/absence for the analysis explained below. Using the revised distributions we registered the total number of species per latitudinal strip (of 1º) and also the number of families. This was done to determine the latitudinal distribution of species richness.

To detect brakes in the latitudinal distribution of pteridophytes species, we conducted a grouping analysis, followed by a significant aggregation detection analysis (Real *et al.* 1992). First, we calculated the floristic similarity between OGUs using the Jaccard's index.

The Jaccard's index is calculated as follow:

$$Jaccard'sindex = \frac{C}{(A+B-C)}$$

Where *A* and *B* are the number of species present exclusively in the latitudinal strips *a* and *b*, respectively, and *C* is the number of species present in both strips.

Afterwards, using the UPGMA algorithm (Unweighted Pair Group Method with Arithmetic Mean, a clustering method) we obtained a dendrogram grouping the latitudinal strips according to their floristic similarity. We calculated the statistical significance of each node of the dendrogram following McCoyed *et al.* (1986). In this method, the similarity matrix is transformed to +, -, or 0, depending on whether the similarity value between two adjacent strips is significantly higher, lower, or equal to that expected for a random distribution. The similarity values for the random distribution were obtained from Real (1999) and based on the number of OGUs. The matrix is then separated in a sub-matrix of signs that includes only the latitudinal strips of the evaluated node. In this sub-matrix three zones are established: zone A and zone B, which correspond to the latitudinal strips separated by the node, and zone A x B, corresponding to the intersection of zone A and B. The significance of each node was evaluated through an independence test (G-test) for the distribution of +, -, and 0 signs among the three zones. Additionally, we calculated GS and GW parameters that determine whether the separation produced by the node is a strong or weak segregation, respectively (McCoyed 1986). For the present study we considered only the strong segregations or brakes (GS).

After establishing the floristic zones, we analyzed whether there is latitudinal variation in the distribution of pteridophyte habitat in Chile. To achieve this we plotted the habitat preference of the species (hygrophytic, xerophytic, aquatic and epiphytic) across the latitudinal zones obtained in the previous analysis. Habitat data followed the species descriptions found in Rodríguez (1995). Hygrophytic referred to plants found in moist environments, xerophytic to plants found in dry environments, aquatic to plants living totally or partially submerged, and epiphytic to plants that live on other plants.

RESULTS

We found five significantly differents in the cluster analysis of pteridophyte latitudinal distribution on continental Chile (Fig. 1). The significance values of the G-test for weak segregation (GW) and strong segregation (GS) are shown (Table I). The results show that continental Chile has five significantly different floristic areas of pteridophytes from North to South (Fig. 2). OGUs at 27º S and 48º S separated early from the rest due to reduced pteridophyte records. These OGUs correspond to extremely arid zones (27°S) and areas with reduced available land (48°S). We registered 124 pteridophyte taxa in total, distributed in continental Chile, with differences in species number per floristic area (Table II).
The 5 areas correspond to:
Area 1: Extends from 17º S to 22º S and it contains 18 taxa (Table II). The most characteristic species (present in most quadrants within the area) are: *Asplenium gilliesii*, *Woodsia montevidensis, Cheilanthes arequipensis, Ch. myriophylla, Ch. pruinata, Ch. sinuate* and *Argyrochosma nivea*.

Area 2: Extends from 23º S to 26º S and it contains 12 taxa (Table II). The most characteristic species species are: *Asplenium peruvianum, Cheilanthes bonariensis* and *Polypodium pycnocarpum.*
Area 3: Extends from 28º S to 34º S and it contains 42 taxa (Table II). The most characteristic species species are: *Adiantum capillus-veneris*, *A. gertrudis*, *A. pearcei, Isoetes hieronymi, Marsilea mollis, Pellaea myrtillifolia, Salvinia auriculata.*

Area 4: Is the larger area, it extends from 35º S to 46º S, and it contains 98 taxa (Table II). The most characteristic species species are: *Asplenium trilobum, Blechnum arcuatum, B. asperum, B. blechnoides, B. corralense*, *B. microphyllum, B. mochaenum* var. *mochaenum, Dryopteris filix-mas, Elaphoglossum gayanum, E. fonkii, E. porteri, Sticherus squamulosus* var. *gunckeliana, S. esquamulosus* var. *squamulosus, Hymenophyllum cuneatum* var. *cuneatum, H. dentatum, H. dicranotrichum, H. ferrugineum, H. fusiforme, H. krauseanum, H. nahuelhuapiense, H. plicatum, H. tunbringense* var. *tumbrigense, H. umbratile, Lophosoria quadripinnata*, *Diphasium gayanum*, *Lycopodium paniculatum*, *Megalastrum spectabile*, *Ophioglossum crotalophoroides*, *Polypodium feuillei* var. *ibañezii*, *Polystichum chilense* var. *chilense*, *P. chilense* var. *dusenii*, *P. multifidum* var. *pearcei*, *P. subinterrigemum*, *Pteris semiadnata*, and *Trichomanes exsectum*.

Area 5: Extends from 47º S to 55º S and it contains 50 taxa (Table II). The two most characteristic species species are *Botrychium dusenii* and *Huperzia fuegiana*.

The full species list per floristic area with the species' authors is found in Table II.
We also obtained two major clusters within the dendrogram

Table I. Significant segregations between latitudinal strips (OGUs) separated by each node in the dendrogram. Numbers in bold indicate significant strong segregation or breaks. GW = weak breaks, GS = strong breaks. Only GS were considered.

Tabla I. Segregaciones significativas entre franjas latitudinales (OGUs) separadas por cada nodo en el dendrograma. Los números en negrita indican separaciones (o quiebres) fuertes significativas. GW = quiebres débiles, GS = quiebres fuertes. Solo GS fueron considerados.

