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A floristic survey of the temporary wetlands in the mediterranean-climate region of Chile

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Abstract

This survey of the temporary ponds of central Chile had two primary objectives: 1) to locate and characterize vernal pools with respect to vegetation and topography; and 2) to compare the Chilean vernal pools to their counterparts in California, with which they share a number of disjunct genera (*Lasthenia*) as well as cosmopolitan taxa such as *Isoetes*. Temporary pools were found between Puerto Oscuro (31°S 23') and the Chol Chol Valley (38°S 36'). The pools are dominated by native, annual species often from generalist wetland genera. Many species had very wide latitudinal ranges; in fact some were present over the whole range of pools studied. In addition to indications that large areas of pool habitat may have been lost due to development, most of the remaining pools were moderately to severely disturbed, and in some areas the pool flora appears primarily in man-made basins. The evidence suggests, as in California, temporary ponds were probably a common and characteristic feature of the pre-agricultural landscape of Chile.

Introduction

Vernal pools, defined here as temporary wetlands in a mediterranean-type climate, fill with rain water in autumn or winter and dry during the late spring and summer. Such wetlands are known from all five of the mediterranean-climate areas in the world

(Australia: Morton and Bayly, 1977; California: Purer, 1939; Chile: Ornduff, 1966; South Africa: Stephens, 1929; Mediterranean Basin: Rivas Goday, 1970). All of these areas have some taxa associated with this community type, but California has the most strongly differentiated flora and fauna with over 80 species and several genera specializing in vernal pool habitats (Holland and Jain, 1977; Thorne, 1984).

Several of the characteristic vernal pool genera are restricted to western North America, except for one or two species in Chile (Ornduff, 1963; Raven, 1963). Molecular and cladistic/taxonomic analysis of some of these taxa suggest they originated in California and reached Chile by long distance dispersal (Crampton, 1954; Ornduff 1963; Raven, 1963). These amphitropical genera, which are present in northern and southern temperate areas but absent in the intervening areas, provide a link which suggests that there might be other similarities between vernal pools in California and the corresponding habitats in Chile.

Although there were anecdotal or incidental accounts of Chilean pools and one regional study (C. Ramirez, pers com), they had not been systematically studied. We therefore undertook to verify the existence of pools in Chile, determine their geographical range and physical setting, characterize their floral composition, and finally come to a better understanding of why Chilean pools were susceptible to the invasion of the North American floral element.

Methods

We surveyed for vernal pools over the length of the mediterranean-climate region of Chile from 30° to 40° south, during the two rainy seasons, 1994 and 1995 (Figure 1). We directed our search on the basis of recommendations by local scientists, locations of known vernal pool species obtained from herbarium collections, and a visual search of areas whose topography and soils seemed similar to those of vernal pools of California.

Throughout the range, we collected plant voucher specimens and took lists of species present in the pools. In selected areas we ran transects across the pools from the edge to edge though the deepest point. For every other dm^2 on the transect we listed all the species present in the quadrat. To correlate the species presence data with characteristics of the hydrology, we recorded elevations along the transect, allowing us to form a topographic profile of the pools.

In the species summaries presented, we classify species into several types. Tolerant upland species are those that have their primary occurrence outside of pools but that do commonly occur within the inundated area. Wetland generalists are species that we found in vernal pools, but they are in genera that are found in a wider range of aquatic habitats. Amphitropical species are those that belong to genera that are more speciose in North America and that are absent from the intervening tropical and montane habitats.

Results and discussion

Pool characteristics

Over 5,300 km of roads were surveyed for this project (Figure 1) resulting in the detection of more than thirty pool areas with a range of latitudes from 31°S 23' to 38°S 36'. Historic records for vernal pool species go farther north than our sites.

