

Vascular plant assemblages of ephemeral wetland vegetation along the Mediterranean-temperate gradient in Chile

Ensamblajes de plantas vasculares asociadas a humedales temporales a lo largo del gradiente mediterráneo-templado en Chile

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ABSTRACT

Plant species composition and geographical distribution of vernal pools in Mediterranean Chile are poorly studied. In order to overcome this gap we collected 73 floristic samples in the Mediterranean-temperate gradient from Chile (31-44°S). Additionally, we carried out an exhaustive collection of published phytosociological relevés made in this area including some relevés from the East side of the Andes in Argentina. The resulting dataset contains 228 observations of 269 species. Hierarchical clustering was applied in order to get co-occurrence assemblages. These sets were compared with diagnostic groups defined *a priori*, life forms and their status in South America (introduced vs native species). In order to detect geographic and climatic distribution patterns of the assemblages, we extracted climatic summary variables from the WorldClim database and performed a principal component analysis (PCA). We detected seven species assemblages with a significant correspondence to diagnostic groups defined *a priori* ($P < 0.01$), though their association is relatively low (Cramér's $V = 0.49$). Native species dominate over adventive ones in each assemblage suggesting low risk of out-competition by introduced species adapted to these habitats. The annual life form is over represented in most of the co-occurrence groups. Despite the huge temperature and precipitation gradient in the studied transect, plant assemblages are occurring almost along the whole range, supporting the hypothesis of azonality (low dependence on macro-climate). Assemblages defined in this work can be potentially used for further supervised classification strategies in order to define plant community types within vernal pool vegetation.

KEYWORDS: Ecological groups, phytosociology, syntaxonomic classification, vernal pools, vegetation database.

RESUMEN

Actualmente se conoce muy poco sobre la composición florística y la distribución geográfica de humedales temporales en Chile mediterráneo. Con el fin de llenar este vacío, se realizaron 73 inventarios florísticos en el gradiente mediterráneo-templado de Chile (31-44°S). Además, se llevó a cabo una búsqueda bibliográfica exhaustiva de inventarios fitosociológicos en publicaciones científicas, incluyendo algunos inventarios de la parte argentina de la Cordillera de los Andes. Se obtuvo una matriz con 228 observaciones y 269 especies. Se aplicó una clasificación jerárquica para generar ensambles de co-ocurrencia. Dichos ensambles fueron comparados con grupos de especies diagnósticas definidas *a priori*, con formas de vida y tipos de origen (especies introducidas en Sudamérica vs especies nativas). Para determinar patrones de distribución geográfica y climática, se extrajeron variables del modelo WorldClim y se aplicaron a un análisis de componentes principales (PCA). Según la clasificación jerárquica se determinaron siete ensambles de especies con una alta correspondencia a los grupos definidos *a priori* ($P < 0,01$), sin embargo con un nivel relativamente bajo de asociación (índice V de Cramér = 0,49). En la vegetación estudiada dominan las especies nativas sobre las introducidas, lo que sugiere un bajo riesgo de extinción por competencia con especies introducidas adaptadas a este tipo de ambientes. La forma de vida anual está sobrerrepresentada en la mayoría de los ensambles. Pese al enorme gradiente de temperatura y precipitación incluido en el rango de las muestras, los ensambles se distribuyen a lo largo de todo este gradiente, apoyando la hipótesis de azonalidad (indiferencia al macro-clima). Los ensambles definidos en este trabajo pueden ser potencialmente utilizados para posteriores clasificaciones supervisadas con el fin de definir tipos de comunidades vegetales en lagunas temporales.

PALABRAS CLAVE: Grupos ecológicos, fitosociología, clasificación sintaxonomica, lagunas temporales, bases de datos vegetacionales.

INTRODUCTION

Ephemeral wetlands are habitats with a restricted time window for plant growth due to the alternation of flooding periods with dry ones. In a global revision, Deil (2005) classified these habitats in three main types: seasonal pools, shorelines of lakes and rivers with fluctuating water level and ephemeral flushes on inselbergs. Seasonal pools and in particular vernal pools occur in the Mediterranean biomes of the world, namely in Australia, South of Africa (Capensis region), the Circum-Mediterranean area (southern Europe and northern Africa), California (eastern USA) and central Chile (Deil 2005). According to Keeley & Zedler (1998), vernal pools are defined as pools filled by winter rains and desiccating in summer. Growth and generative reproduction of the plant species are concentrated on the aquatic phase in spring and the amphibic phase in early summer. The occurrence of these habitats is determined by strong seasonality of temperature and rainfall. Low water permeability of the substrate and an undulating relief with small depressions are further preconditions (Deil 2005). Since vernal pools are not affected by long-distance drainage (Keeley & Zedler 1998), soil chemistry and water properties are locally determined.

Vernal pools are colonized by a highly specialized flora, adapted to a strong seasonal dynamic on water availability. Such specialists are frequently accompanied by opportunistic species from the surrounding habitats. The spatial isolation of the vernal pools favours allopatric speciation, resulting in endemic taxa and geographical vicariants, especially in taxa with restricted dispersal capacity. On the other hand, ephemeral wetland species with long-distance dispersal capacity can reach a cosmopolitan distribution (Deil 2005).

In Chile vernal pools are poorly studied. Most of the research is restricted to floristic surveys done at the local scale. A first floristic analysis and vegetation study over a broader geographical area and along the north-south precipitation gradient from the semi-arid via the subhumid Mediterranean to the temperate bioclimate in Chile was realized by Bliss *et al.* (1998). These authors collected data along transects, crossing the whole vernal pool and including habitats of very different inundation period and becoming amphibic in different seasons. Hence such data are not suitable to look for phytocoenoses related to specific environmental conditions.

Vernal pools offer a habitat to native annuals, many of them endemic in Chile (Arroyo *et al.* 1990). Additionally, many of these annual species belong to mono-specific genera, such as the Asteraceae *Blennosperma*, *Centipeda*, *Lasthenia*, *Micropsis* and *Microseris* (Moreira-Muñoz & Muñoz-Schick 2007, Moreira-Muñoz 2011). The distribution and ecology of vernal pool plant species is poorly known (Alvarez *et al.* 2008, 2012b). An analysis, which species are restricted to the vernal pool habitat and how they are distributed can be

a first step to evaluate their vulnerability and the extinction risk and to assess their importance for conservation of plant diversity at the regional, national and even continental scale. On the other hand, Chilean vernal pools often occur in man-made pastures and in other disturbed areas such as trampling paths (Deil *et al.* 2007), livestock watering ponds (San Martín *et al.* 1998) and gravel quarries (Ramírez *et al.* 1996), resulting in a significant participation of European alien plants in Chilean vernal pools. This phenomenon is also mentioned for vernal pools in California, where the high frequency of *Briza minor*, *Leontodon taraxacoides*, *Lythrum hyssopifolia*, *Picris echioides*, *Medicago polymorpha*, *Sonchus asper*, *Trifolium dubium* and *Vulpia bromoides* is recorded (Barbour *et al.* 2003, Gerhardt & Collinge 2003). All these species of Palaearctic origin are also occurring in Chilean vernal pools. The dominance of non-native species may reflect the degree of disturbance in those habitats.

Vernal pools in Chile are distributed over a long gradient of temperature and rainfall, for instance annual rainfall ranges from less than 100 to more than 1,000 mm (Bliss *et al.* 1998). This huge gradient is reflected in the zonal vegetation dominated by semi-desert coastal scrubs in the north respectively temperate evergreen forests in the south (Luebert & Plissock 2006). Although this gradient is crossing through four floristic regions defined by Bannister *et al.* (2012), we hypothesise that vernal pools specialists react more sensitively to local conditions along the inundation gradient by forming different plant assemblages in the pool bottom, the fringes and the surrounding upland areas (see examples from other Mediterranean areas in the world in Deil 2005), but are less affected by macro-climatic conditions, showing an azonal character.