Node	Group 1	Group 2	Coefficient	Gw	Gs
1	17 - 27	35 - 48	0,048	52,56	337,77
2	17-34	27	0,055	1,06	14,76
3	35 - 49	48	0,101	6,61	0,49
4	17- 22	23- 34	0,077	4,82	5,40
5	23-26	28- 34	0,123	5,35	12,83
6	17	18-22	0,173	$8,08 \times 10^{-22}$	$8,08 \times 10^{-22}$
7	35- 44	47-49	0,233	50,89	55,98
8	28 - 29	30- 34	0,246	4,94	1,02
9	35-45	44	0,365	11,99	1,81
10	47-55	49	0,371	2,12	$1,59 \times 10^{-20}$
11	23-24	25-26	0,344	$8,07 \times 10^{-21}$	$8,07 \times 10^{-21}$
12	35-37	38-45	0,408	15,82	$1,25 \times 10^{-21}$
13	38-46	45	0,442	23,14	0,34
14	28	29	0,455	$1,02 \times 10^{-27}$	$1,02 \times 10^{-27}$
15	30-31	32-34	0,502	3,05	$3,09 \times 10^{-21}$
16	35	36-37	0,594	$8,08 \times 10^{-21}$	$8,08 \times 10^{-21}$
17	38-42	43-46	0,570	1,02	1,02

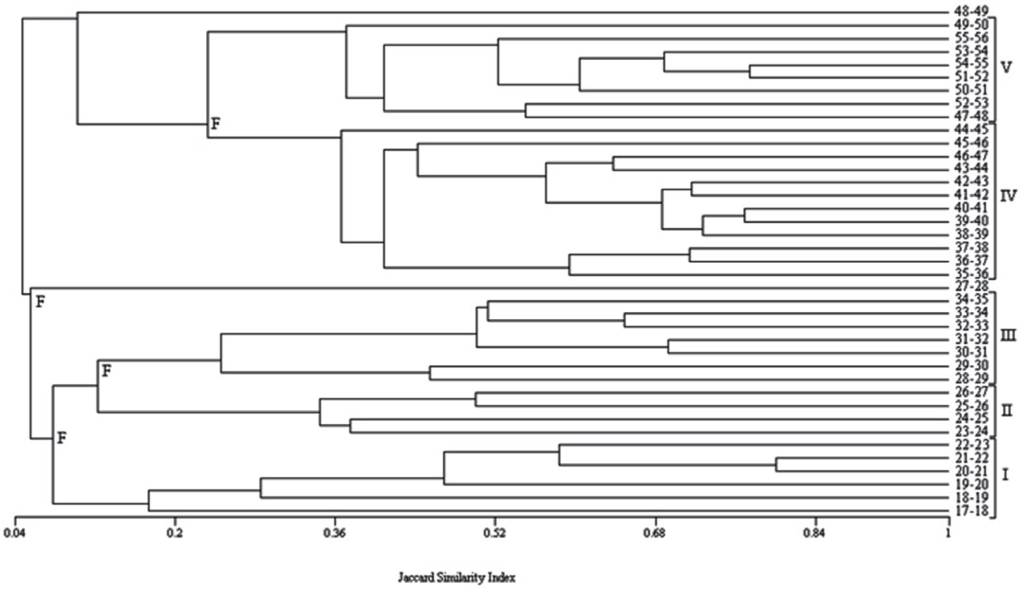

Figure 1. Dendrogram obtained with UPGMA and Jaccard's index of similarity. F indicates strong segregations. Numbers represent latitudinal strips of 1°.

Figura 1. Dendrograma obtenido con UPGMA y el índice de similitud de Jaccard. F indica segregaciones (quiebres) fuertes. Los números representan franjas latitudinales de 1°.

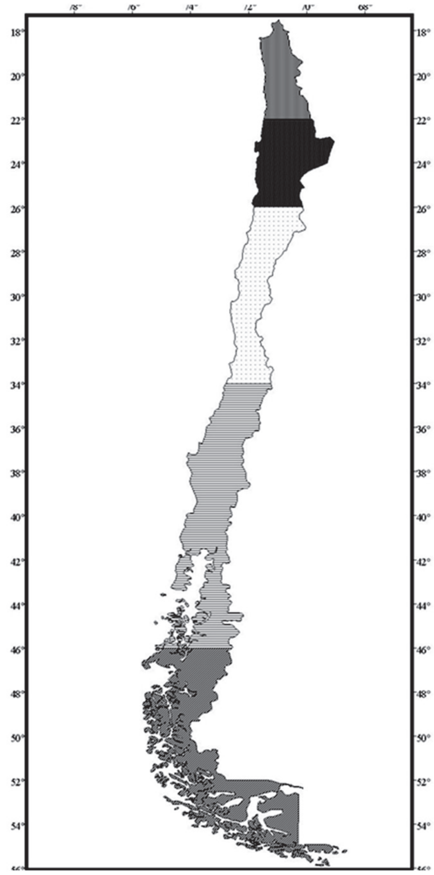

Figure 2. Distribution map showing the 5 pteridophytic zones of continental Chile obtained.

Figura 2. Mapa de distribución que muestra las 5 zonas pteridofíticas obtenidas de Chile continental.

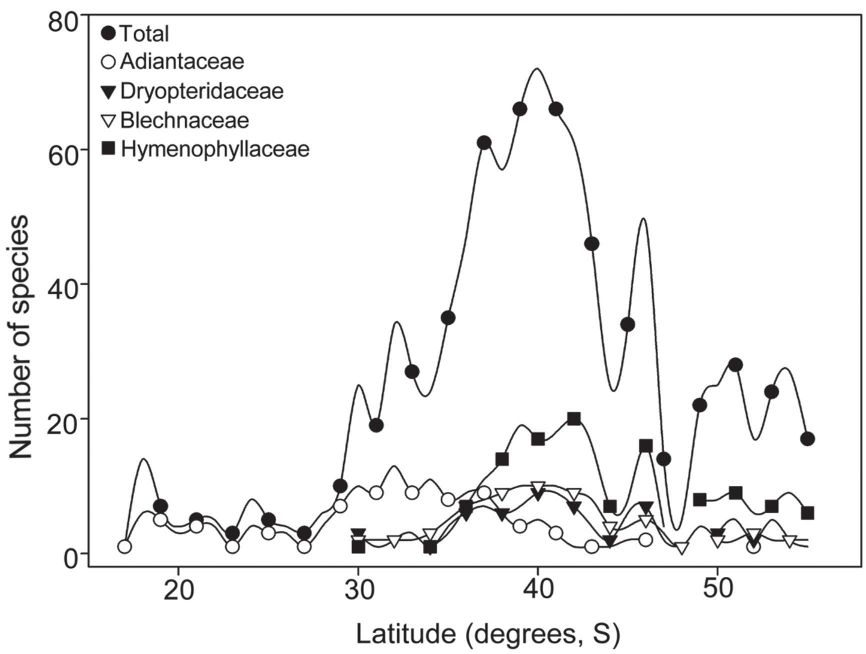

FIGURE 3. Latitudinal richness distribution of Pteridophytes in continental Chile. Black circles = total, open circles = Adiantaceae, black triangles Dryopteridaceae, open triangles = Blechnaceae, black square = Hymenophyllaceae. Lines show smoothed distribution of number of species per latitudinal degree.