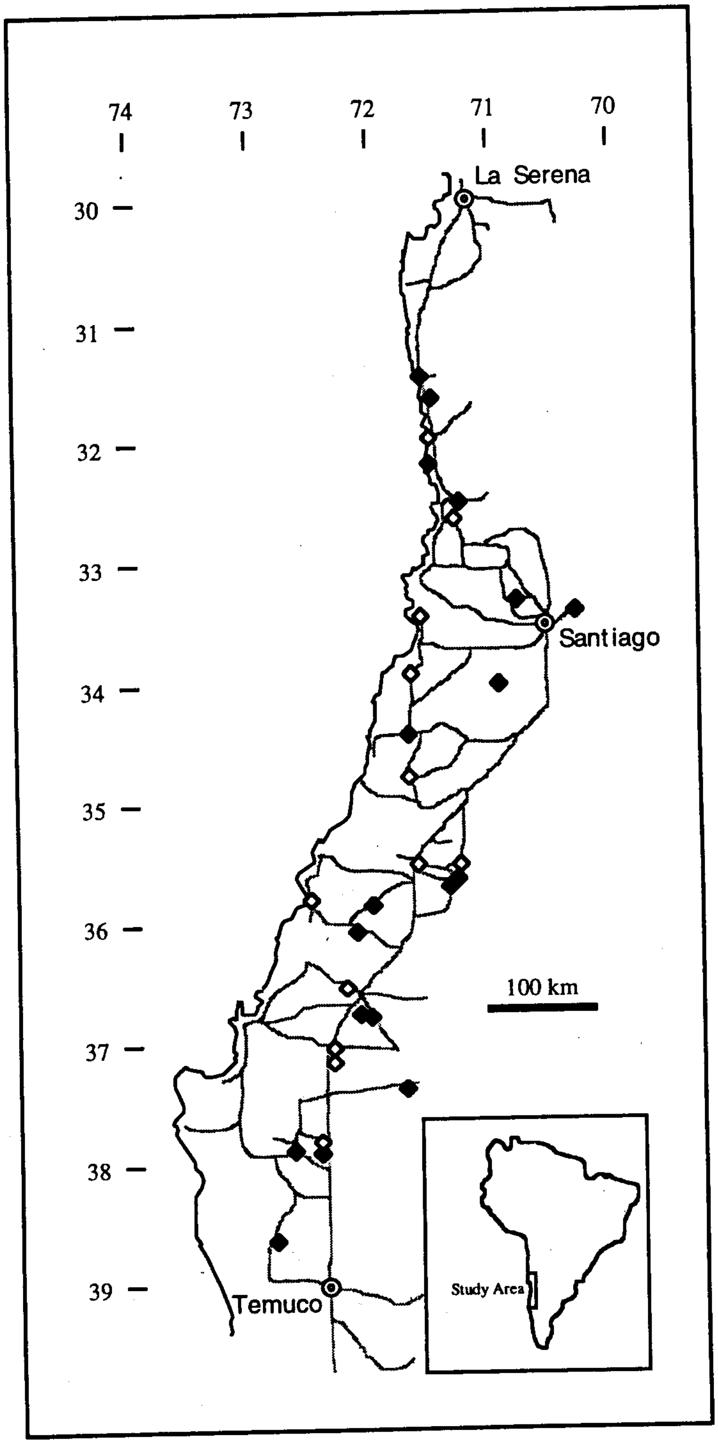

Figure 1. The mediterranean-climate region of Chile with the vernal pool areas located in this study. Closed diamonds represent sites with transects. Gray network indicates over 5,300 km of roads searched.

Table 1. Site characteristics for 30 vernal pool locations in Chile in order of increasing latitude. Precipitation and distance to coast are estimates.