The aims of this work are to classify Chilean vernal pool species into co-occurrence groups (assemblages) and to check the correlation between their distribution along the studied gradient (31° to 43° south latitude) and macro-climatic parameters (temperature and rainfall). Additionally we aim to compare the resulting assemblages with current syntaxonomical lists of diagnostic species, life forms and species status (i.e. native or introduced species).

METHODS

DATA COLLECTION

In early spring of 2009 (September-October) we searched for vernal pools in Mediterranean Chile from 31° to 38° S and at localities recorded by Bliss *et al.* (1998). To get data from homogeneous plots concerning inundation period and time of emergence, sample sites were delimited according to their actual eco-phase. Following Pott & Remy (2000), we separated in each of the pools the hydrophase, littoral, limose, and terrestrial eco-phases. Plot size was 1 or 2 m² depending on the size of the whole stand and the slope angle towards the pool centre. In total 73 relevés were sampled in

33 pools. The number of relevés per pool varies from 1 to 4.

Complementing the relevés sampled in 2009, we included in the dataset published records focussing on the syntaxonomic classes *Limoselletea australis*, *Littorelletea australis* and *Nanojuncetea australis* (community groups G, H and I in Deil *et al.* 2011, respectively). These records are not only restricted to Chile but some are located in the Western Argentinean Patagonia area (Eskuche 2005). Since previous studies (Alvarez 2008, Deil *et al.* 2007, Ramírez *et al.* 1994) and field observations showed close floristic relationships between seasonal wetland vegetation in the late terrestrial eco-phase and surrounding annual dry grassland communities we also added to this analysis the communities studied by Deil *et al.* (2007), which were included into the *Helianthemetea guttati*, a class of annual dry grassland in Mediterranean climate regions. The final

dataset included records from 228 plots. Though most of the ephemeral wetlands studied here may correspond to vernal pools, typical of the Mediterranean belt and the temperate areas with dry summer, some of the stands can be also representing autumnal pools (*sensu* Deil 2005) occurring at the shoreline of lakes with fluvio-nival regimes, such as the case of the relevés collected in the Argentinean Andes by Eskuche (2005).

Relevés analysed in this work (Table I) are stored in CL-Dataveg, a database formatted for Turboveg (Hennekens & Schaminée 2001), focussing on Chilean herb vegetation (Alvarez *et al.* 2012a) and indexed with the code SA-CL-001 in the Global Index of Vegetation-Plot Databases (Dengler *et al.* 2011). The nomenclature of plant species follows Zuloaga *et al.* (2008).

TABLE I. Sources of relevés used for the determination of plant assemblages in seasonal wetlands of Chile and Argentina. Some of the plant community names are tentative. ID is the access number in the database CL-Dataveg.

TABLE I. Fuentes de inventarios usados para la determinación de ensambles de plantas asociadas a lagunas temporales de Chile y Argentina. Algunos de los nombres de comunidades vegetales son tentativos. ID es el número de acceso en la base de datos CL-Dataveg.

SOURCE	PLANT COMMUNITY	NUMBER OF RELEVÉS	ID
DATA SAMPLED IN CHILE			
Original for this work	Several communities	73	1-73
Alvarez (2008)	<i>Leontodo saxatilis</i> - <i>Piptochaetietum navarretietosum</i>	4	(98-105)
	<i>Leontodo saxatilis</i> - <i>Piptochaetietum micropsietosum</i>	4	(98-105)
Deil <i>et al.</i> (2007)	<i>Crassula closiana</i> - <i>Microseris pygmaea</i> comm.	11	74-84
	<i>Hypochaeris glabra</i> - <i>Leontodon taraxacoides</i> comm.	5	85-89
San Martín <i>et al.</i> (1998)	<i>Eleocharietum pachycarpae</i>	11	183-193
	<i>Eleocharietum macrostachyae</i>	7	194-200
	<i>Gnaphalio cymatoidis</i> - <i>Polygonetum hydropiperoidis</i>	7	201-207
	<i>Eleocharis pachycarpa</i> - <i>Lythrum portula</i> comm.	5	215-219
	<i>Phyla nodiflora</i> -comm.	4	224-227
Ramírez <i>et al.</i> (1996)	<i>Polygono aviculare</i> - <i>Crassuletum paludosae</i>	2	106-107
Ramírez <i>et al.</i> (1994)	<i>Leontodo</i> - <i>Piptochaetietum navarretietosum</i>	20	108-127
	<i>Leontodo</i> - <i>Piptochaetietum micropsietosum</i>	20	128-147
	<i>Mentha pulegium</i> - <i>Juncus procerus</i> -comm.	4	148-151
Oberdorfer (1960)	<i>Gratiolo peruviani</i> - <i>Littorelletum australis</i>	2	90-91
	<i>Juncetum planifolii</i>	3	92-94
	<i>Anagallis alternifolia</i> - <i>Juncus planifolius</i> comm.	1	95
	<i>Scirpo inundati</i> - <i>Limoselletum aquaticae</i>	2	96-97
DATA SAMPLED IN ARGENTINA			
Eskuche (2005)	<i>Arenario serpentis</i> - <i>Azorelletum trifoliatae</i>	9	230-238
	<i>Carici deciduae</i> - <i>Senecionetum zostaerifolii</i>	10	239-248
	<i>Senecioni zostaerifolii</i> - <i>Littorelletum australis</i>	10	249-258
	<i>Crassulo peduncularis</i> - <i>Limoselletum lineatae</i>	4	259-262
	<i>Downingio pusillae</i> - <i>Isoëtetum chubutiana</i>	4	263-266
	<i>Hydrocotylo chamaemori</i> - <i>Juncetum arctici</i>	6	267-272

The subset used for this work is restricted to vascular plants (269 taxa in total; mosses, lichens and algae are excluded). We added the coordinates of sampling localities, which were either recorded in the field by using a GPS device (i.e. plots sampled in 2009) or read from digital maps according to the descriptions of study sites in the respective bibliographic sources. The relevés are distributed in a range over about 1,000 km in the North-South direction (Fig. 1), from the Mediterranean into the temperate bioclimate according to Amigo & Ramírez (1998), and the ombrotypes semi-arid to hyper-humid according to Luebert & Pliscoff (2006). This gradient includes sites with annual mean temperatures ranging from 6.3 to 17.2°C and annual rainfall ranging from 171 to 2,417 mm.

CLASSIFICATION OF SPECIES AND COMPARISON WITH GROUPS DEFINED A PRIORI, LIFE FORMS AND STATUS

In order to produce sociological groups of species (species of similar ecological requirements), we classified them into co-occurrence groups (inverse classification according to Wilson *et al.* 1990). Previous to analysis the input dataset was formatted in a vegetation matrix of species as rows and relevés as columns (transposed vegetation table). Rare species, occurring in less than 7 plots, were excluded from the input matrix. Such species could be recorded by chance or due to introgression from the local neighbouring vegetation and may interfere in the statistical analyses. Hence the 269 vascular plant species included in the original dataset were reduced to 114 species. In order to enhance the discrimination capacity of the classification, abundance was rescaled to 4 classes using 25%-steps (Van der Maarel 1979). A distance matrix comparing species was calculated after logarithmic transformation of abundance, using the formula $x' = \ln(1+x)$, and calculation of Bray-Curtis index as $1 - index$. The resulting dissimilarity matrix was submitted to hierarchical clustering using the algorithm Ward1 (Murtagh & Legendre 2014). The clustering displayed as a dendrogram was visually assessed to define clusters' cut level according to the length of branches. The clusters were contrasted against a null hypothesis of "no class structure" using the Multiple Response Permutation Procedure (MRPP) according to Mielke *et al.* (1981) and Van Sickle & Hughes (2000). This test was applied to the same dissimilarity matrix as for classification and running 1,000 permutations. In this analysis the index A (chance corrected within-group agreement) estimates the proportion of the distances explained by group identity and varies from 1 (all sample within groups are identical) to 0 (within-group heterogeneity equals the expectation by chance). Both, hierarchical clustering and MRPP were carried out using the package *vegan* (<http://CRAN.R-project.org/package=vegan>) in the statistical computing language R (<http://www.R-project.org>). For a direct import of the Turboveg database to the R console we used the package

vegdata (Jansen & Dengler 2010). For the manipulation and display of the classification dendrogram we used the package *ggdendro* (<http://CRAN.R-project.org/package=ggdendro>).