FIGURA 3. Distribución latitudinal de la riqueza de Pteridofitas en Chile continental. Círculos negros = total, círculos blancos = Adiantaceae, triángulos negros = Dryopteridaceae, triángulos blancos = Hymenophyllaceae. Las líneas muestran la distribución suavizada del número de especies por grado latitudinal.

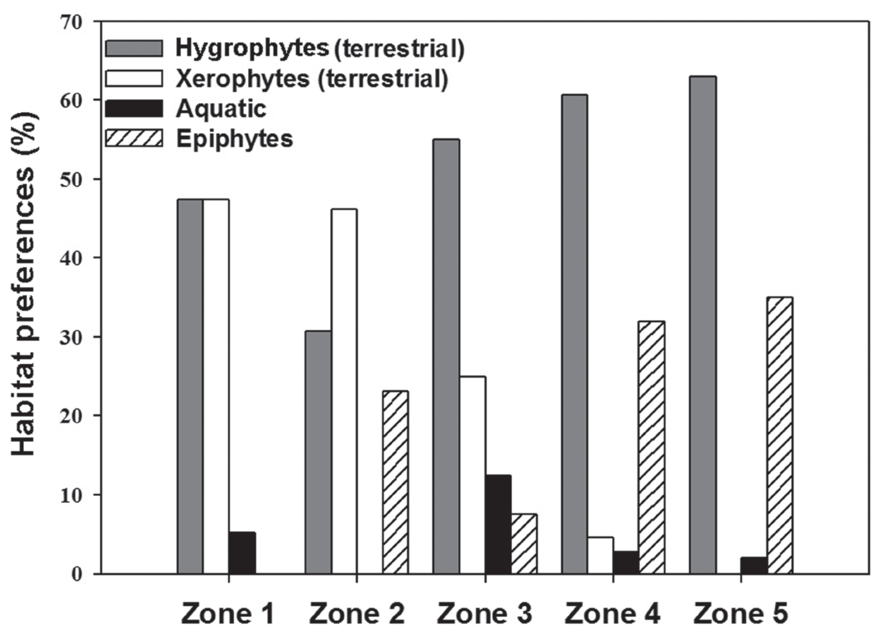

FIGURE 4. Habitat distribution in different pteridophytic zones of continental Chile.

FIGURA 4. Distribución de hábitat en las diferentes zonas pteridofíticas de Chile continental.

Table II. Pteridophyte species in each floristic area of Continental Chile. (Areas 1 To 5).

Tabla II. Especies de Pteridophyta en cada área florística de Chile continental (Áreas 1 A 5).

	Species	Habitat
Area 1	*Adiantum thalictroides* Willd. ex Schltdl. var. *hirsutum* (Hook. & Grev.) de la Sota	Hygrophytic
	Argyrochosma nivea (Poir.) Windham	Xerophytic
	Asplenium gilliesii Hook.	Xerophytic
	Asplenium triphyllum C. Presl	Hygrophytic
	Azolla filiculoides Lam.	Aquatic
	Cheilanthes arequipensis (Maxon) R. et A. Tryon	Xerophytic
	Cheilanthes mollis (Kunze) C. Presl	Xerophytic
	Cheilanthes myriophylla Desv.	Xerophytic
	Cheilanthes pilosa Goldm.	Xerophytic
	Cheilanthes pruinata Kaulf.	Xerophytic
	Cheilanthes sinuata (Sw.) Domin	Xerophytic
	Cystopteris fragilis (L.) Bernh. var. *apiiformis* (Gand.) C. Chr.	Hygrophytic
	Equisetum bogotense Kunth	Hygrophytic
	Equisetum giganteum L.	Xerophytic
	Pellaea ternifolia (Cav.) Link	Xerophytic
	Pityrogramma trifoliata (L.) R. Tryon	Xerophytic
	Thelypteris argentina (Hieron.) Abbiatti	Hygrophytic
	Woodsia montevidensis (Spreng.) Hieron.	Hygrophytic
Area 2	*Adiantum chilense* Kaulf. var. *chilense*	Hygrophytic
	Adiantum thalictroides Willd. ex Schltdl. var. *hirsutum* (Hook. & Grev.) de la Sota	Hygrophytic
	Asplenium peruvianum Desv.	Xerophytic
	Cheilanthes bonaeriensis (Willd.) Proctor	Xerophytic
	Cheilanthes hypoleuca (Kunze) Mett.	Xerophytic
	Cheilanthes mollis (Kunze) C. Presl	Xerophytic
	Notholaena sulphurea (Cav.) J. Sm.	Xerophytic
	Pellaea ternifolia (Cav.) Link	Xerophytic
	Pleopeltis macrocarpa (Bory ex Willd.) Kaulf.	Epiphytic
	Polypodium espinosae Weath.	Epiphytic
	Polypodium pycnocarpum C. Ch.	Epiphytic
	Thelypteris argentina (Hieron.) Abbiatti	Hygrophytic
Area 3	*Adiantum capillus-veneris* L.	Hygrophytic
	Adantum chilense Kaulf. var. *scabrum* (Kaulf.) Hicken	Hygrophytic
	Adiantum thalictroides Willd. ex Schltdl. var. *hirsutum* (Hook. & Grev.) de la Sota	Hygrophytic
	Adiantum chilense Kaulf. var. *chilense*	Hygrophytic
	Adiantum excisum Kunze	Hygrophytic
	Adiantum gertrudis Espinosa	Hygrophytic
	Adiantum pearcei Phil.	Hygrophytic
	Adiantum sulphureum Kaulf.	Hygrophytic
	Asplenium dareoides Desv.	Hygrophytic
	Asplenium obtusatum G. Forster var. *sphenoides* (Kunze) C. Chr. ex Skottsb.	Hygrophytic
	Azolla filiculoides Lam.	Aquatic
	Blechnum chilense (Kaulf.) Mett.	Hygrophytic
	Blechnum hastatum Kaulf.	Hygrophytic
	Blechnum microphyllum (Goldm.) C. V. Morton	Hygrophytic
	Cheilanthes glauca (Cav.) Mett.	Xerophytic
	Cheilanthes hypoleuca (Kunze) Mett.	Xerophytic
	Cheilanthes mollis (Kunze) C. Presl	Xerophytic