Site #	Site Name	Latitude	Longitude	Altitude (m)	Km to Coast	Ppt '95 (mm)	Usage
1	Puerto Oscuro	31°24'	71°35'	200	3	97	light grazing
2	Huentelauquen	31°33'	71°33'	25	1	105	heavy goat grazing
3	Mincha	31°35'	71°29'	150	10	105	grazing excluded-3 years
4	Los Vilos	31°55'	71°30'	25	1	135	not fenced-moderate grazing
5	Pichidangui	32°08'	71°31'	25	1	145	not fenced–moderate grazing
6	La Ligua	32°27'	71°16'	50	15	222	moderate cattle grazing
7	Catapilco	32°34'	71°19'	125	16	225	basin augmented
8	Batuco	33°15'	70°49'	475	81	95	light grazing
9	Colina	33°16'	70°48'	480	85	95	irrigated with very saline water, light grazing
10	Farellones	33°21'	70°18'	2475	123	360	not fenced–moderate grazing
11	Algarrobo	33°24'	71°36'	360	6	294	basin augmented, light horse grazing
12	Cantillana	33°57'	70°57'	2200	70	370	little impact
13	Alcones	34°23'	71°43'	150	24	367	horse grazing
14	Lolol	34°44'	71°42'	110	35	532	receives overflow water from river
15	Vilches-north	35°28'	71°17'	275	100	700	moderate grazing
16	Talca	35°28'	71°39'	100	70	640	not fenced–moderate grazing
17	Vilches	35°34'	71°18'	400	112	800	low mixed grazing
18	Colbun	35°38'	71°23'	260	101	730	pools created by soil removal (20+ years ago)
19	Parral	35°38'	72°12'	125	40	725	moderate mixed grazing
20	Cauquenes	35°48'	72°01'	125	52	725	heavy mixed grazing
21	Cauquenes 2	35°51'	72°26'	130	50	725	moderate sheep grazing
22	San Nicolas	36°28'	72°18'	100	62	920	light grazing
23	Chillan-created	36°39'	72°08'	100	75	1000	pools created by gravel removal, low grazing
24	Chillan-natural	36°43'	72°08'	100	73	1000	unfenced, light grazing
25	Cabrero	37°00'	72°21'	125	75	950	moderate grazing
26	Antuco	37°20'	71°45'	500	130	1400	not fenced–light grazing
27	Mininco-natural	37°51'	72°28'	200	93	1100	low impact, open spaces between pine plantings
28	Mininco-disturb.	37°51'	72°29'	200	93	1100	hydrology disturbed to increase drainage
29	Angol	37°51'	72°41'	125	72	1050	moderate grazing
30	Chol Chol	38°36'	72°51'	30	53	1300	moderate grazing

We searched some of these areas, but this region had low rainfall in the two years of our study and many areas that often have pools appeared not to have them in 1994 and 1995. Future searches using aerial photographs taken in the winter of wet years are certain to reveal more pools throughout the range of the mediterranean-climate region in Chile.

Climate, geomorphology, soils and land use all varied extensively over the seven degrees of latitude where we found pools (Table 1). The estimated precipitation for 1995 varied between 95 mm to 1,400 mm, resulting in very different hydrologic conditions between the dry north and the wetter south. Elevation ranged from 25 m to over 2,400 m; of special notice are the two sets of alpine pools, Farellones and Cerro Cantillana. No site was more than 130 km from the coast. Consequently, the relatively low coastal mountains and many transversely draining valleys, many areas probably experience some maritime influence (Arroyo *et al.*, 1995). Coastal pools were generally restricted to the north where the coastal plain is wider. Most of the pools farther south are in the Central Depression formed between the Coastal Ranges and the Andes. Antuco, one of the most distinctive sites, is on an ancient volcanic flow, with the pools formed in the shallow pockets in the lava.

Land use practices have had a large impact on the pools. The amount of pool habitat has probably been significantly reduced since settlement by Europeans, and very little pristine habitat is left. Pool hydrology has been altered to a large extent by human intervention in some areas: basins have been augmented by berms to serve as stock-watering ponds, basins have been trenched to increase drainage, and in several cases pool areas have been created by removal of top soil to near the bed rock by gravel excavation allowing ponding in new areas. In addition, land conversion to cultivated crops is very extensive in this region of Chile and the reduction in pool habitat is compounded by the fact that almost all land not under cultivation is being grazed. Grazing pressure ranges from light to heavy by sheep, goats, cattle and/or horses. Although grazing may have negative effects on the hydrology of the pools and individual plants, it is believed for pools in California that grazing can help reduce the impact of exotic plant species in drier years (Ferren pers. com.).