An additional a priori classification of species was defined according to available syntaxonomic studies. In such studies, plant species with high fidelity values for a syntaxa (class, order, alliance or association) are defined as diagnostic. Thus a diagnostic species of a class is frequently occurring in this class and absent in other classes due to matching of ecological requirements of this species and the properties of habitats occupied by the class (Bruehlheide 2000). Diagnostic species for the classes *Nanojuncetea australis*, *Limoselletea australis* and *Littorelletea australis*

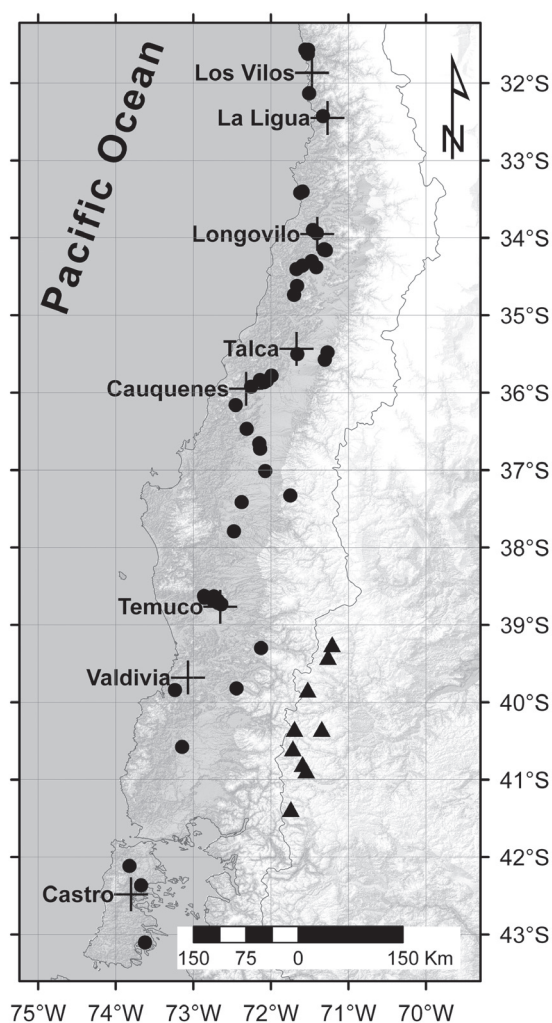


FIGURE 1. Geographical distribution of analyzed samples. Points: sample plots in Chile, triangles: sample plots in Argentina, crosses: localities of the reference weather stations.

FIGURA 1. Distribución geográfica de las muestras analizadas. Puntos: muestras de Chile, triángulos: muestras de Argentina, cruces: estaciones meteorológicas usadas como referencia.

were defined according Deil *et al.* (2011), while species for dry annual turfs (*Helianthemetea guttati*) were extracted from Deil *et al.* (2007) (Table II). Additional information about life forms (Raunkiaer's classes) and status of the species (native or introduced) in Chile was collected from reference checklists (i.e. Arroyo *et al.* 1990 and Zuloaga *et al.* 2008). This information is displayed in Appendix A.

The correspondence of assemblages to groups defined a priori, life forms and status of species was estimated by calculating the Cramér's V coefficient and checked with Pearson's chi squared test (Backhaus *et al.* 2006). For that purpose, the function `assocstats` of the R-package `vcd` (version 1.2-12, <http://CRAN.R-project.org/package=vcd>) was applied.

DESCRIPTION OF CLIMATIC GRADIENTS

To describe the climatic gradient following the latitudinal distribution of sites we superimposed an ESRI-shapefile over climatic raster-dataset obtained from the WorldClim database (Hijmans *et al.* 2005). The climatic information was transferred to the shapefile by using the Hawth's analysis tools plug-in (<http://www.spatial ecology.com>)

in the software ArcGIS (<http://www.esri.com>). We also compared climatic parameters for some stations published in Luebert & Plissock (2006) and shown in Figure 1 against the simulated data stored in the WorldClim database.

In order to reduce the redundancy by highly correlated climatic variables, a principal component analysis (PCA) was carried out using the R-function `prcomp`. Coordinates and climatic information were imported from the ESRI-shapefile to R using the package `maptools` (<http://CRAN.R-project.org/package=maptools>). Herewith we eliminated duplicates in the dataset (plots sampled in the same locality). Previous to analysis we re-scaled the values of each climatic variable to a distribution with mean value 0 and standard deviation 1 by using the R-function `scale`. To determine correlations between variables we used the PCA loadings, where high and low values indicate positive respectively negative correlation of a variable with a PCA axis. To analyse the correspondence between presence of species and PCA dimensions summarizing correlated climatic variables, we exported the PCA scores to the sampling localities into the dataset and draw boxplots showing the dispersal of assemblages in the PCA scores.

TABLE II. Diagnostic groups of plant species defined a priori according to Deil *et al.* (2011) and Deil *et al.* (2007).

TABLA II. Grupos de plantas diagnósticas definidas a priori según Deil *et al.* (2011) y Deil *et al.* (2007).