	Cryptogramma fumariifolia (Phil. ex Baker) Christ	Xerophytic
	Cystopteris fragilis (L.) Bernh.	Hygrophytic
	Dennstaedtia glauca (Cav) C. Chr. ex Looser	Hygrophytic
	Dryopteris filix-mas (L.) Schott	Hygrophytic
	Equisetum bogotense Kunth	Hygrophytic
	Equisetum pyramidale Goldm.	Hygrophytic
	Hymenophyllum peltatum (Poir.) Desv.	Epiphytic
	Hymenophyllum tunbrigense (L.) Sm. var. *tunbrigense*	Epiphytic
	Hymenophyllum umbratile Diem et J. S. Licht.	Epiphytic
	Hypolepis poeppigii (Kunze) R.A. Rodr.	Hygrophytic
	Isoetes hieronymi U. Weber	Aquatic
	Marsilea mollis B.L. Rob. & Fernald	Aquatic
	Megalastrum spectabile (Kaulf.) A.R. Sm. et R.C. Moran	Hygrophytic
	Ophioglossum lusitanicum L. ssp. *coriaceum* (A. Cunn.) R.T. Clausen	Hygrophytic
	Pellaea myrtillifolia Mett. ex Kuhn	Xerophytic
	Pellaea ternifolia (Cav.) Link	Xerophytic
	Pilularia americana A. Braun	Aquatic
	Pleurosorus papaverifolius (Kunze) Mett. var. *papaverifolius*	Hygrophytic
	Polypodium feuillei Bertero var. *feuillei*	Epiphytic
	Polystichum andinum Phil.	Hygrophytic
	Polystichum plicatum (Poepp. ex Kunze) Hicken	Hygrophytic
	Rumohra adiantiformis (G. Forst.) Ching	Hygrophytic
	Salvinia auriculata Aubl.	Aquatic
	Thelypteris argentina (Hieron.) Abbiatti	Hygrophytic
Area 4	*Adiantum chilense* Kaulf. var. *chilense*	Hygrophytic
	Adiantum excisum Kunze	Hygrophytic
	Adiantum scabrum Kaulf.	Hygrophytic
	Adiantum sulphureum Kaulf.	Hygrophytic
	Adiantum thalictroides Willd. ex Schltdl. var. *hirsutum* (Hook. & Grev.) de la Sota	Hygrophytic
	Asplenium dareoides Desv.	Hygrophytic
	Asplenium monanthes L.	Hygrophytic
	Asplenium obtusatum G. Forst. var. *sphenoides* (Kunze) C. Chr. ex Skottsb.	Hygrophytic
	Asplenium trilobum Cav.	Epiphytic
	Azolla filiculoides Lam.	Aquatic
	Blechnum arcuatum J. Remy	Hygrophytic
	Blechnum asperum (Klotzsch) W. Sturm	Hygrophytic
	Blechnum blechnoides Keyserl.	Hygrophytic
	Blechnum chilense (Kaulf.) Mett.	Hygrophytic
	Blechnum corralense Espinosa	Hygrophytic
	Blechnum hastatum Kaulf.	Hygrophytic
	Blechnum magellanicum (Desv.) Mett.	Hygrophytic
	Blechnum microphyllum (Goldm.) C. V. Morton	Hygrophytic
	Blechnum mochaenum G. Kunkel var. *mochaenum*	Hygrophytic
	Blechnum penna-marina (Poir.) Kuhn	Hygrophytic
	Cheilanthes glauca (Cav.) Mett.	Xerophytic
	Cheilanthes hypoleuca (Kunze) Mett.	Xerophytic
	Cheilanthes mollis (Kunze) C. Presl	Xerophytic
	Cryptogramma fumariifolia (Phil. ex Baker) H. Christ	Xerophytic
	Cystopteris fragilis (L.) Bernh.	Hygrophytic
	Dennstaedtia glauca (Cav.) C. Chr. ex Looser	Hygrophytic
	Dryopteris filix-mas (L.) Schott	Hygrophytic
	Elaphoglossum fonkii (Phil.) T. Moore	Hygrophytic
	Elaphoglossum gayanum (Fée) T. Moore	Hygrophytic