Species composition

Over 140 species were recorded in the pools, but 50 species accounted for nearly 90% of the total occurrence of plants in the pools (Table 2). Almost half of these species are from generalist wetland genera, for example *Crassula* and *Hydrocotyle*. Four species with generic or specific disjunct distributions from North America's vernal pool flora were important in the composition of the pools. The remaining, generally less abundant, species in the pools are upland species that appear to be at least partially tolerant of inundation. There was a surprising lack of representation of local elements in the pool basins.

Compared to the surrounding uplands in which introduced plants are prominent, native species make up over 80% of the common species in the pools (Table 3). The same tendency for vernal pools to have much lower levels of exotic invasion has been noted in the pools of California (Holland and Jain, 1977). The very high incidence of annual species (70% of the common species) is remarkable considering that only 15% of the native flora in the mediterranean-climate region of Chile are annual plants (Arroyo *et al.*, 1995).

Despite the wide range of latitudes and other natural features of the pools, many species were found along most or all of the latitudinal gradient, for example *Lasthenia kunthii* and *Crassula peduncularis* (Table 4). Other species were more common in the northern pools (*Psilocarphus brevissimus* and *Callitriche sp.*) or in the southern region (*Hydrocotyle cryptocarpa* and *Navarretia involucrata*, a species that also appears to exploit lake edge habitat in the south of Chile from 39°–51°S) Although species were generally distributed across a wide latitudinal range, it was quite common for species to be missing from individual pool areas; there was especially low species richness at the areas with created basins (Colbun and Chillan-created) and with unusual substrates (Antuco).

Table 2. The 50 most abundant species found in the vernal pools of Chile arranged by family, with the characteristics amphitropical disjunct, generalist wetland, annual indicated. Non-natives are indicated with an (*).

	Amp	Wet.	Ann.	Rank
Fern Allies				
Isoetaceae				
Isoetes savatieri Franchet		•		15
Marsileaceae				
Marsilea mollis		•		24
Pilularia americana Braun		•		50
Dicots				
Apiaceae				
Eryngium depressum H. et A.		•	•	26
Eryngium psuedojunceum Clos		•		38
Eryngium rostratum Cav.		•	•	4
Asteraceae				
Lasthenia kunthii (Less.) H. et A.	•		•	7
Leontodon saxatilis *			•	17
Micropsis nana D.C.			•	45
Microseris pygmaea D. Don			•	41
Psilocarphus brevissimus Nutt.	•		•	9
Senecio zosterifolius H. et A.			•	29
Boraginaceae				
Plagiobothrys spp.		•	•	2
Brassicaceae				
Capsella bursa-pastoris (L.)			•	49
Cardamine spp.			•	20
Callitrichaceae				
Callitriche lechleri (Hegelm.) Fassett		•	•	10
Campanulaceae				
Downingia pusilla (Don) Torrey	•		•	14
Convolvulaceae				
Convolvulus arvensis (L.) *				40
Dichondra seriea Sw.				43
Crassulaceae				
Crassula spp. (J.E. Sm.) Meigan		•	•	1
Cuscutaceae				
Cuscutta spp.				42
Elatinaceae				
Elatine triandra Schkuhr		•	•	27
Fabaceae				
Trifolium spp. *			•	28
Gentianaceae				
Cicendia quadrangularis (Lam.) Griseb.			•	36
Geraniaceae				
Erodium cicutarium (Cav.) Bertol. *			•	33
Lamiaceae				
Mentha suaveolens Ehrg. *		•		30
Lythraceae				
Lythrum hyssopifolium L. *		•	•	47
Plantaginaceae				
Plantago firma Kunze ex Walp.			•	23
Polemoniaceae				
Collomia biflora (R. et P.)Brand			•	31
Navarretia involucrata R.et P.	•		•	5
Primulaceae				
Centunculus minima L.		•	•	16
Ranunculaceae				
Ranunculus bonariensis Poir.		•	•	6
Scrophulariaceae				
Limosella australis R. Br.		•	•	21
Veronica spp. *				35
Verbenaceae				
Phyla canescens (H.B.K.) Greene *				34
Monocots				
Cyperaceae				
Eleocharis spp.		•		19
Scirpus spp.		•		12
Dioscoreaceae				
Dioscorea longipes Phil.				37
Lilaeaceae				
Lilaea scilloides (Poir.) Haum.		•	•	17
Liliacaceae				
Nothoscordum sp.				13
Poaceae				
Amphibromus scabrivalvis (Trin.)Swallen				44
Bromidium anomalum (Trin.) Doell			•	11
Deschampsia airiformis (Steud.)		•	•	39
Deschampsia spp.		•	•	8
Hordeum spp. *			•	32
Nassella spp.				43
Vulpia spp. *			•	25
Juncaceae				
Juncus bufonius L.		•	•	22
Juncus spp.		•		46

