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Biogeography of Chilean charophytes

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ABSTRACT

Although charophytes have been studied from South America since the 19th century, large regional gaps in their distribution and manifold taxonomic problems hinder a trans-Andean comparison of charophyte diversity. In total, 14 charophyte species have been previously published for Chile. This number is very low compared to countries east of the Andean barrier.

Here we present the results of a series of expeditions that gathered data concerning charophyte distribution in Chile between Patagonia and the Peruvian border. About one-third of the several hundred sites investigated between 2011 and 2013 exhibited rich charophyte communities. Accordingly, the number of species known for Chile has increased to a total of 31 and includes two species (*Chara fulgens* and *Nitella asagrayana*) reported from South America for the first time. Our results show some marked differences between charophyte communities west and east of the Andes, notably the absence of the Willdenowia group in the region west of the Andes.

Possible reasons for this discrepancy are discussed, and different types of charophyte habitats are characterized in order to widen our knowledge about global distribution and dispersal routes of charophytes.

1. Introduction

Charophytes are a group of morphologically highly differentiated green algae, belonging to the Streptophyta (Jeffrey, 1967; Mattox and Stewart, 1984). They are assumed to be closely related to the ancestors of land plants (Laurin-Lemay et al., 2012) or even thought to be the closest living relatives of land plants (McCourt, 1995; Melkonian and Surek, 1995; Karol et al., 2001; Martin-Closas, 2003), and therefore are commonly exploited as model organisms for the development of acclimation mechanisms allowing survival in terrestrial habitats (Braun et al., 2007). Besides this academic interest, charophytes attract attention for applied aspects. They are exploited for bioremediation (e.g. Marquardt and Schubert, 2009; Schneider and Nizzetto, 2012) and used as bioindicators for environmental quality control (e.g. Krause, 1981; Steinhardt et al., 2009; Selig et al., 2009). In shallow aquatic ecosystems, they form a dense biomass and strongly affect all levels of the ecosystem's food web by a number of stabilizing feedback interactions (Hargeby et al., 1994).

The application of charophytes for bioindication requires detailed knowledge about the ecological niche structure of these algae, which can best be achieved by analyzing occurrence data (Hiltermann and Mädler, 1977). During the last few decades, charophytes from many regions of the world have been catalogued (e.g. Schubert and Blindow, 2004; Caisová and Gąbka, 2009; Naz et al., 2011), providing a sound basis for large-scale biogeographical analysis (e.g. Mann et al., 1999).

Whereas the first survey of charophytes (restricted to Chareae) of North America was published in 1906 (Robinson, 1906), the first survey for Latin America, assumed to be rather fragmentary by the author himself, was published much later (Horn af Rantzien, 1950a). Since then, a number of thorough studies filled gaps in knowledge for North America (e.g. Wood, 1949; Mann et al., 1999) as well as for large regions of South America (e.g. Argentina: Tell, 1985; Cáceres, 1978, 1979; Cáceres and Garcia, 1989; Bolivia, Ecuador, Guiana: Guerlesquin, 1981; Brazil: Bicudo, 1969; Bicudo and Martau, 1974; Bueno et al., 2009).

Covering 10 bioclimatic regions (Walther and Breckle, 1991), mainland Chile provides a broad variety of different aquatic habitats, which should support a large number of charophyte

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species. Mainland Chile stretches about 4400 km in a N–S direction, covering a broad variety of bioclimatic zones. The tropical macrobioclimate in the northernmost region is followed by the Mediterranean macrobioclimate, stretching between the southern limit of the tropics (a diagonal between 23° at the coast and 31° in the mountains) and 37–39° in the south. Further south, the temperate macrobioclimate and the antiboreal macrobioclimate follow, the latter restricted to the islands off southern Patagonia and the southern part of Tierra de Fuego (Moreira-Muñoz, 2011). Due to the steep elevation gradient of the Andes, these macrobioclimatic zones are subdivided additionally into several bioclimatic regions in order to match the distribution of characteristic terrestrial vegetation (e.g. Schmithüsen, 1956), which give rise to the delimitation of the 10 bioclimatic regions defined by Walther and Breckle (1991). Considering this variety of terrestrial vegetation types, one would expect comparable variability with respect to aquatic life.

Furthermore, part of Chile is a world biodiversity hotspot (Andean biodiversity hotspot; Pennington et al., 2010; Särkinen et al., 2012) in terms of species richness and endemism. A high diversity can therefore be expected in Chile especially for organisms such as charophytes, which are well known for their high colonization potential (e.g. Feist et al., 2005; Schaible et al., 2009).

In this context, the 14 charophyte species previously published for Chile (see Table 1) are very few compared with the 58 taxa reported from South America by Van Raam (2009) or the 32 taxa reported from Argentina by Tell (1985), a country with an almost similar latitudinal gradient, but separated from Chile by the Andes.