NAA: NANOJUNCETEA AUSTRALIS (cf. Isoëtales, Isoëto-Nanojuncetea)
<i>Blennosperma chilense</i> , <i>Bromidium trisetoides</i> , <i>Calotheca brizoides</i> , <i>Cardamine valdiviana</i> , <i>Centipeda elatinoides</i> , <i>Centunculus minimus</i> , <i>Cicendia quadrangularis</i> , <i>Cyperus eragrostis</i> , <i>C. reflexus</i> , <i>Deschampsia danthonioides</i> , <i>Dichondra sericea</i> , <i>Dioscorea fastigiata</i> , <i>Eryngium humifusum</i> , <i>E. pseudojunceum</i> , <i>Gamochoaeta spiciformis</i> , <i>Pseudognaphalium cymathoides</i> , <i>Gratiola peruviana</i> , <i>Hydrocotyle cryptocarpa</i> , <i>Juncus bufonius</i> , <i>J. capitatus</i> , <i>J. imbricatus</i> , <i>J. planifolius</i> , <i>J. procerus</i> , <i>Lasthenia kunthii</i> , <i>Leontodon taraxacoides</i> , <i>Lotus subpinnatus</i> , <i>Lythrum hyssopifolia</i> , <i>L. portula</i> , <i>Mentha pulegium</i> , <i>Micropsis nana</i> , <i>Nassella poeppigiana</i> , <i>Navarretia involucrata</i> , <i>Nierembergia repens</i> , <i>Nothoscordum gramineum</i> , <i>Oldenlandia salzmännii</i> , <i>Paspalum dasyleurum</i> , <i>Phyla canescens</i> , <i>Piptochaetium montevidense</i> , <i>Plagiobothrys pratensis</i> , <i>Polygonum hydropiperoides</i> , <i>Sisyrinchium graminifolium</i> , <i>Stenandrium dulce</i> , <i>Triptilion spinosum</i>
LMO: LIMOSELLETEA AUSTRALIS (cf. Nanocyperetalia, Isoëto-Nanojuncetea)
<i>Crassula peduncularis</i> , <i>Elatine triandra</i> , <i>Juncus ebracteatus</i> , <i>J. pallescens</i> , <i>J. uruguensis</i> , <i>Lilaeopsis macloviana</i> , <i>Limosella australis</i> , <i>Soliva triniifolia</i>
LTT: LITTORELLETEA AUSTRALIS (cf. Littorelletalia uniflorae, Isoëto-Littorelletea)
<i>Anagallis alternifolia</i> , <i>Azorella trifoliolata</i> , <i>Carex decidua</i> , <i>C. sangei</i> , <i>Downingia pusilla</i> , <i>Eleocharis maculosa</i> , <i>E. pachycarpa</i> , <i>Equisetum bogotense</i> , <i>Hydrocotyle chamaemorus</i> , <i>Isoëtes chubutiana</i> , <i>Isolepis inundata</i> , <i>Juncus balticus</i> ssp. <i>andicola</i> , <i>J. stipulatus</i> , <i>Leptophyllochloa micrathera</i> , <i>Lindernia procumbens</i> , <i>Littorella australis</i> , <i>Myosurus apetalus</i> , <i>Plagiobothrys corymbosus</i> , <i>Ranunculus hydrophilus</i> , <i>R. trullifolius</i> , <i>Senecio zosterifolius</i>
ANN: COMMUNITIES DOMINATED BY DWARF ANNUALS (cf. Chaetanthero-Vulpion, Helianthemetea guttati)
<i>Aira caryophyllea</i> , <i>Briza minor</i> , <i>Cerastium glomeratum</i> , <i>Chaetanthera ciliata</i> , <i>Crassula closiana</i> , <i>Hypochaeris glabra</i> , <i>Logfia gallica</i> , <i>Medicago polymorpha</i> , <i>Microseris pygmaea</i> , <i>Oxalis micrantha</i> , <i>Ozoroë biflora</i> , <i>Plagiobothrys procumbens</i> , <i>Rumex acetosella</i> , <i>Soliva sessilis</i> , <i>Trifolium amabile</i> , <i>T. glomeratum</i> , <i>T. suffocatum</i> , <i>Vulpia bromoides</i>

RESULTS

SPECIES ASSEMBLAGES

According to hierarchical clustering we defined 7 co-occurrence groups and arranged them from north to south according to their median latitudinal distribution. The classification dendrogram is presented in Fig. 2, indicating species groups defined *a priori* for a preliminary overview of correlations between those groups. According to the MRPP, the null hypothesis of no-cluster structure was rejected (P -value < 0.01). In the analysis the value of the chance corrected within-group agreement is relatively low ($A = 0.23$). The size of the groups ranges from 9 (assemblage 6) to 22 species (assemblage 7).

CLASSIFICATION *A PRIORI*, LIFE FORMS AND STATUS VERSUS ASSEMBLAGES

From the 114 species used for the classification, 40% were considered as companion species, while 32% of them were considered as diagnostic species for the class *Nanojuncetea australis*. Most of the dwarf wetland annuals were clustered in assemblage 1, while assemblage 6 is dominated by *Nanojuncetea australis* and assemblage 7 by *Littorelletea australis* species. *Limoselletea australis* species are assigned to the assemblages 5 and 7 (Table III, see also Fig. 2).

53% of the species are therophytes (annuals), followed by hemicryptophytes (34%). Therophytes dominate the assemblages 1, 2, 4 and 5, while hemicryptophytes are dominating the assemblages 3, 6 and 7. About 73% of the analysed species are native ones. They are also the majority in every assemblage.

According to the Pearson's chi-squared test, significant p -values ($P < 0.05$) were observed in the comparisons of assemblages versus groups defined *a priori* and versus life forms (Table III). Therefore, the null-hypothesis of non-dependency was rejected in those cases, while the status of species (native/non-native) is not related to assemblages ($P = 0.12$). Despite to these findings, the correspondence of assemblages with groups defined *a priori* and life forms is relatively weak considering values of the Cramér's V (0.49 for species groups and 0.42 for life forms), since the values of this index vary between 0 (no correlation) and 1 (perfect correlation).

GEOGRAPHIC DISTRIBUTION AND MACRO-CLIMATIC GRADIENT

The latitudinal distribution of species is in general very variable within co-occurrence groups (Fig. 3, bottom). Most of the groups occur along the whole gradient. Assemblages 1 to 5 have a latitudinal median between 34 °S and 37 °S, while assemblages 6 to 7 have their medians between 38 °S and 40 °S.

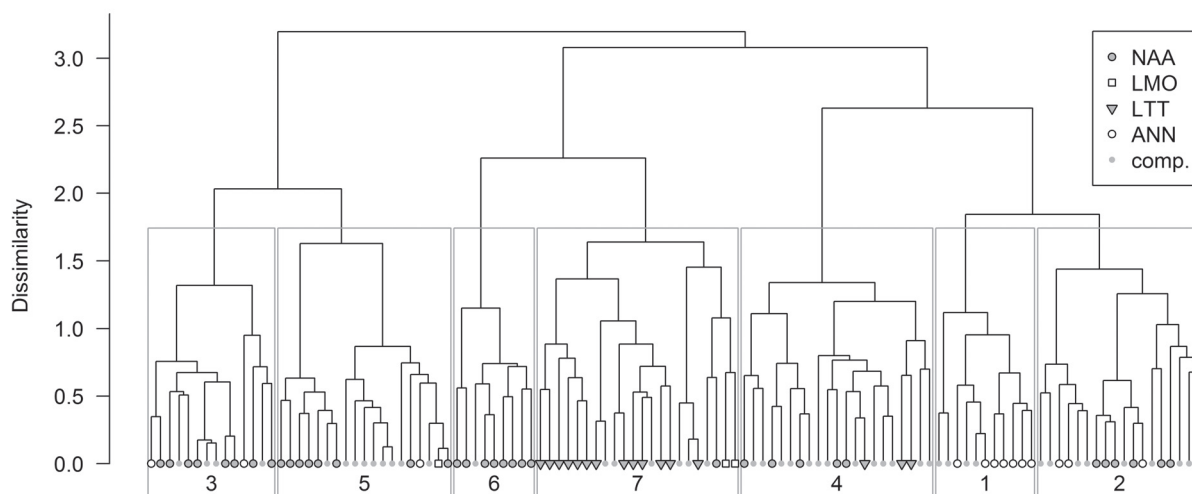


FIGURE 2. Classification dendrogram of species according to hierarchical clustering. Symbols of single species show groups defined *a priori* (see legend): *Nanojuncetea australis* (NAA), *Limoselletea australis* (LMO), *Littorelletea australis* (LTT), communities dominated by annual dwarf species (ANN) and companion species (comp.). Grey frames show the single assemblages with assigned numbers (identifiers) below.

FIGURA 2. Dendrograma de clasificación jerárquica de especies. Los símbolos para las especies muestran los grupos definidos *a priori* (ver leyenda): *Nanojuncetea australis* (NAA), *Limoselletea australis* (LMO), *Littorelletea australis* (LTT), comunidades dominadas por especies nano-terófitas (ANN) y especies acompañantes (comp.). Los rectángulos grises muestran los ensambles con los números asignados (identificadores) debajo.

