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RESEARCH PAPER

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Chilean vegetation in the context of the Braun-Blanquet approach and a comparison with EcoVeg formations

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Abstract

Aims: The Braun-Blanquet approach has been widely implemented to generate classification schemes at the country level and Chile is not an exception. In spite of numerous studies, a revised system for the whole country is still missing and most of the current surveys are restricted to a small set of vegetation groups or specific study sites. To fill this gap, we established a vegetation-plot database and updated the classification into a single syntaxonomic scheme. We also performed a comparison of this scheme with the formation system following the EcoVeg approach. **Study area**: Continental Chile. **Methods:** We compiled a database of 1,582 plot observations, which are classified into 29 classes, 43 orders, 65 alliances, and 162 associations according to the Braun-Blanquet approach. **Results**: These observations were assigned to 7 formation classes, 10 subclasses and 19 formations in the EcoVeg approach. There are several mismatches between phytosociological classes and EcoVeg formations, which indicates some inconsistencies in the current stage of syntaxonomy in Chile. Besides a big contrast on bioclimatic conditions within the country's territory, the occurrence of intrazonal vegetation may explain the high diversity of phytosociological associations recorded in this database. **Conclusions**: This work may constitute the basis for the implementation of the EcoVeg classification at the levels of alliance and association and can be extended for other countries in the South American sub-continent.

Keywords

Braun-Blanquet approach, cross-classification, EcoVeg formation, South America, syntaxonomy, taxlist, vegetation-plot database, vegtable

Introduction

Chile is characterized by a broad latitudinal extension and a rugged terrain. The country stretches over 4,000 km of North-to South distance, from 17° to 56°S, approximately. Chile's relief is in part dominated by two mountain ranges, a coastal range in the western margin reaching up to 3,000 m a.s.l. in its northern portion, and the Andes Cordillera in the East reaching around 7,000 m a.s.l. These attributes result into a wide spectrum of bioclimates, ranging from tropical to antiboreal, as well as ombrotypes, ranging from ultraperarid to ultraperhumid (Amigo and Ramírez 1998; Luebert and Pliscoff 2017), which, added to soil and geological variety (Casanova et al. 2013), render a wide environmental diversity.

The environmental diversity is reflected in the plant species diversity and endemism. The catalogue of Chilean vascular plants (Rodríguez et al. 2018) reports 4,655 native species. Of those, 2,145 species are endemic to the country, highlighting the uniqueness of the Chilean flora, and indicative of both high vegetation diversity and unique vegetation types. Human activities, especially urban settlements, industries, transport networks, agronomic production and wood exploitation have strongly impacted the integrity of natural vegetation and probably eradicated some vegetation types from the country (Torrejón and Cisternas 2002; Otero 2006).

To date there is an unequal degree of knowledge about vegetation diversity in Chile. While some authors classify it at a coarse scale and focus on zonal vegetation (Hueck and Seibert 1981; Luebert and Pliscoff 2017), more detailed works are restricted to specific localities and only few plant communities.

The Braun-Blanquet approach is a classification system based on physiognomy, floristics (species composition), and ecology (or biogeography) (Dengler et al. 2008). This classification is usually based on plot observations (also known as phytosociological relevés), and classification schemes have a hierarchical structure, where the association is the fundamental unit and class is the highest rank (Westhoff and van der Maarel 1978; Dengler et al. 2008). Despite criticisms regarding the common preferential sampling strategy and the heterogeneity in the use of plot sizes and abundance scales (Dengler et al. 2008; De Cáceres et al. 2015), current development of classification methods including the implementation of expert systems (Tichý et al. 2019; Bruelheide et al. 2021) and the proliferation of initiatives compiling and sharing records in vegetation-plot databases (Dengler et al. 2011; Alvarez et al. 2012), enhance the potential application of the Braun-Blanquet approach as a reference system for the summary of vegetation diversity at a national level.

In Chile, a pioneer phytosociological study – and still the most extensive vegetation survey in terms of geographical coverage and diversity of assessed plant communities – is the work of Oberdorfer (1960). Further botanists and vegetation ecologists used this classification as a skeleton for the assignment of new syntaxa, but most of these works handle either a small set of associations or are highly restricted to specific study sites. Recent publications have started with critical reviews of classes or groups of related classes targeting the consolidation of the Braun-Blanquet system applied to the Chilean vegetation (Amigo et al. 2007, 2017; Amigo and Rodríguez-Guitián 2015). However, there is no modern work that has tried to systematize the syntaxonomy of all Chilean vegetation down to association level.