One hypothesis explaining this low species number could be that the Andean barrier isolates the Chilean bioregion from the rest of South America. This isolation is further strengthened by the Atacama Desert in the North and the ice fields in the South (Campo de Hielo Sur), where dispersal is hampered by restricted habitat availability. The low number of species is thus the result of the species number–area relationship (first published by Arrhenius, 1921) because the Chilean bioregion, irrespective of stretching about 4400 km, is on average about 150 km wide. These 150 km are furthermore extremely heterogeneous because of a steep climatic gradient, which sub-divides the zonobiomes (climatic regions, classified by their temperature and precipitation regimes) in several orobiomes (modifications of the respective zonobiom caused by elevation: "mountain biomes"; Walther and Breckle, 1991). If this hypothesis is correct, diversity should be largest in the southernmost region of Chile (Tierra de Fuego and Magellan Strait) which lacks a barrier with Argentina. A similar assumption was made by Musacchio (2000) based on analysis of Cretaceous charophytes in South America. He assumed that southern Chile and southern Argentina should have more species in common than the northern regions of these countries.

An alternative hypothesis is that the low number of species results from lack of knowledge about charophyte distribution in Chile. Research on charophytes has, however, a long history in Chile and was performed by specialists. A number of prominent collectors (e.g. F. Philippi, W. Lechler) as well as taxonomists (e.g. A. Braun, T.F. Allen) were active in this region, and a check of different herbaria reveals a rather high number of collectors of Chilean charophytes. Data about Chilean sites and species are abundant in the literature, starting with Braun (1839) and Kützing (1849, 1857). Several species were first described from Chilean material (*Chara calveraënsis*; *C. magellanica*, *Nitella lechleri*, *Tolypella apiculata*). Altogether, this does not support the idea of undersampling, especially if compared to the large areas of countries like Brazil or Argentina. Even the northern desert region, which came to Chile after the "Salpeter Wars", was catalogued carefully in 1884/1885 by the botanist F. Philippi who sampled aquatic macrophytes including charophytes (Philippi, 1891). Two arguments, however, indicate lack of knowledge. First, some species, which were reported as widespread in South America such as *C. zeylanica*, *C. hydropitys*, *N. hyalina*, *N. gracilis*, *N. mucronata* (Van Raam, 2009), have never been reported from Chile (Table 1), though their distribution maps in some cases include Chile (Corillion, 1973). Second, published charophyte records are rare from the southern part of the country. Thus, the most recent review on charophytes in Chilean herbaria (Falcon and Hauenstein, 2000) could not trace any material from sites south of Chaitén. There are no published data from Northern Patagonia between Chaitén and the Campo de Hielo Sur, a large region of lakes and rivers, but with difficult access.

Therefore the present paper utilizes data from a series of expeditions to ~500 sites on mainland Chile and the Islands of Chiloe and Tierra de Fuego to provide get a more complete picture of the occurrence and species distribution of charophytes in Chile.

2. Materials and methods

2.1. Field work and study area

Field work was conducted during 3 expeditions in southern late summer (February and March) of 2011, 2012 and 2013. During these expeditions, the entire latitudinal gradient of the macrobioclimatic zones of Mainland Chile was sampled. The 4 macrobioclimatic zones of Chile are divided into 10 different (bioclimatic) vegetation zones, accounting for differences in the climatic conditions within the macrobioclimatic zones due to elevation (orobiomes, i.e. mountain biomes) or characteristic conditions at the borders between the zones ("Zonoecotones"): 1. northern high Andes (Orobiome III & IV); 2. Atacama desert (Zonobiome III); 3. dwarf-shrub and xerophytic shrublands (Zonoecotone II/IV); 4. dry broadleaf forest (Zonobiome IV); 5. deciduous broadleaf forest (Zonobiome V); 6. temperate evergreen rainforest (Zonoecotone V/VIII); 7. subantarctic deciduous broadleaf forest (Zonobiome VIII); 8. Patagonian steppe (Zonobiome VII); 9. southern Andes (Orobiome VIII); and 10. tundra-like cold-zone vegetation (Zonoecotone VIII/IX, Walther and Breckle, 1991). Fig. 1 (left panel) gives an overview of the vegetation zones of Chile based on the boundaries of Walther (1968) in its most recently published modified form (Walther and Breckle, 1991). Except for no. 10, which is an insular ecotone in southern coastal Chile and accessible only by boat, all zones were sampled. However, the climatic differences with respect to precipitation and seasonality of temperature between no. 10 and no. 6 (the latter sampled extensively) are minor. The main difference between these two types is the absence of freeze–thaw-days in the tundra-like cold zone (no. 10) which is, because of the high thermal capacity of water, probably less important for submerged aquatic organisms than for terrestrial plants.

Sites for sampling were selected from satellite images (Google Earth). Additionally, small water bodies such as ephemeral ponds and creeks were sampled along the route between the preselected sampling sites. In each water body, occurrence of submerged vegetation (if not immediately visible) was investigated at least three times by means of a double-fork as described by Krause (1997). Larger lakes were investigated at several locations along the shoreline; about 100 sites were sampled by snorkelling or diving.

2.2. Species determination and taxonomic concept

Herbarium sheets were prepared for all material presented in this study. A complete set, consisting of sheets of all species from all sites sampled is preserved in the herbarium of the University of Rostock (ROST). Some duplicates are present in the herbarium of the Ernst-Moritz-Arndt University of Greifswald, Germany (GFW), the William and Lynda