Table 3. Summary of the life history strategies for the 50 most abundant species in the Chilean pools.

	Amphi-tropical	Wetland General	Tolerant Upland	Total
Origin				
Native	4	21	15	40
Introduced	n/a	2	8	10
Longevity				
Annual	4	15	14	33
Perennial	0	8	9	17

Table 4. The representation of the 15 most abundant species on transects in 16 locations in order of latitude from north to south.

	Huente	Mincha	Pichi	Ligua	Batuco	Alcones	Vilches	Colbun	Parral	Cauq	Chi-c	Chi-n	Antuco	Minico	Angol	Chol
E. rostratum	•	•	•				•		•							
P. brevissimus	•	•	•	•	•	•		•		•		•				
C. lechleri	•		•	•	•	•	•	•	•	•	•	•				
Nothoscordum spp.	•	•	•	•			•		•	•		•		•	•	•
Plaigiobothrys spp.	•	•	•		•	•	•	•	•	•	•	•	•	•	•	•
Crassula spp.	•		•	•	•	•	•	•	•	•	•	•	•	•	•	•
Scirpus spp.	•		•	•			•		•	•		•		•	•	•
L. kunthii		•	•		•	•	•		•	•	•	•	•	•		•
R. bonariensis		•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
H. cryptocarpa			•				•		•	•	•	•		•	•	•
Deschampsia spp.						•			•	•	•			•	•	•
N. involucrata							•	•		•	•	•	•	•	•	•

When species distributions of some important species are examined in relation to the hydrological gradient, several patterns emerge. *Lasthenia kunthii* and *Crassula peduncularis* tend to be abundant over a wide range of pool depths (Figure 2). *Marsilea mollis*, a very important species in the north, is found over a wide range of hydrologic conditions, but it appears to be excluded from the deepest portions of the pools. *Navarretia involucrata* and *Plagiobothrys* spp. tend to be most abundant on the edges and absent from the middle of the pools, while *Lilaea scilloides* was often restricted to the deepest portions of the pools. *Psilocarphus brevissimus* and *Ranunculus bonariensis* appear to be the species that respond most to the changing environmental conditions found across the latitudinal gradient and move from the pool edges in wetter south to deeper in the pool basin in the north.