In contrast to Braun-Blanquet, EcoVeg is a relatively new approach for vegetation classification, which is also hierarchical arranging units in eight levels (Faber-Langendoen et al. 2014). While the lower levels (i.e., alliance and association) are based on floristic composition and physiognomy, the higher levels (formation class, formation subclass and formation) are strictly based on physiognomy and bioclimatic patterns. Mid levels in this classification (division, macrogroup and group) are defined by constant species, physiognomy, and ecological preferences of the vegetation. This is an important difference to the Braun-Blanquet approach, which does not include categories for plant formations. There is no current description of associations applying the EcoVeg approach for the Chilean vegetation, but Luebert and Pliscoff (2022) suggest a classification down to the macrogroup level and a map for the distribution of zonal vegetation. Furthermore, most recent applications of the Braun-Blanquet approach in Europe (e.g., Mucina et al. 2016) have attempted to restrict the scope of higher-level syntaxa (i.e., orders and classes) to physiognomically and ecologically homogeneous units, making the potential linkage between the Braun-Blanquet and the EcoVeg approaches more straightforward (see Willner and Faber-Langendoen 2021). The task of reassessing syntaxa in the latter sense has not been fully acknowledged yet in the scientific community. However, the large amount of vegetation data produced by studies employing the Braun-Blanquet approach make them a valuable source of information to be used in the context of the EcoVeg approach.

The aims of this work are (1) to provide a review of Chilean vegetation based on plot observations available from scientific publications; (2) to produce a first syntaxonomic database as starting point for further phytosociological studies; and (3) to match the units of the Braun-Blanquet approach with the plant formations of the EcoVeg approach.

Methods

Data collection

The initial data set was composed of plot observations stored in the database "sudamerica" (https://www.givd.info/ID/SA-CL-001, Alvarez et al. 2012). This database already includes assignments of plot observations to phytosociological associations. While the first version of this database focused on grassland vegetation in Chile, its geographic and syntaxonomic focus have now been expanded to all kind of vegetation across the South American continent. The initial collection of references started by searching the phrases "vegetation survey", "phytosociological classification", and "syntaxonomy" in combination with the term "Chile" in electronic libraries (e.g. ScienceDirect, Wiley, Springer and Scielo) as well as in Google Scholar. Those searches were done in Spanish, English, and German, which are, according to our experience, the main languages used to publish vegetation surveys done in Chile. After the assessment of each publication, we also screened the respective reference lists and repeated a search using the names of handled syntaxa, leading to additional references, especially from the gray literature. All references including relevés were considered.

In a second step, we reviewed the literature for additional vegetation surveys meeting the following two criteria: 1) abundance of plant species in plots was recorded, 2) plot observations were assigned to associations.

Only header information was considered, avoiding the time-demanding digitizing of abundance tables and further assessment of species nomenclature and synonymy.

The header data of each plot observation, which is usually a table column in the original source, include page, table and column numbers, data source (bibliographic reference), assignment to a plant community, elevation and plot coordinates. If not provided by the source, coordinates of plot observations were inferred from information of study sites using geonames (http://www.geonames.org/) and indications of directions and roads by locating them in Google Maps (https://www.google.com/maps).

For further bioclimatic descriptions, we also collected information on annual temperature and total annual precipitation from CHELSA version 1.2 (Karger et al. 2017).

Our syntaxonomic assessment used, as an initial stage, the classification of Oberdorfer (1960). This classification was expanded and adjusted as we assessed more recent publications (Suppl. material 1). Each plot record was inserted in the database by its original syntaxonomic assignment and was linked to a syntaxonomic concept using the relational model proposed by Alvarez and Luebert (2018). For the delimitation of higher syntaxonomic ranks we accepted the newest proposals as syntaxonomic references (see Suppl. material 2).

We respected all syntaxonomic ranks mentioned in the consulted references (principal and secondary ranks according to Theurillat et al. 2021). Relevés where the principal rank order or alliance was not assigned, were marked with question marks (i.e., "order?" and "alliance?", respectively).