Elaphoglossum porteri Hicken	Hygrophytic
Equisetum bogotense Kunth	Hygrophytic
Equisetum pyramidale Goldm.	Hygrophytic
Grammitis magellanica Desv.	Epiphytic
Grammitis patagonica (C. Chr.) Parris	Epiphytic
Grammitis poeppigiana (Mett.) Pic. Serm.	Epiphytic
Histiopteris incisa (Thunb.) J. Sm.	Hygrophytic
Huperzia fuegiana (Roiv.) Holub	Hygrophytic
Hymenophyllum caudiculatum Mart.	Epiphytic
Hymenophyllum cruentum Cav.	Epiphytic
Hymenophyllum cuneatum Kunze var. *cuneatum*	Epiphytic
Hymenophyllum darwinii Hook.f. ex Bosch	Epiphytic
Hymenophyllum dentatum Cav.	Epiphytic
Hymenophyllum dicranotrichum (C. Presl) Hook. ex Sadeb.	Epiphytic
Hymenophyllum falklandichum Baker	Epiphytic
Hymenophyllum ferrugineum Colla	Epiphytic
Hymenophyllum fuciforme Sw.	Epiphytic
Hymenophyllum krauseanum Phil.	Epiphytic
Hymenophyllum nahuelhuapiense Diem & J.S. Licht.	Epiphytic
Hymenophyllum pectinatum Cav.	Epiphytic
Hymenophyllum peltatum (Poir.) Desv.	Epiphytic
Hymenophyllum plicatum Kaulf.	Epiphytic
Hymenophyllum secundum Hook. & Grev.	Epiphytic
Hymenophyllum seselifolium C. Presl	Epiphytic
Hymenophyllum tortuosum Hook. & Grev.	Epiphytic
Hymenophyllum tunbrigense (L.) Sm. var. *tunbrigense*	Epiphytic
Hymenophyllum umbratile Diem & J.S. Licht.	Epiphytic
Hypolepis poeppigii (Kunze) R.A. Rodr.	Hygrophytic
Isoetes araucaniana Macluf & Hickey	Aquatic
Isoetes chubutiana Hickey, Macluf & W.C. Taylor	Aquatic
Lophosoria quadripinnata (J. F. Gmel.) C. Chr.	Hydrophytic
Lycopodium alboffii Rolleri	Hygrophytic
Lycopodium confertum Willd.	Hygrophytic
Lycopodium gayanum J. Remy	Hygrophytic
Lycopodium magellanicum (P. Beauv.) Sw. var. *magellanicum*	Hygrophytic
Lycopodium magellanicum (P. Beauv.)Sw. var. *erectum* (Phil.) Looser	Hygrophytic
Lycopodium paniculatum Desv.	Hygrophytic
Lycopodium gayanum J. Remy	Hygrophytic
Megalastrum spectabile (Kaulf.) A.R. Sm. & R.C. Moran	Hygrophytic
Ophioglossum crotalophoroides Walter	Hygrophytic
Ophioglossum lusitanicum L. spp. *coriaceum* (A. Cunn.) R.T. Clausen	Hygrophytic
Ophioglossum nudicaule L. f. var. *robustum* J.S. Licht.	Hygrophytic
Pellaea ternifolia (Cav.) Link	Xerophytic
Pilularia americana A. Braun	Aquatic
Pleopeltis macrocarpa (Bory ex Willd.) Kaulf.	Epiphytic
Pleurosorus papaverifolius (Kunze) Mett. var. *papaverifolius*	Hygrophytic
Polypodium feuillei Bertero var. *feuillei*	Epiphytic
Polypodium feuillei Bertero var. *ibañezii* Looser	Epiphytic
Polystichum andinum Phil.	Hygrophytic
Polystichum chilense (H. Christ) Diels var. *chilense*	Hygrophytic
Polystichum chilense (H. Christ) Diels var. *dusenii* (C. Chr.) Looser ex R. A. Rodr.	Hygrophytic
Polystichum multifidum (Mett.) H. Christ var. *multifidum*	Hygrophytic
Polystichum multifidum (Mett.) T. Moore var. *pearcei* (Phil.) R. A. Rodr.	Hygrophytic
Polystichum plicatum (Poepp. ex Kunze) Hicken	Hygrophytic

	Polystichum subintegerrimum (Hook.& Arn.) R. A. Rodr.	Hygrophytic
	Pteris chilensis Desv.	Hygrophytic
	Pteris semiadnata Phil.	Hygrophytic
	Rumohra adiantiformis (G. Forst.) Ching	Hygrophytic
	Schizaea fistulosa Labill.	Hygrophytic
	Selaginella apoda (L.) Spring	Hygrophytic
	Serpyllopsis caespitosa (Gaudich.) C. Chr. var. *caespitosa*	Epiphytic
	Sticherus cryptocarpus (Hook.) Ching	Hygrophytic
	Sticherus litoralis (F. Phil.) Nakai	Hygrophytic
	Sticherus quadripartitus (Poir.) Ching	Hygrophytic
	Sticherus squamulosus (Desv.) Nakai var. *gunckelianus* (Looser) R.A. Rodr. & Ponce	Hygrophytic
	Sticherus squamulosus (Desv.) Nakai var. *squamulosus*	Hygrophytic
	Thelypteris argentina (Hieron.) Abbiatti	Hygrophytic
	Trichomanes exsectum Kunze	Epiphytic
Area 5	*Adiantum chilense* Kaulf. var. *chilense*	Hygrophytic
	Asplenium dareoides Desv.	Hygrophytic
	Asplenium obtusatum G. Forst. var. *sphenoides (*Kunze) C. Chr. ex Skottsb.	Hygrophytic
	Asplenium triphyllum C. Presl	Hygrophytic
	Lycopodium alboffii Rolleri	Hygrophytic
	Lycopodium confertum Willd.	Hygrophytic
	Lycopodium magellanicum P. Beauv. var. *magellanicum*	Hygrophytic
	Blechnum arcuatum J. Remy	Hygrophytic
	Blechnum chilense (Kaulf.) Mett.	Hygrophytic
	Blechnum magellanicum (Desv.) Mett.	Hygrophytic
	Blechnum mochaenum G. Kunkel var. *mochaenum*	Hygrophytic
	Blechnum penna-marina (Poir.) Kuhn	Hygrophytic
	Botrychium dusenii (H. Christ) Alston	Hygrophytic
	Cystopteris fragilis (L.) Bernh.	Hygrophytic
	Grammitis magellanica Desv.	Epiphytic
	Grammitis patagonica (C. Chr.) Parris	Epiphytic
	Grammitis poeppigiana (Mett.) Pic. Serm.	Epiphytic
	Histiopteris incisa (Thunb.) J. Sm.	Hygrophytic
	Huperzia fuegiana (Roiv.) Holub	Hygrophytic
	Hymenophyllum caudiculatum Mart.	Epiphytic
	Hymenophyllum cruentum Cav.	Epiphytic
	Hymenophyllum darwinii Hook.f. ex Bosch	Epiphytic
	Hymenophyllum dentatum Cav.	Epiphytic
	Hymenophyllum falklandichum Baker	Epiphytic
	Hymenophyllum ferrugineum Colla	Epiphytic
	Hymenophyllum nahuelhuapiense Diem & J.S. Licht.	Epiphytic
	Hymenophyllum pectinatum Cav.	Epiphytic
	Hymenophyllum peltatum (Poir.) Desv.	Epiphytic
	Hymenophyllum plicatum Kaulf.	Epiphytic
	Hymenophyllum secundum Hook. & Grev.	Epiphytic
	Hymenophyllum seselifolium C. Presl	Epiphytic
	Hymenophyllum tortuosum Hook. & Grev.	Epiphytic
	Hypolepis poeppigii (Kunze) R. A. Rodr.	Hygrophytic
	Isoetes savatieri Franch.	Aquatic
	Megalastrum spectabile (Kaulf.) A.R. Sm. & R.C. Moran	Hygrophytic
	Ophioglossum crotalophoroides Walter	Hygrophytic
	Pleurosorus papaverifolius (Kunze) Mett. var. *papaverifolius*	Hygrophytic
	Polystichum andinum Phil.	Hygrophytic
	Polystichum chilense (H. Christ) Diels var. *chilense*	Hygrophytic