TABLE III. Cross classification table comparing species assemblages obtained by hierarchical clustering versus species groups defined *a priori* (A), life forms (B) and status of the species in South America (C). Groups defined *a priori* are coded as NAA (Nanajuncetea australis species group), LMO (Limoselletea australis species group), LTT (Littorelletea australis species group), ANN (dwarf annuals or Chaetanthero-Vulpion species group), and comp. (companion species). Life forms are coded as T (therophytes, i.e. annuals), Cr (cryptophytes, including bulb plants), H (hemicryptophytes), and Ch (chamaephytes). Species status is either native (nat.) or introduced (int.). Cramér's V coefficient (V) and the p-value of the Pearson's chi-squared test (P) are indicated for each factor.

TABLA III. Tabla de clasificación cruzada de la comparación de ensambles de especies obtenidos de la clasificación jerárquica con grupos definidos *a priori* (A), formas de vida (B) y origen de especies (C). Los grupos definidos *a priori* están codificados como NAA (especies de Nanajuncetea australis), LMO (especies de Limoselletea australis), LTT (especies de Littorelletea australis), ANN (nano-terófitas o especies del Chaetanthero-Vulpion), y comp. (especies acompañantes). Formas de vida son abreviadas como T (terófitas, i.e. plantas anuales), Cr (criptófitas, inclusive plantas bulbosas), H (hemicriptófitas), y Ch (caméfitas). El origen corresponde a plantas nativas (nat.) o introducidas (int.). Además se indica para cada factor el coeficiente V de Cramér's (V) y el valor de p para el test de chi cuadrado de Pearson (P).

FACTOR	CLASSES	ASSEMBLAGES							SUM	V	P
		1	2	3	4	5	6	7			
A: Groups a priori	NAA	-	6	8	5	8	8	1	36	0.49	<0.01
	LMO	-	-	-	-	1	-	2	3		
	LTT	-	-	-	3	-	-	13	16		
	ANN	7	3	2	-	1	-	-	13		
	comp.	4	9	4	13	9	1	6	46		
B: Life forms	T	9	17	4	14	10	1	5	60	0.42	<0.01
	Cr	2	1	-	5	2	-	4	14		
	H	-	-	10	2	6	8	13	39		
	Ch	-	-	-	-	1	-	-	1		
C: Status	int.	4	8	5	2	7	2	3	31	0.30	0.12
	nat.	7	10	9	19	12	7	19	83		
Total species		11	18	14	21	19	9	22	114		

The sampling localities show a clear geographic and climatic pattern from higher mean temperatures and lower rainfall in the North to cooler and wetter climate in the South. Mean annual temperature ranges from 17.2 to 6.3 °C, while annual rainfall varies between 171 and 2,417 mm. Climatic stations used as reference show a very similar trend in the latitudinal direction. Although Argentinean plots are located at higher altitudes at same latitudes of Chilean plots, they do not divert too much in the mentioned climatic patterns (Fig. 3).

According to the PCA loadings, 4 groups of climatic variables could be defined, highly correlated between each other (Table IV). The first group contains variables negatively correlated with PCA 1, most of them related

with mean temperature (bio_1) but also precipitation seasonality (bio_15). The second group is positively correlated with PCA 1 and contains variables related with annual precipitation (bio_12). A third group of variables with highly positive loadings in PCA 2 is related with temperature oscillation patterns like the annual range (bio_7) and the temperature seasonality (bio_4). The isothermality (bio_3) has low loadings in PCA 1 and PCA 2 but a high negative correlation with PCA 3. The three first PCA dimensions used to build these groups resume about 92% of the total variability of the data. The latitude, also included in this analysis, is mainly correlated with PCA 1, indicating the geographic trend in the ordination from low (North) to high scores (South).

DISCUSSION

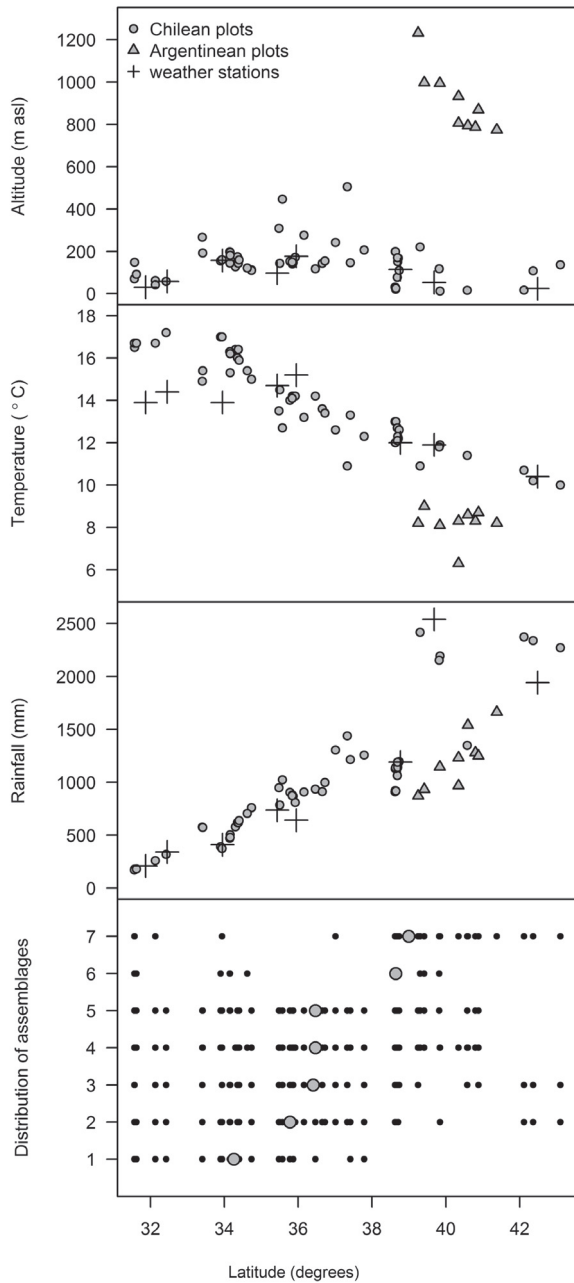


FIGURE 3. Geographic distribution of sampling localities and weather stations versus gradients of altitude, temperature and rainfall at the sampling localities according to the WorldClim database (Hijmans *et al.* 2005). Bottom plot shows the occurrence of species assemblages defined by hierarchical clustering (black dots), indicating their respective latitudinal medians (grey circles).

FIGURA 3. Distribución geográfica de las localidades muestreadas y de las estaciones meteorológicas comparadas con gradientes de altitud, temperatura y precipitación en los lugares de muestreo según el modelo WorldClim (Hijmans *et al.* 2005). El plot inferior muestra la presencia de ensambles definidos por la clasificación jerárquica (puntos negros), indicando sus respectivas medianas latitudinales (círculos grises).

SPECIES ASSEMBLAGES, SYNTAXONOMY AND MICRO-ENVIRONMENT
 Character species of vernal pool habitats are related to the Nanojuncetea australis (Deil 2005). Therefore this class is well represented in our dataset and is discriminated by the hierarchical clustering in the assemblages 3, 5 and 6 (Table III). Most of these clusters are dominated by annuals. On the other hand, assemblages 3, 6 and 7 are dominated by hemicryptophytes.