Formation types

Plot observations were assigned to plant formations according to the EcoVeg classification (Faber-Langendoen et al. 2014). For this we used the keys and definitions by Faber-Langendoen et al. (2016). We also considered the additions done by Luebert and Pliscoff (2022).

For the comparison of formations and phytosociological units, we produced Sankey diagrams, weighting the assessed units by their relative number of phytosociological associations and linking Braun-Blanquet classes and alliances with EcoVeg formations.

Software

Data management, statistical assessment and plotting was done in R version 4.1.0 (https://cran.r-project.org/). To build and adjust syntaxonomic classifications, we used the R-package "taxlist" version 2.2.3 (https://docs.ropensci.org/taxlist/, Alvarez and Luebert 2018). For linking plot observations with the syntaxonomy, we used the R-package "vegtable" version 0.1.8 (https://github.com/kamapu/vegtable). Data sources and syntaxonomic views (references for syntaxonomic concepts) were formatted by using the R-package "biblio" version 0.0.7 (https://github.com/kamapu/biblio). To draw Sankey diagrams we used the R-package "networkD3" version 0.4 (https://github.com/christophergandrud/networkD3). The final data set was stored in a PostgreSQL database.

Results

Syntaxonomic diversity and distribution

The compiled database contains 1,776 plot observations extracted from 37 publications (see also Suppl. material 1). Most of the publications (34) are journal articles, while the rest are a book (Oberdorfer 1960), a book chapter (Roig et al. 1985) and a thesis (Ackermann 2001). The most frequent journals in this list are Agro Sur (6 articles), edited at the Universidad Austral de Chile in Valdivia, and the International Journal of Geobotanical Research (5 articles), edited in Spain. The year of publication spans from 1954 (Schmithüsen 1954) until 2019 (Amigo 2009; Amigo et al. 2019).

The collected plot observations account for a total of 29 classes, 43 orders, 66 alliances, and 175 associations (full list included as Suppl. material 2). The most diverse classes in terms of number of associations are *Wintero-Nothofagetea* (31 associations), *Lithraeo causticae-Cryptocaryetea albae* (15 associations), and *Myrteolo nummulariae-Sphagnetea magellanici* (14 associations). While the distribution of plot observations is very clustered along the latitudinal gradient, they cover a large proportion of the country from the northernmost to the southernmost extremes (Figure 1). Nevertheless, huge gaps are observed from the 30°S northwards and from the 45°S southwards. The classes with the broadest latitudinal distribution are *Lemnetea minoris*, *Wintero-Nothofagetea*, and *Nothofagetea pumilionis-antarcticae*.

Correspondence between phytosociological units and formations

Vegetation plots recorded in Chile were assigned to 7 formation classes including 10 subclasses and 20 formations. From 29 phytosociological classes, 11 are associated to more than one formation, with *Wintero-Nothofagetea* linked to 5 formations, *Phragmito-Magnocaricetea* to 4, *Parastrephio lepidophyllae-Fabianetea densae* and *Potametea* to 3, and other 7 classes to 2 formations. On the other hand, 12 out of 20 formations are linked to more than one phytosociological class (Figure 2).

Out of 66 recorded alliances, 19 are associated to more than one formation. *Wintero-Nothofagetea* is the phytosociological class including the highest number of alliances, which is 10, whereas the rest of the classes include 4 or less alliances.

The formation classes, sorted by decreasing number of assigned associations, were Shrub & Herb Vegetation class (66 associations), Forest & Woodland class (50 associations), Polar & High Montane Scrub, Grassland & Barrens class (16 associations), Agricultural & Developed Vegetation class (15 associations), Aquatic Vegetation class (11 associations), Desert & Semi-Desert class (9 associations), and Open Rock Vegetation class