Polystichum chilense (H. Christ) Diels var. *dusenii* (C. Chr.) Looser ex R. A. Rodr.	Hygrophytic
Polystichum multifidum (Mett.) H. Christ var. *multifidum*	Hygrophytic
Polystichum multifidum (Mett.) T. Moore var. *pearcei* (Phil.) R. A. Rodr.	Hygrophytic
Polystichum plicatum (Poepp. ex Kunze) Hicken	Hygrophytic
Polystichum subintegerrimum (Hook.& Arn.) R. A. Rodr.	Hygrophytic
Rumohra adiantiformis (G. Forst.) Ching	Hygrophytic
Schizaea fistulosa Labill.	Hygrophytic
Serpyllopsis caespitosa (Gaudich.) C. Chr. var. *caespitosa*	Epiphytic
Sticherus cryptocarpus (Hook.) Ching	Hygrophytic
Sticherus litoralis (F. Phil.) Nakai	Hygrophytic
Sticherus quadripartitus (Poir.) Ching	Hygrophytic

(Fig. 1). The first group included area 1, 2 and 3. The second included areas 4 and 5. This separation corresponds to an increase in moisture and marked seasons, passing from mediterranean to temperate-moist climate at 36°S (Di Castri & Hajek 1976, Luebert & Pliscoff 2006).

The pteridophyte species richness changed with latitude in an almost unimodal pattern. Richness increased from 17º S southward, reaching a maximum at 40º S, and descending further South (Fig. 3). Regarding the diversity distribution of the main pteridophytes families, we found a high presence of the Adiantaceae family (now included in the Pteridaceae) from the northern limit up to 30º S. At that latitude (30ºS), the Blechnaceae and Dryopteridaceae families appear. Around 34º S the Hymenophyllaceae family starts to increase in richness, peaking between 40º S and 43º S (Fig. 3).

The habitats of pteridophytes in continental Chile change with latitude (Fig. 4). The terrestrial xerophytic species tend to decrease with latitude, disappearing in area 5 (47º to 55º S). Epiphytes appear in area 2 (23º to 26º S), and increase with latitude, peaking in area 5. Hygrophytic pteridophytes are more or less homogeneously distributed along Chile, but are more abundant in area 3, 4, and 5 compared to areas 1 and 2. Aquatic pteridophytes are the least represented in Chile, and have a maximum diversity in area 3 (28º to 34º S) and are absent from area 2.

DISCUSSION

The results show that continental Chile can be divided into five latitudinal regions (areas) based on the geographic distribution of pteridophytes. Each zone possesses a particular pteridophytic diversity, although a number of species are shared among areas. The number of areas found here differs from previous studies that divided continental Chile in three areas: north, central, and south (Looser 1932, Godoy & Figueroa 1989). This suggests a finer grain of latitudinal variation than previously appreciated. Looser (1932) did a purely descriptive analysis of the Pteridophyte distribution, delimiting the areas based on visual criteria. Godoy & Figueroa (1989) used latitudinal strips of 2º, larger than those used in the present study and probably too large to detect finer gradients of floristic variation recognized here. Recent biogeographical studies on ferns species of Central America have also used a 1° resolution, and have also found higher diversity on central latitudes (Sanginés-Franco *et al.* 2011, Luna-Vega *et al.* 2012).

The pteridophyte zones recognized in this study are characterized by a latitudinal exchange in the dominant families. This taxonomic replacement follows the habitat characteristic change found from north to south. In the north, xerophytic terrestrial pteridophytes, like those belonging to the Adiantaceae are found, replaced by exclusively hygrophytes and epiphytes in the south, like those belonging to the Dryopteridaceae and Hymenophyllaceae, respectively. This taxonomic and habitat preference replacement sequence suggest a key role of the precipitations in the distribution of Pteridophyte in continental Chile, where average rainfall increases with latitude (Di Castri & Hajek 1976). Water availability has been suggested as the main factor determining pteridophyte distribution (Karst *et al.* 2005, Qian *et al.* 2012). However, temperature and elevation have been also found to be positively related to pteridophyte species richness (Zhang *et al.* 2011, Qian *et al.* 2012). In Chile, temperature decreases with latitude, leaving precipitation as possibly the main determinant of pteridophyte distribution. Elevation effects were not explicitly tested in this study and should be addressed in future studies.

Ferns from the Adiantaceae represent almost 80% of the species of the first (northern-most) area. Many ferns taxa from this family, like *Cheilanthes*, are desiccation-tolerant plants (Rodríguez 1995). This area also presented high-altitudes species found in Peru, Mexico, and United States. These species could have reached Chile through the Andes, and can only be found above 3,000 m.a.s.l. Many species that are found exclusively in area 1, such as *Cheilanthes myriophylla* and *Cheilanthes sinuata*, are rare in Chile, with only a few records close to Parinacota (Arica y Parinacota Region). *Pityrogramma trifoliata* is the only species from area 1 that can be found at lower altitudes (close to 200 m). This species comes from tropical and subtropical America and grows in Chile associated to river banks from Parinacota to Loa River (Rodríguez 1995).

Area 2 has the greatest desert influence of all continental Chile. Here, two epiphyte species exclusive of area 2 can be found: *Polypodium espinosae* and *P. pycnocarpum*. These species live on short woody plants (shrubs, and small trees) like

Berberis litoralis Phil., *Proustia cuneifolia* D. Don f. *tipia* (Phil.) Fabris., *Ophryosporus triangularis* Meyen, *Bahia ambrosioides* Lag., *Monttea chilensis* Gay, and *Euphorbia lactiflua* Phil. These woody plants grow mainly close to the coast, where their presence is sustained by marine climate and "camanchacas", climatic phenomena of low clouds produced by sea water evaporation. Another epiphyte species present in this area is *Pleopeltis macrocarpa*, a fern more typical of higher latitudes. In continental Chile, it is found north of 36º S, where its presence can be explained by the moisture contribution of camanchacas.

Area 3 corresponds to the semi-arid zone of Chile. Here, the rainfall is closely related to cyclic climatic phenomena called "El Niño" y "la Niña" (El Niño/La Niña-Southern Oscillation, ENSO), with oscillations between dry and wet years. This results in pteridophytic vegetation characterized by drought-avoidance (mainly through dormancy) and drought-tolerance (Rundel *et al.* 1991). In this area only three aquatic species are found; *Isoetes hieronymi*, *Marsilea mollis*, and the introduced fern *Salvinia auriculata* grow in ephemeral ponds close to the Pacific Ocean (Rodríguez 1995).