Within annuals, two groups can be distinguished according to flooding resistance: *Centunculus minimus*, *Cicendia quadrangularis* or *Micropsis nana* are dwarfish species, characterized by short life spans and a low tolerance to flooding duration (up to 30 days according to Keeley & Zedler 1998), growing on pond edges. They belong to the “terrestrial damp species” sensu Casanova & Brock (2000), which are able to germinate in water-saturated soils, finishing their life cycle in the terrestrial ecophase. Amphibious annuals like *Hydrocotyle cryptocarpa*, *Navarretia involucrata* or *Ranunculus bonariensis* var. *trisepalus* belong to the second group: These species are amphibious annuals, tolerating longer flooding periods. They respond to water level variations with a morphological plasticity (“amphibious fluctuation responders” sensu Casanova & Brock 2000), mainly by changes in leaf morphology (Urban 1999). These species occur with preference in the bottom of seasonal pools (Bliss *et al.* 1998, Keeley & Zedler 1998). Despite these two strategies allow the annuals to colonize different sites in an inundation gradient, the numerical classification mixed them in the assemblages, suggesting their co-occurrence due to a gradual transition from the aquatic to the terrestrial ecophase. Such intra-seasonal dynamic in the species composition was analysed by Rudner (2005) in the south of the Iberian Peninsula, where Isoëto-Nanojuncetea communities are replaced in early summer by Helianthemetea guttati communities. A classification of seasonal wetland annuals according to the scheme proposed by Casanova & Brock (2000) for Australia will require a detailed analysis of the phenology of the species in Chile.

Species grouped in assemblage 1 also belong to the dwarf annual growth form (nanism sensu Alvarez *et al.* 2012b). They characterize dry annual grassland (Deil *et al.* 2007) and are probably diagnostic species for the alliance Chaetanthero-Vulpion described by Oberdorfer (1960). Some of them are neophytes of European origin, linking their communities with the class Helianthemetea guttati of the Mediterranean area of the Western Palaearctic subkingdom. Among them we also find the native species *Lepuropetalon spathulatum*, one of the smallest dicotyledonous plants worldwide. The distribution of this species and its relation to vernal pools was studied in detail by Alvarez *et al.*

(2012b). The syntaxonomic linkage between assemblage 1 and the vernal pool species suggest their assignment to *Nanojuncetea australis*.

Limoselletea australis species are poorly represented in our data set and not discriminated by the classification. For instance, *Crassula peduncularis* and *Limosella australis*, both considered as diagnostic for this class, join the *Littorelletea* species in assemblage 7. Though *Limoselletea australis* is considered by some authors as synonymous of *Nanojuncetea australis* (e.g. Galán de Mera 2005), its distribution along the Andean belt differs from the species of *Nanojuncetea australis*, clearly linked to the Mediterranean bioclimate. Additional samples of *Limoselletea australis* communities may be required to elucidate this question.

Species related to *Littorelletea australis* are mainly grouped in assemblage 7. These species colonize shorelines of oligotrophic lakes and streams with gravel or sand and are more frequent in the southern part of the study area (Oberdorfer 1960, Deil *et al.* 2011). Though some of these species are co-occurring with *Nanojuncetea australis*, there is a clear discrimination between both syntaxa (Deil *et al.* 2011), which is also reflected in our classification. Dynamic of this vegetation is strongly affected by a fluvio-glacial hydrological regime. The vegetation period is restricted by cool temperatures in winter and by submersion in summer (Deil 2005). *Littorelletea* species are able to grow permanently submerged as mentioned for example for *Lilaeopsis macloviana* by Affolter (1985). These species belong to the “long growing amphibious fluctuation tolerators” *sensu* Casanova & Brock (2000).

MACRO-CLIMATE AND PHYTOGEOGRAPHY OF SEASONAL WETLAND VEGETATION

The occurrence of vernal pools specialists depends from local conditions like duration of inundation, small catchments triggered by rainfall, a subsurface hardpan with low water permeability and the chemical properties of soil and waterbody (Deil 2005, Deil *et al.* 2011). These conditions are on the one hand side strong environmental filters; on the other hand they can be quite similar over a broad macroclimatic gradient. These environmental conditions result in an azonal distribution of vernal pool vegetation, stated in this study for Chile, but also observed in Californian vernal pools (Zedler 1990). Since latitudinal distribution as well as rainfall and temperature are strongly correlated with PCA 1 (62.5% of explained variance), the macro-climatic gradient contained in the dataset is near unidimensional. Dwarf annuals (assemblage 1), which probably depend more on the conditions of the surrounding environment, are more frequent in the dryer and warmer conditions in Northern Chile. On the other hand, *Littorelletea australis* species (assemblage 7) are more frequent in the humid and colder climate in the South. Most of the species assemblages take a high position in PCA 2, indicating their

preferences to a strong seasonality of the temperature (Table IV, Fig. 4). Only the assemblages 6 and 7 tend to lower PCA 2 scores. The PCA 3 scores have a high negative correlation with isothermality (10.7% of explained variance), which is defined as the mean diurnal range divided by the annual range. They show a less clear trend in the distribution of assemblages (Fig. 4).

The occurrence of vernal pools partially resembles the distribution of *Centipeda elatinoides*, *Soliva* spp. (Moreira-Muñoz & Muñoz-Schick 2007), *Hydrocotyle cryptocarpa* (Alvarez *et al.* 2008) and *Lepuropetalon spathulatum* (Alvarez *et al.* 2012b). These diagnostic species are only missing in the plots from the island of Chiloé and from Argentina. *Lasthenia kunthii* is widespread southwards (Moreira-Muñoz & Muñoz-Schick 2007) and occurs also in ephemeral wetlands in Patagonia (San Martín *et al.* 2013).

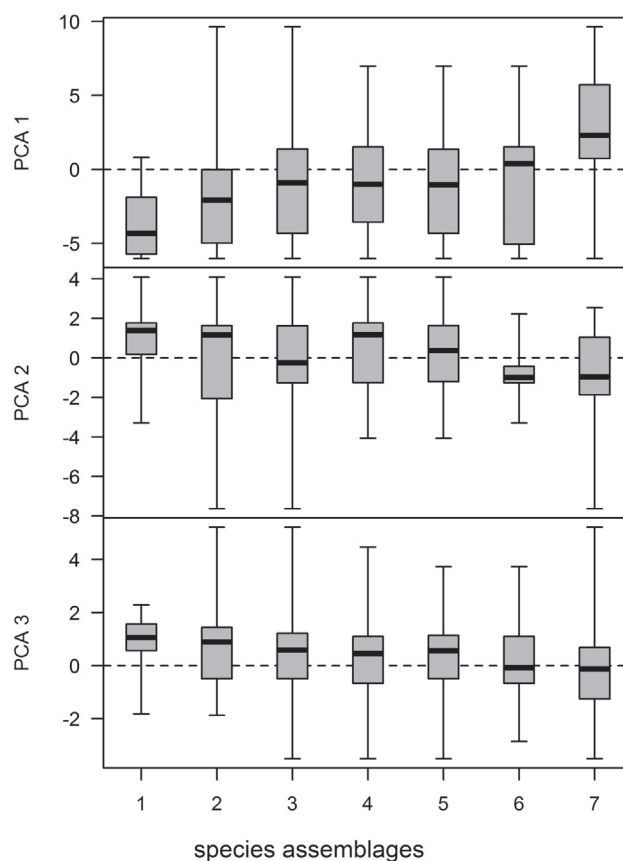


FIGURE 4. Boxplots showing the distribution of species assemblages (x axis) defined by hierarchical clustering in the first three PCA scores.

FIGURA 4. Boxplots mostrando la distribución de ensambles de especies (eje de abscisas) definidos por la clasificación jerárquica en las tres primeras dimensiones del PCA.

The existence of vernal pools in the study area is linked to different ecoregions. In the semi-arid climatic belt in the north (31° to 34° S), vernal pools are scattered over the littoral plains. Southwards from the Mediterranean into the temperate bioclimate (34° to 44° S) they occur preferentially in the Central Valley and along the eastern slopes of the Coastal Mountain Range. Littorelletea species, which are better represented in assemblage 7,

grow preferentially on the fringes of the big lakes in the Chilean Lake District (39° to 42° S) and on shorelines of lakes and streams in the Andes and Patagonian lowlands, in Chile as well as in Argentina (Deil *et al.* 2011). These landscapes were shaped by glaciations, the substrates are stony and sandy and the waters are oligo- to mesotrophic (Oberdorfer 1960).