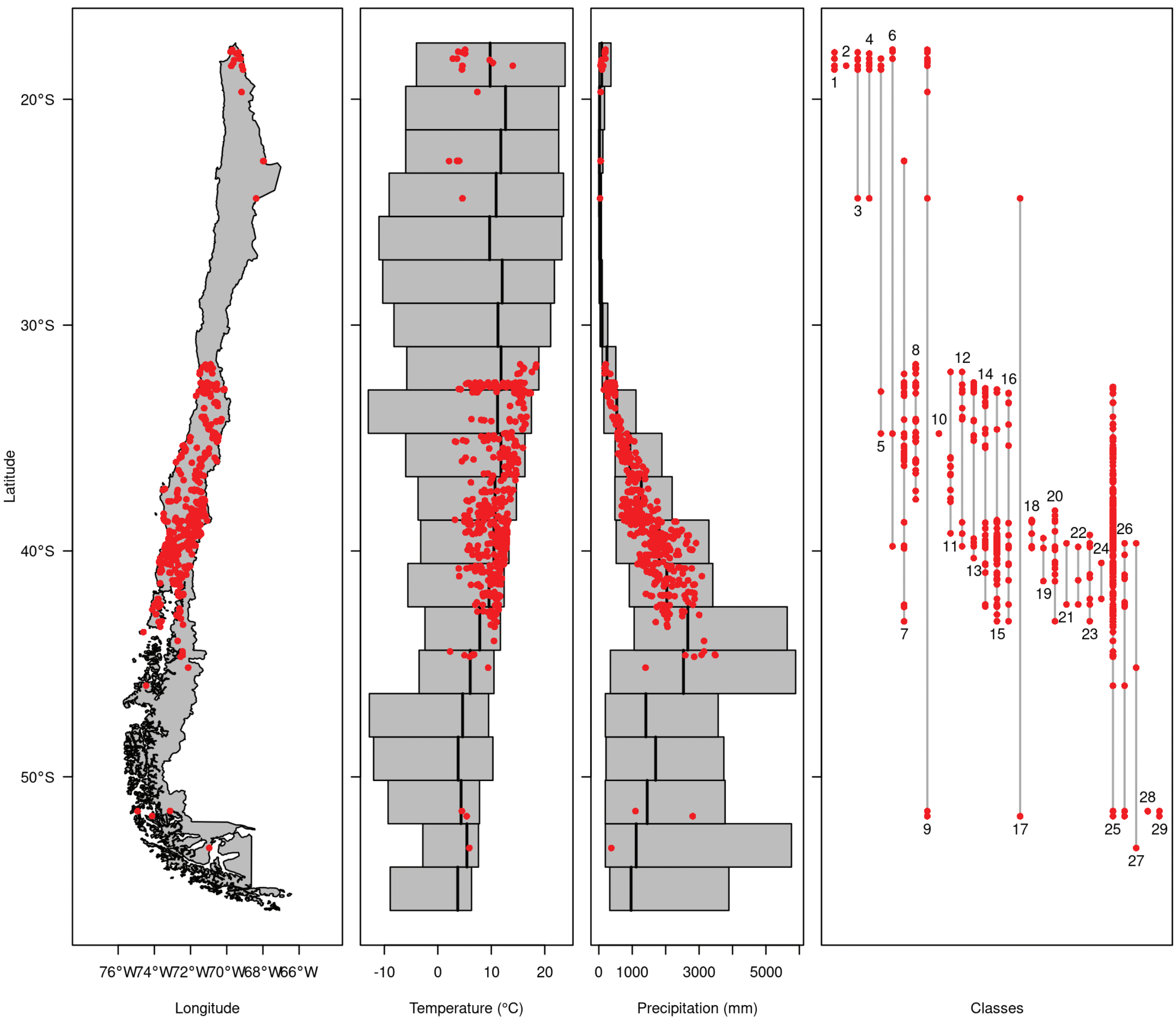

Figure 1. Latitudinal distribution of recorded phytosociological classes. In all panels the positions of vegetation plots are overlaid as red dots. The bars of the two middle panels correspond to mean annual temperature and total annual precipitation values extracted from CHELSA version 1.2 (Karger et al. 2017) for all pixels included in the respective latitudinal segments. The right panel shows the latitudinal distribution of recorded plot observations for each class. All observations belonging to the same class are connected by a vertical line. Classes are numbered by their latitudinal distribution: 1 - *Polylepidetea tarapacano-besseri*, 2 - *Parastrephio lepidophyllae-Fabianetea densae*, 3 - *Anthochloo lepidulae-Dielsiochloetea floribundae*, 4 - *Plantagini rigidae-Distichietea muscoidis*, 5 - *Opuntietea sphaericae*, 6 - *Lemnetea minoris*, 7 - *Ambrosietea chamissonis*, 8 - *Gutierrezio paniculatae-Trichoceretea chilensis*, 9 - *Ephedro chilensis-Chuquiragetea oppositifoliae*, 10 - *Mayteno boariae-Salicetea humboldtianae*, 11 - *Helianthemetea guttati*, 12 - *Tessario integrifoliae-Baccharidetea salicifoliae*, 13 - *Lithraeo causticae-Cryptocaryetea albae*, 14 - *Stellarietea mediae*, 15 - *Molinio caerulae-Arrhenatheretea elatioris*, 16 - *Plantaginetea majoris*, 17 - *Phragmito-Magnocaricetea*, 18 - *Potametea*, 19 - *Littorelletea australis*, 20 - *Bidentetea tripartiti*, 21 - *Senecionetea chilensis*, 22 - *Loasetea*, 23 - *Nanojuncetea australis*, 24 - *Empetro rubrum-Pernettyetea*, 25 - *Wintero-Nothofagetea*, 26 - *Nothofagetea pumilionis-antarcticae*, 27 - *Myrteolo nummulariae-Sphagnetea magellanici*, 28 - *Rostkovietea magellanicae*, and 29 - *Deschampsio-Asteretea vahlii*.

(1 association). The most important formations in term of assigned associations were Cool Temperate Forest & Woodland formation (33 associations), Temperate to Polar Bog & Fen formation (17 associations), Fallow Field & Weed Vegetation formation (15 associations), Tropical High Montane Scrub & Grassland formation (15 associations), and Temperate Grassland & Shrubland formation (14 associations).

Discussion

Syntaxonomy of Chilean vegetation

In spite of the lack of a plot-based summary of the vegetation syntaxonomy in Chile, we found a surprisingly high number of recorded syntaxa. While we may focus on