Area 4 includes 35º S to 46º S, where the pteridophytes diversity and abundance is highest. This area coincides with the pteridophytes diversity center for temperate Southern Chile and Argentina (Ponce *et al*. 2002), in the temperate and cold-temperate Andes. The dominant pteridophytic flora includes species from Hymenophyllaceae and Blechnaceae. These families have high endemism, indicating strong biogeographical isolation due to the Arid Diagonal (see Villagrán *et al.* 1996, Villagrán & Hinojosa 1997) and the Andes (Ponce *et al.* 2002). The Arid Diagonal corresponds to a hyper-arid zone in northern Chile that appeared 7-4 million years ago (Villagrán *et al.* 1996, Villagrán & Hinojosa 1997). In this area, the individuals of some fern species such as *Lophosoria quadripinnata* and *Blechnum chilense* can grow very tall, reaching 2-3 meters or more (Rodríguez 1995). Epiphytic pteridophytes, e.g. Hymenophyllaceae, are characteristic of this area.

The last area (area 5) of our study has few endemic species, sharing most of the pteridophytic flora with area 4 (Table II). Here, the abundance of some of species, like *Blechnum penna-marina* and *Lycopodium alboffii* in Magallanes, can be very high.

The pteridophyte species richness changed with latitude, increasing southward from the northern limit peaking around 40º S, and decreasing sharply between 47º S and 48º S. This result agrees with previous studies of the richness distribution of trees, lianas, and ferns of the temperate rain forest in South America (Arroyo *et al.* 1995). Dominant pteridophyte families also exchange along a latitudinal gradient in continental Chile. In the north the Adiantaceae is the dominant family. Close to 30º S the Blechnaceae and Dryopteridaceae families appear, with the Adiantaceae still dominating. This could be related to the xeric conditions of the area. From the 34º S the available moisture increases due to occasional rain, fog, and low clouds. Here the Hymenophyllaceae appear and increase in diversity southward reaching a maximum around 40º S. Further south, the pteridophyte richness decreases, with some families like the Adiantaceae disappearing around 47º S. This could be related to the decrease in land mass area at those latitudes, and the presence of large ice masses and glaciers.

The latitudinal taxonomic replacement parallels the latitudinal change in habitat. The predominant terrestrial xerophytic forms give way to epiphytes in the south, probably related to the southward increase in precipitation and appearance of temperate forests. Terrestrial hygrophytes and aquatic pteridophytes are more or less evenly distributed in continental Chile. However, no aquatic pteridophytes were found in area 2, possibly due to incomplete sampling of water bodies and the inaccessibility of many locations.

Our results differ from previous studies on the biogeographic distribution of pteridophytes (Looser 1932, Godoy & Figueroa 1989). Based on pteridophytes, we define five biogeographic areas in continental Chile from north to south, matching the richness distribution and habitat requirements of these plants. Our study did not take into account the altitudinal variation found from East to West in Chile. It is possible that altitudinal segregation could also exist (see Cabrera & Willink 1973) and future studies on pteridophytes distribution should include longitudinal zonation. Incomplete pteridophytes sampling in Chile could result in errors in the interpretation of the obtained patterns. However, this plant group is relatively well studied in Chile (Rodríguez 1995, Rodríguez *et al.* 2009), especially the most diverse families like Blechnaceae, Adiantaceae, Dryopteridaceae and Hymenophyllaceae.

This is the first study to use 1° OGUs for pteridophytes in Chile, a latitudinal scale that allowed for finer segregation of the distribution of pteridophytes. Pteridophytes are a good proxy for environmental conditions since they are somewhat sensible to pollution and other anthropic effects (i.e. Deng *et al.* 2014, Soare *et al.* 2013). Few to none conservation initiatives are now focused on this plant group despite the fact that some species are considered endangered (Baeza *et al.* 1998, Squeo *et al.* 2008). The highest pteridophyte diversity is found in Central-South Chile, which coincides with the most densely populated areas of the country. Extensive land-use change and deforestation threatens this high diversity area. Future studies should include predictive models to determine priority areas for pteridophyte conservation.

REFERENCES

Arana, M. & B. Øllgaard. 2012. Revisión de las Lycopodiaceae (Embryopsida, Lycopodiidae) de Argentina y Uruguay. Darwiniana 50: 266-295.

Arroyo, M.T.K., L.A. Cavieres, A. Peñaloza, M. Riveros & A.N. Faggi. 1995. Relaciones fitogeográficas y patrones regionales de riqueza de especies en la flora del bosque lluvioso templado de Sudamérica. En: J.J. Armesto, C. Villagrán & M.T.K. Arroyo (eds.), Ecología de los Bosques Nativos de

Chile, pp. 71-99. Editorial Universitaria, Santiago, Chile.

Baeza, M., E. Barrera, J. Flores, C. Ramírez, & R. Rodríguez. 1998. Categorías de conservación de Pteridophyta nativas de Chile. Boletín del Museo Nacional de Historia Natural 47: 23-46.

Cabrera, A.L. & A. Willink. 1973. Biogeografía de América Latina. Monografía 13, Serie de Biología, OEA, Washington D.C. 152 pp.

Castán, D.F. & O.R. Vetaas. 2005. Pteridophyte richness, climate and topography in the Iberian Peninsula: comparing spatial and nonspatial models of richness patterns. Global Ecology and Biogeography 14: 155-165.

Deng, G., M. Li, H. Li, L. Yin & W. Li. 2014. Exposure to cadmium causes declines in growth and photosynthesis in the endangered aquatic fern (*Ceratopteris pteridoides*). Aquatic Botany 112: 23-32.

Di Castri, F. & E.R. Hajek. 1976. Bioclimatología de Chile. Editorial de la Universidad Católica de Chile, Santiago, Chile. 129 pp.

Frahm, J.-P. & S.R. Gradstein. 1991. An altitudinal zonation of tropical rain forests using bryophytes. Journal of Biogeography 18: 669-678.

Gajardo, R. 1994. La vegetación Natural de Chile. Clasificación y distribución geográfica. Editorial Universitaria, Santiago, Chile. 165 pp.