TABLE IV. Loadings of the environmental factors in the three first PCA axes and summarizing statistics of the principal component analysis (PCA). Variables are separated in four groups: 1) strong negative correlation with the first axis, 2) strong positive correlation with the first axis, 3) strong positive correlation with the second axis, and 4) strong negative correlation with the third axis.

TABLA IV. Vectores de los factores ambientales para las primeras tres dimensiones de PCA y estadísticas del análisis de componentes principales (PCA). Las variables están separadas en cuatro grupos: 1) correlacionadas negativamente con la primera dimensión, 2) correlacionadas positivamente con la primera dimensión, 3) correlacionadas positivamente con la segunda dimensión, y 4) correlacionadas negativamente con la tercera dimensión.

CODE	FACTOR	PCA 1	PCA 2	PCA 3
bio_9	Mean temperature of the driest quarter	-0.265	0.004	0.226
bio_10	Mean temperature of the warmest quarter	-0.265	0.010	0.234
bio_1	Annual mean temperature	-0.262	-0.113	0.202
bio_5	Max temperature of the warmest month	-0.244	0.164	0.207
bio_15	Precipitation seasonality (coefficient of variation)	-0.241	0.132	0.125
bio_8	Mean temperature of the wettest quarter	-0.243	-0.207	0.185
bio_11	Mean temperature of the coldest quarter	-0.242	-0.219	0.171
bio_6	Min temperature of the coldest month	-0.226	-0.265	0.183
lat	Latitude	0.265	-0.013	-0.045
bio_17	Precipitation of the driest quarter	0.267	-0.126	0.112
bio_18	Precipitation of the warmest quarter	0.265	-0.134	0.116
bio_14	Precipitation of the driest month	0.261	-0.152	0.121
bio_12	Annual precipitation	0.255	-0.020	0.260
bio_19	Precipitation of the coldest quarter	0.230	0.059	0.333
bio_16	Precipitation of the wettest quarter	0.227	0.074	0.343
bio_13	Precipitation of the wettest month	0.222	0.128	0.348
bio_7	Temperature annual range (bio_5 - bio_6)	-0.047	0.497	0.049
bio_4	Temperature seasonality (standard deviation)	-0.035	0.486	0.110
bio_2	Mean diurnal temperature range	-0.042	0.454	-0.141
bio_3	Isothermality (bio_2/bio_7)	-0.012	-0.095	-0.451
	SUMMARIZING PCA STATISTICS			
	Standard deviation	3.535	1.950	1.463
	Proportion of Variance	0.625	0.190	0.107
	Cumulative Proportion	0.625	0.815	0.922

Though neophytes are very frequent in Chilean vernal pools, the high dominance of native species in most of the co-occurrence groups suggests low risks of extinction by out-competition. Nevertheless, more detailed synecological studies are required for a proper assessment.

The species assemblages defined here can be used as starting groups for supervised classification strategies (e.g. Cocktail method; Bruelheide 2000) as well as to search for indicator species of seasonal wetland types. An enlargement of the database and further collection of field data will improve the knowledge about the vegetation ecology of vernal pools and will allow a better classification of the communities in Chile and elsewhere in South America.

ACKNOWLEDGEMENTS

Financial support for data collection during a field survey in 2009 by the Faculty of Biology, University of Freiburg is greatly acknowledged. Also crucial for this work were later field surveys in Chile supported by the Otti Wilmanns Foundation and the A.F.W. Schimper Foundation, both placed in Germany. The authors also thank to Prof. Dr. Michael Rudner (University Weihenstephan-Triesdorf) for his valuable comments to a first version of this manuscript.

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APPENDIX A. List of species used for the classification and respective attributes (groups defined *a priori*, life forms, status and assigned assemblage). Nomenclature of species according Zuloaga *et al.* (2008). Groups defined *a priori* (according to Deil *et al.* 2011 and Deil *et al.* 2007) are coded as NAA (Nanajuncetea australis), LMO (Limoselletea australis), LTT (Littorelletea australis), ANN (dwarf annuals), and comp. (companion species). Life forms are coded as T (therophytes), Cr (cryptophytes), H (hemicryptophytes), and Ch (chamaephytes). Species status is either native (N) or introduced (I).

APÉNDICE A. Lista de especies usadas para la clasificación y sus respectivos atributos (grupos definidos *a priori*, formas de vida, estatus y ensamble asignado). Nomenclatura de especies según Zuloaga *et al.* (2008). Los grupos definidos *a priori* (según Deil *et al.* 2011 y Deil *et al.* 2007) son codificados como NAA (Nanajuncetea australis), LMO (Limoselletea australis), LTT (Littorelletea australis), ANN (nanoterófitas), y comp. (especies acompañantes). Las formas de vida son abreviadas como T (terófitas), Cr (criptófitas), H (hemicriptófitas), y Ch (caméfitas). Origen de especies es nativo (N) o introducido (I).

CODE	SCIENTIFIC NAME	GROUP	LIFE FORM	STATUS	ASSEMB.
AGROCAP	<i>Agrostis capillaris</i>	comp.	H	I	3
AGROMAG	<i>Agrostis magellanica</i>	comp.	H	N	7
AIRACAR	<i>Aira caryophyllea</i>	ANN	T	I	2
ANAGALT	<i>Anagallis alternifolia</i>	LTT	H	N	7
ANTHCOT	<i>Anthemis cotula</i>	comp.	T	I	1
APHAARV	<i>Aphanes arvensis</i>	comp.	T	I	2
ARENSER	<i>Arenaria serpens</i>	comp.	H	N	7
AZORTRI	<i>Azorella trifoliolata</i>	LTT	H	N	7
BLENCHI	<i>Blennosperma chilense</i>	NAA	T	N	2
BRIZMIN	<i>Briza minor</i>	ANN	T	I	3
BROMTRI	<i>Bromidium trisetoides</i>	NAA	T	N	2
CALL.SP	<i>Callitriche</i> sp.	comp.	T	N	4

APPENDIX A. Continuation.

APÉNDICE A. Continuación.