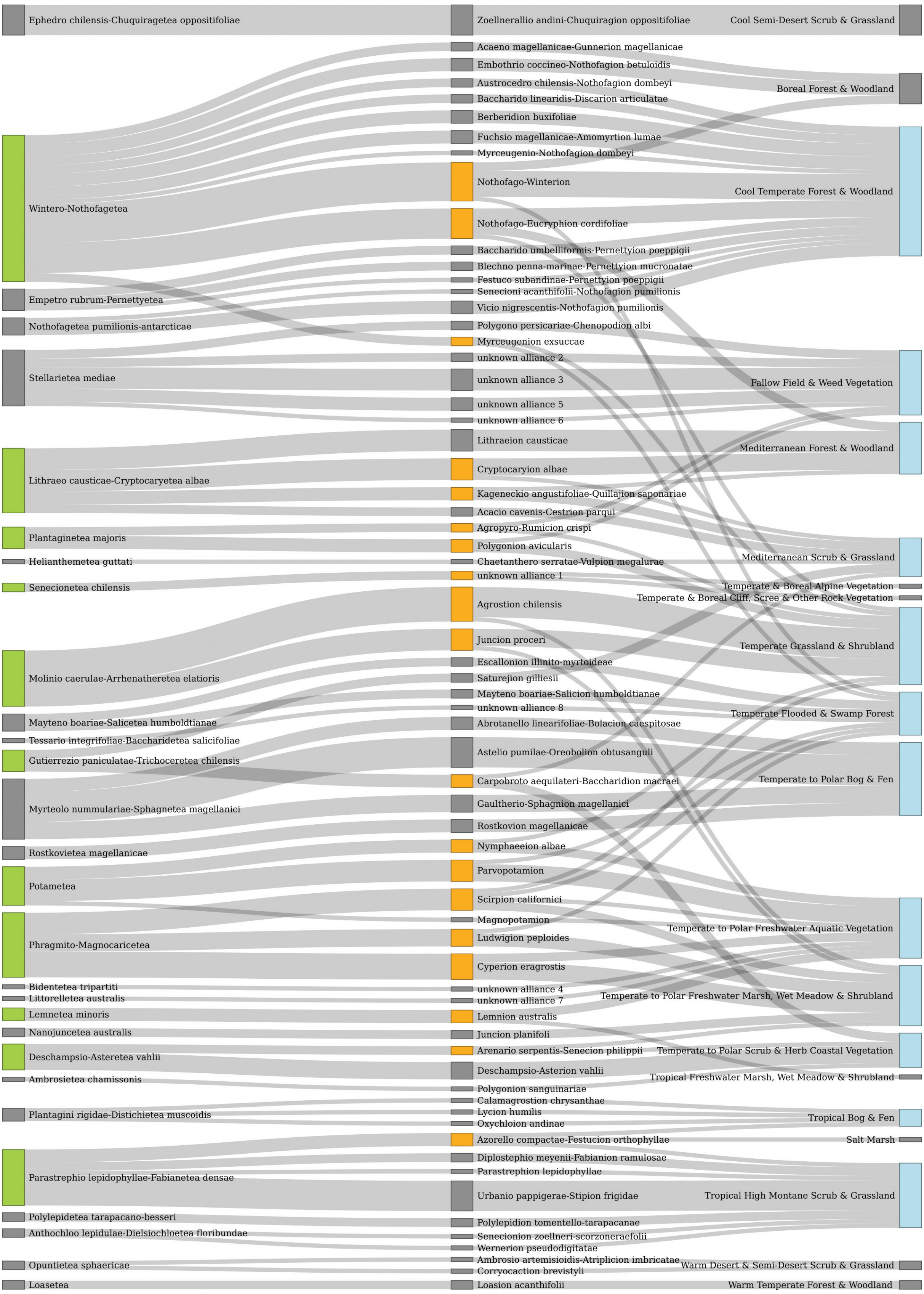

Figure 2. Correspondence between phytosociological classes and EcoVeg formations. The height of columns represents the relative number of associations included in each unit. The first and second columns from the left are phytosociological classes and alliances. The third column corresponds to formations. Green bars show phytosociological classes linked to more than one formation. Orange bars show alliances linked to more than one formation. Blue bars show formations linked to more than one phytosociological class.

acquiring resources to continue digitizing data (see Suppl. material 1 for some references still in the queue), discovering further data sources may further increase the vegetation diversity from the perspective of the Braun-Blanquet approach. This is also expected in consideration of the strong bioclimatic gradients of the country and the huge data gaps from 30°S northwards and 45°S southwards (Figure 1). The database presented here may be an important complement to classifications applying expert systems (Bruelheide et al. 2021) and vegetation maps (Luebert and Pliscoff 2022). We also show the usefulness of this database for comparing different classification approaches based on plot observations.

Our assessment focused on principal syntaxomic ranks, namely class, order, alliance, and association (Theurillat et al. 2021), but secondary ranks are also distinctly applied in this scheme. On the other hand, there are gaps in the classification, where orders or alliances are not yet defined, as in the case of *Bidentetea tripartiti*, *Helianthemetea guttati*, *Littorelletea australis*, *Phragmito-Magnocaricetea*, *Senecionetea chilensis*, *Stellarietea mediae*, and *Tessario integrifoliae-Baccharidetea salicifoliae* (Suppl. material 2).