Godoy, R. & H. Figueroa. 1989. Composition and distribution of the pteridophyte flora of continental and insular Chile. Nova Hedwigia 48: 437-453.

Grau, J. 1995. Aspectos geográficos de la flora de Chile. En: C. Marticorena & R. Rodríguez (eds.), Flora de Chile, Vol. 1, pp. 63-83. Ediciones Universidad de Concepción, Concepción, Chile.

Hemp, A. 2002. Ecology of the pteridophytes on the southern slopes of Mt. Kilimanjaro. Part I: Altitudinal distribution. Plant Ecology 159: 211-239.

Karst, T., B. Gilbert & M. J. Lechowicz. 2005. Fern community assembly: The roles of chance and the environment at local and intermediate scales. Ecology 86: 2473-2486.

Larsen, C., M. Ponce & M. Scataglini. 2013. Revisión de las especies de *Hymenophyllum* (Hymenophyllaceae) del sur de Argentina y Chile. Gayana Botánica 70(2): 274-329.

Looser, G. 1932. Ensayo sobre la distribución geográfica de los helechos chilenos. Revista de Historia y Geografía 69: 162-198.

Luebert, F. & P. Pliscoff. 2006. Sinopsis bioclimática y vegetacional de Chile. Editorial Universitaria, Santiago, Chile. 316 pp.

Luna-Vega, I., J.D. Tejero-Díez, R. Contreras-Medina, M. Heads & G. Rivas. 2012. Biogeographical analysis of two *Polypodium* species complexes (Polypodiaceae) in Mexico and Central America. Biological Journal of the Linnean Society 106: 940-955.

Macluf, C.C. & R.J. Hickey. 2007. *Isoetes araucaniana*, a New Species from Southern South America. American Fern Journal 97: 220-224.

McCoyed, E.D., S.S. Bell & K. Walters. 1986. Identifying biotic boundaries along environmental gradients. Ecology 67: 749-759.

Oberdorfer, E. 1960. Pflanzensoziogische Studien in Chile, Ein Vergleichmit Europa. Flora Vegetatio Mundi 2: 1-128.

Pausas, J.G. & L. Sáez. 2000. Pteridophyte richness in the NE Iberian Peninsula: biogeographic patterns. Plant Ecology 148:195-205.

Ponce, M., K. Mehltreter & E. de la Sota. 2002. Análisis biogeográfico de la diversidad pteridofítica en Argentina y Chile continental. Revista Chilena de Historia Natural 75: 703-717.

Qian, H., S. Wang, Y. Li, M. Xiao & X. Wang. 2012. Disentangling the relative effects of ambient energy, water availability, and energy-water balance on pteridophyte species richness at a landscape scale in China. Plant Ecology 213: 749-756.

Real, R. 1999. Tables of significant values of Jaccard`s index of similarity. Miscellanea Zoológica 22: 29-40.

Real, R., J.M. Vargas & J.C. Guerrero. 1992. Análisis biogeográfico de clasificación de áreas y especies. Herpetological Monographs 2: 73-84.

Rodríguez, R. 1989. Comentarios fitogeográficos y taxonómicos de Pteridophyta chilenos. Gayana Botánica 46: 199-208.

Rodríguez, R. 1995. Pteridophyta. En: C. Marticorena & R. Rodríguez (eds.), Flora de Chile, Vol. 1, pp. 119-309. Ediciones Universidad de Concepción, Concepción, Chile.

Rodríguez, R., D. Alarcón & J. Espejo. 2009. Helechos Nativos del Centro y Sur de Chile. Guía de Campo. Ed. Corporación Chilena de la Madera, Concepción, Chile. 212 pp.

Rodríguez, R. & M. Ponce. 2007. Nuevas combinaciones en Gleicheniaceae. En: F. Zuloaga, O. Morrone & M.J. Belgrano (eds.). Novedades taxonómicas y nomenclaturales para la flora vascular del Cono Sur de Sudamérica. Darwiniana 45(2): 238.

Rundel, P.W., M.O. Dillon, B. Palma, H.A. Mooney & S.L. Gulmon. 1991. The phytogeography and ecology of the coastal Atacama and Peruvian deserts. Aliso 13: 1-49.

Sanginés-Franco, C., I. Luna-Vega, O. Alcántara & R. Contreras-Medina. 2011. Distributional patterns and biogeographic analysis of ferns in the Sierra Madre Oriental, Mexico. American Fern Journal 101: 81-104.

Schmithüsen, J. 1956. Forschungen in Chile. Die räumliche Ordnungderchilenischen Vegetation. Bonner Geographische Abhandlungen 17: 1-86.

Soare, L.C., C.M. Dobrescu, M. Popescu & A.G. Boeru. 2013. The Effects of Some Pesticides on Spore Germination and Gametophyte Differentiation in *Athyrium filix-femina* (L.) Roth. and *Polypodium vulgare* L. Notulae Botanicae Horti Agrobotanici Cluj-Napoca 41: 458-462.

Squeo, F.A., G. Arancio, J.R. Gutiérrez, L. Letelier, M.T.K. Arroyo, P. León-Lobos & L. Rentería-Arrieta. 2008. Flora Amenazada de la Región de Atacama y Estrategias para su Conservación. Ediciones Universidad de La Serena, La Serena. Viii. 72 pp.

Villagrán, C. & L.F. Hinojosa. 1997. Historia de los bosques de Sudamérica. II: Análisis fitogeográfico. Revista Chilena de Historia Natural 70: 241-267.

Villagrán, C., P. Moreno & R. Villa. 1996. Antecedentes palinológicos acerca de la historia Cuaternaria de los bosques chilenos. En: J.J. Armesto, C. Villagrán & M.T.K. Arroyo (eds.), Ecología de los bosques nativos de Chile, pp. 51-69. Editorial Universitaria, Santiago, Chile.

Zhang, Q., Z. Wang, M. Ji, Z. Fan & J. Deng. 2011. Patterns of species richness in relation to temperature, taxonomy and spatial scale in eastern China. Acta Oecologica 37: 307-313.

Zuloaga, F., O. Morrone & M. Belgrano (eds.). 2008. Catálogo de las Plantas Vasculares del Cono Sur (Argentina, Sur de Brasil, Chile, Paraguay y Uruguay). Missouri Botanical Garden Press, U.S.A. 3348 pp.

Recibido: 26.03.14
Aceptado: 0711.14