CODE	SCIENTIFIC NAME	GROUP	LIFE FORM	STATUS	ASSEMB.
CALOBRI	<i>Calotheca brizoides</i>	NAA	H	N	3
CARDCHI	<i>Cardamine chilensis</i>	comp.	T	N	4
CARDVAL	<i>Cardamine valdiviana</i>	NAA	Cr	N	5
CAREDEC	<i>Carex decida</i>	LTT	H	N	7
CAREFUS	<i>Carex fuscua</i>	comp.	H	N	5
CASTLAC	<i>Castilleja laciniata</i>	comp.	T	N	2
CENTELA	<i>Centipeda elatinoidea</i>	NAA	H	N	6
CENTMIN	<i>Centunculus minimus</i>	NAA	T	I	4
CERAGLO	<i>Cerastium glomeratum</i>	ANN	T	I	1
CICEQUA	<i>Cicendia quadrangularis</i>	NAA	T	N	5
CLARTEN	<i>Clarkia tenella</i>	comp.	T	N	1
CONACAM	<i>Conanthera campanulata</i>	comp.	Cr	N	1
CRASCLO	<i>Crassula closiana</i>	ANN	T	N	1
CRASPAL	<i>Crassula paludosa</i>	comp.	T	N	4
CRASPED	<i>Crassula peduncularis</i>	LMO	T	N	7
CUSC.SP	<i>Cuscuta</i> sp.	comp.	T	N	4
CYNOECH	<i>Cynosurus echinatus</i>	comp.	T	I	3
CYPEREF	<i>Cyperus reflexus</i>	NAA	H	N	6
DESCDAN	<i>Deschampsia danthonioides</i>	NAA	T	N	2
DICHSER	<i>Dichondra sericea</i>	NAA	H	N	5
DOWNPUS	<i>Downingia pusilla</i>	LTT	T	N	4
ELEOMAC	<i>Eleocharis macrostachya</i>	comp.	Cr	N	4
ELEOPAC	<i>Eleocharis pachycarpa</i>	LTT	Cr	N	7
EPILSUB	<i>Epilobium subdentatum</i>	comp.	T	N	3
EQUIBOG	<i>Equisetum bogotense</i>	LTT	Cr	N	7
ERODCIC	<i>Erodium cicutarium</i>	comp.	T	I	1
ERODMAL	<i>Erodium malacoides</i>	comp.	T	I	2
ERYNPSE	<i>Eryngium pseudojunceum</i>	NAA	H	N	6
ERYN.SP	<i>Eryngium</i> sp.	comp.	H	N	4
EUPHMEI	<i>Euphrasia meiantha</i>	comp.	T	N	2
GAMOSPI	<i>Gamochoaeta spiciformis</i>	NAA	H	N	3
GLINRAD	<i>Glinus radiatus</i>	comp.	T	N	7
GRATPER	<i>Gratiola peruviana</i>	NAA	H	N	6
HERBLAH	<i>Herbertia lahue</i>	comp.	Cr	N	5
HORDMAR	<i>Hordeum marinum</i>	comp.	T	I	5
HYDRCHA	<i>Hydrocotyle chamaemorus</i>	LTT	H	N	7
HYDRCRY	<i>Hydrocotyle cryptocarpa</i>	NAA	T	N	4
HYPOGLA	<i>Hypochaeris glabra</i>	ANN	T	I	2
HYPORAD	<i>Hypochaeris radicata</i>	comp.	H	I	3
HYP.SP	<i>Hypochaeris</i> sp.	comp.	H	N	5
ISOESAV	<i>Isoetes chubutiana</i>	LTT	Cr	N	4
ISOLCER	<i>Isolepis cernua</i>	comp.	T	N	4

APPENDIX A. Continuation.

APÉNDICE A. Continuación.

CODE	SCIENTIFIC NAME	GROUP	LIFE FORM	STATUS	ASSEMB.
ISOLINU	<i>Isolepis inundata</i>	LTT	Cr	I	7
JUNCB.A	<i>Juncus balticus</i> subsp. <i>andicola</i>	LTT	H	N	7
JUNCBUF	<i>Juncus bufonius</i>	NAA	T	I	2
JUNCCAP	<i>Juncus capitatus</i>	NAA	T	I	2
JUNCIMB	<i>Juncus imbricatus</i>	NAA	H	N	3
JUNCPAL	<i>Juncus pallescens</i>	LMO	H	N	5
JUNCPLA	<i>Juncus planifolius</i>	NAA	H	N	3
JUNCPRO	<i>Juncus procerus</i>	NAA	H	N	6
JUNC.SP	<i>Juncus</i> sp.	comp.	H	N	4
JUNCSTI	<i>Juncus stipulatus</i>	LTT	H	N	7
LASTKUN	<i>Lasthenia kunthii</i>	NAA	T	N	4
LEONTAR	<i>Leontodon taraxacoides</i>	NAA	T	I	5
LEPTMIC	<i>Leptophyllochloa micrathera</i>	LTT	H	N	7
LEPUSPA	<i>Lepuropetalon spathulatum</i>	comp.	T	N	2
LILASCI	<i>Lilaea scilloides</i>	comp.	T	N	4
LIMOAUS	<i>Limosella australis</i>	LMO	T	N	7
LINUCHA	<i>Linum chamissonis</i>	comp.	Ch	N	5
LITTAUS	<i>Littorella australis</i>	LTT	Cr	N	7
LOLITEM	<i>Lolium temulentum</i>	comp.	T	I	5
LOTUSUB	<i>Lotus subpinnatus</i>	NAA	T	N	5
LYTHHYS	<i>Lythrum hyssopifolia</i>	NAA	T	I	4
LYTHPOR	<i>Lythrum portula</i>	NAA	T	I	7
MEDIPOL	<i>Medicago polymorpha</i>	ANN	T	I	1
MENTPUL	<i>Mentha pulegium</i>	NAA	H	I	5
MICRNAN	<i>Micropsis nana</i>	NAA	T	N	3
MICRPYG	<i>Microseris pygmaea</i>	ANN	T	N	1
MONTFON	<i>Montia fontana</i>	comp.	T	N	2
NASSPOE	<i>Nassella poeppigiana</i>	NAA	H	N	3
NAVAINV	<i>Navarretia involucrata</i>	NAA	T	N	5
NOTHGRA	<i>Nothoscordum gramineum</i>	NAA	Cr	N	4
OXALMIC	<i>Oxalis micrantha</i>	ANN	T	N	1
OXAL.SP	<i>Oxalis</i> sp.	comp.	Cr	N	4
OZIRBIF	<i>Oziroë biflora</i>	ANN	Cr	N	1
PASPDAS	<i>Paspalum dasyleurum</i>	NAA	H	N	3
PHALAME	<i>Phalaris amethystina</i>	comp.	T	N	5
PHYLNOD	<i>Phyla nodiflora</i>	NAA	H	N	6
PILUAME	<i>Pilularia americana</i>	comp.	Cr	N	4
PIPTMON	<i>Piptochaetium montevidense</i>	NAA	H	N	3
PLAGCMB	<i>Plagiobothrys corymbosus</i>	LTT	T	N	4
PLAGPRA	<i>Plagiobothrys pratensis</i>	NAA	T	N	5
PLAGPRO	<i>Plagiobothrys procumbens</i>	ANN	T	N	1
PLANFIR	<i>Plantago firma</i>	comp.	T	N	2

APPENDIX A. Continuation.

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CODE	SCIENTIFIC NAME	GROUP	LIFE FORM	STATUS	ASSEMB.
PLANLAN	<i>Plantago lanceolata</i>	comp.	H	I	5
POLYHDS	<i>Polygonum hydropiperoides</i>	NAA	H	I	6
POLYAUS	<i>Polypogon australis</i>	comp.	H	N	7
GNAPCYM	<i>Pseudognaphalium cymathoides</i>	NAA	T	N	6
PSILBRE	<i>Psilocarphus brevissimus</i>	comp.	T	N	4
RANUB.T	<i>Ranunculus bonariensis</i> var. <i>trisepalus</i>	comp.	T	N	4
RANUHYD	<i>Ranunculus hydrophilus</i>	LTT	T	N	7
RUMEACE	<i>Rumex acetosella</i>	ANN	H	I	3
RUMECRI	<i>Rumex crispus</i>	comp.	H	I	7
SENEZOS	<i>Senecio zosterifolius</i>	LTT	H	N	7
SISYGRA	<i>Sisyrinchium graminifolium</i>	NAA	Cr	N	2
SOLISES	<i>Soliva sessilis</i>	ANN	T	N	2
SPERRUB	<i>Spergula rubra</i>	comp.	H	I	6
SYMPVAH	<i>Symphyotrichum vahlii</i>	comp.	H	N	7
TRIFDUB	<i>Trifolium dubium</i>	comp.	T	I	2
TRIFSUB	<i>Trifolium subterraneum</i>	comp.	T	I	2
VEROP.X	<i>Veronica peregrina</i> subsp. <i>xalapensis</i>	comp.	T	I	5
VULPBRO	<i>Vulpia bromoides</i>	ANN	T	I	5

Recibido: 14.01.15
Aceptado: 06.07.15