Some classes are cosmopolitan in their native distribution, especially aquatic and semi-aquatic vegetation as in the case of *Lemnetea minoris*, *Phragmito-Magnocaricetea*, and *Potametea*. These classes are defined by their physiognomy and ecology and have few species in common (Landucci et al. 2015).

Other classes collate associations dominated by introduced plant species and therefore of anthropogenic origin, as in the case of the classes *Molinio caerulae-Arrhenatheretea elatioris*, *Plantaginetea majoris* and *Stellarietea mediae*, which represent grassland, ruderal and weed vegetation, respectively. Most of the associations assigned to these communities are characterized by a mixture of native and introduced plant species, whereby the allochthonous elements use to be dominant. For instance, Oberdorfer (1960) classified the Chilean temperate grasslands into an own alliance called *Agrostion chilensis*, which was later assigned to an own order called *Agrostietalia capillaris* (San Martín et al. 1993). Oberdorfer (1960) argued for the benefits of this classification because of the occurrence of characteristic South American species as well as the generally species poor communities in comparison with their European counterparts. The classification of such communities is not yet aligned to the current state of the European syntaxonomy (compare with Mucina et al. 2016), nor assessed by a jointly review to date.

Conversely, some classes are endemic to the continent or even smaller areas. For instance, *Wintero-Nothofagetea* and *Nothofagetea pumilionis-antarcticae* represent South American temperate forests and woodlands.

Oberdorfer (1960) proposed some names for native vegetation corresponding to their ecological counterparts from the Northern Hemisphere. For instance *Littorelletea australis* corresponds to the southern hemisphere counterpart of *Littorelletea uniflorae*, as well as *Nanojuncetea australis* with respect to *Isoëto-Nanojuncetea* (see also Amigo 2009).

Oberdorfer (1960) established a backbone syntaxonomy for the transition area between the Mediterranean and temperate zones in central Chile. Additional publications complemented the geographical coverage for the Braun-Blanquet approach. Here we highlight the project "Transecta Botánica de la Patagonia Austral" (Roig et al. 1985) for the extreme South and the works by Ruthsatz (1995) and Luebert and Gajardo (2000, 2005) for the extreme north of the country.

Our analysis also highlights the lack of phytosociological work in north-central Chile between 25° and 32°S, where only one azonal class (*Lemnetea minoris*) was recorded (see Figure 1). While this gap may be partially filled when including further references (see Suppl. material 1), this zone has already been acknowledged as one of the least known in Chile from the point of view of its vegetation (Luebert and Pliscoff 2017), suggesting it as a priority for further field studies. Another big gap is observed from ca. 45°S southwards, which may be caused by the low population density in these areas, resulting in few research institutions or vegetation ecologists residing and researching in these areas, as well as due to the low accessibility, rugged topography, and harsh weather conditions. As consequence, less than a 50% of the country's surface is covered by the current database, advising for more efforts on new, complementary vegetation surveys.

Phytosociological classes versus EcoVeg formations

Plot observations are associated with 20 formations belonging to 10 subclasses and 7 classes from the EcoVeg approach. Considerable disagreement is observed between formations and phytosociological classes (Figure 2). The main reasons for this mismatch is probably the physiognomic heterogeneity of plant communities belonging to the same phytosociological class. For instance, the class *Wintero-Nothofagetea*, which mainly corresponds to the Cool Temperate Forest & Woodland formation, currently also includes swamp forests (order *Myrceugenietalia exsuccae*), which is azonal vegetation belonging to the Temperate Flooded & Swamp Forest formation (Figure 2). Excluding swamp forests from *Wintero-Nothofagetea* into a new class can be a solution to this problem. In this context, the implementation of the EcoVeg approach can be very useful for enhancing the consistency in the classification of Chilean vegetation as complementary to the Braun-Blanquet approach. Such kind of comparison have been done by Willner and Faber-Langendoen (2021) for phytosociological units in Europe. They also observed discrepancies between EcoVeg formation and phytosociological classes and proposed some adjustments to solve some of those issues.

As a consequence of the bioclimatic diversity of the country, plant formations observed in Chile are very diverse, including formations from all 7 classes proposed by Faber-Langendoen et al. (2016). However, part of this diversity is due to the fact that syntaxa also capture intrazonal and azonal vegetation, thus contrasting with the lower diversity of zonal vegetation formations identified for Chile by Luebert and Pliscoff (2022).

Potential applications of the database

The database presented here also covers other countries in South America and can be accessed at https://syntax.kamapu.net. This database can be potentially used to support the consolidation of a syntaxonomic classification at the national or continental level, providing access to floristic tables for meta-analyses, and for implementing the development of expert systems.

The database can also be used to compare different plot-based classifications, as shown here. Further comparisons may include the mid and lower levels of the EcoVeg approach (Faber-Langendoen et al. 2014) or the classification of plant formations by Ellenberg and Mueller-Dombois (1966). In Chile, this database may be used to complement intrazonal units to the proposal of zonal vegetation formations by Luebert and Pliscoff (2022) and to incorporate EcoVeg units at the lower levels of alliance and association, not covered by Luebert and Pliscoff (2022).

Data availability

Data used for this work will be updated at https://syntax.kamapu.net/. This data is only visualized at this time but it will be made free accessible in the near future.

Author contributions

M.A. is the custodian of the database and performed the statistical assessment. Both authors planed the structure and content of this manuscript.

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Supplementary material

Supplementary material 1
Data Sources of Vegetation-Plot Observations in Chile
Link: https://doi.org/10.3897/VCS.72194.suppl1

Supplementary material 2
Syntaxonomy Chilean Vegetation
Link: https://doi.org/10.3897/VCS.72194.suppl2