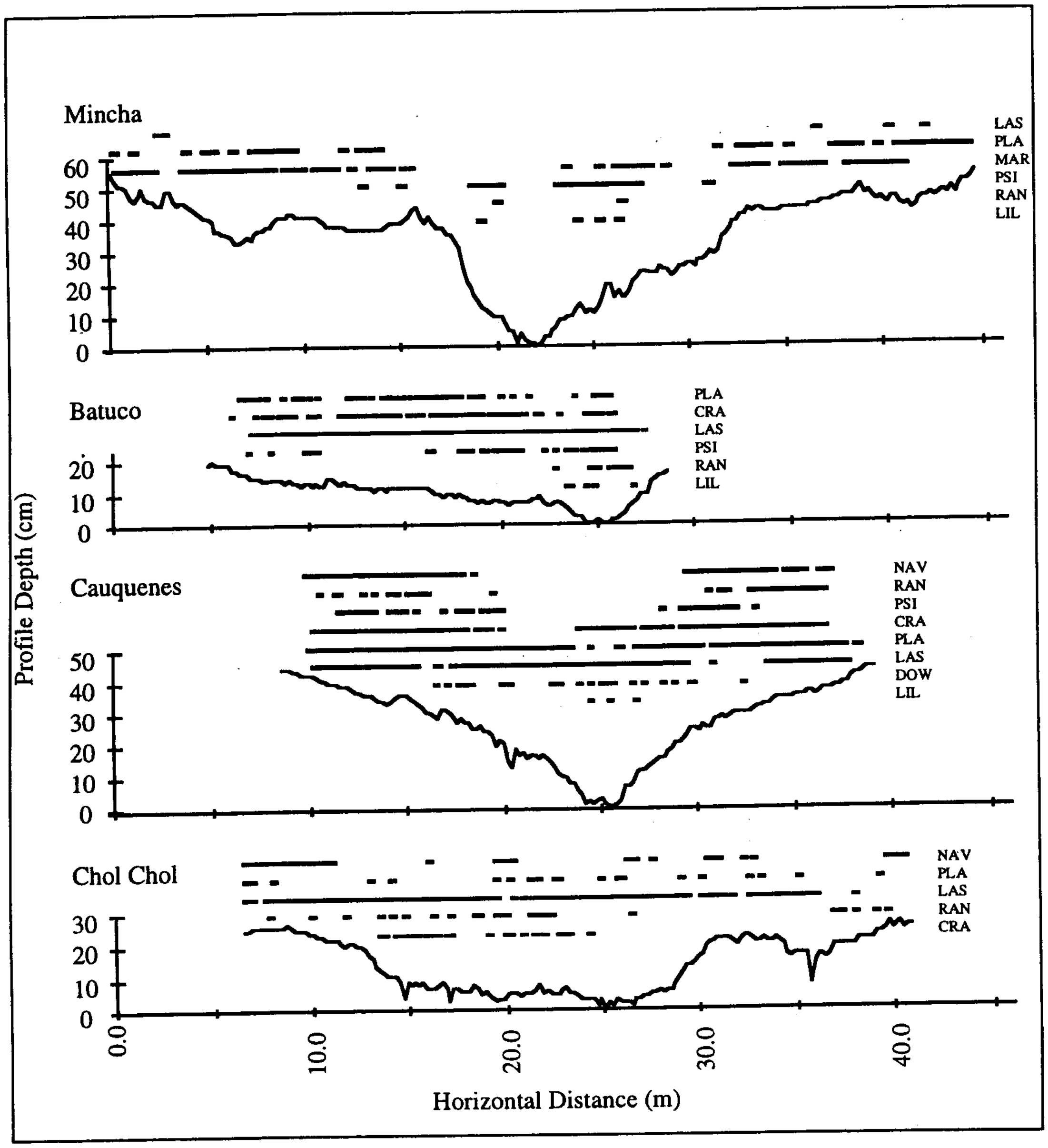

Figure 2. The presence of 10 important species in relation to pool elevation profile for four vernal pools along the latitudinal gradient from north to south. Species code is the first 3 letters of the genus name: CRA-*Crassula*, DOW-*Downingia*, LAS- *Lasthenia*, LIL-*Lilaea*, MAR-*Marsilea*, NAV-*Navarretia*, PLA- *Plagiobothrys*, PSI-*Psilocarphus*, RAN-*Ranunculus*.

Conclusions

Chilean pools act as a repository of significant biodiversity, especially in the annual part of the flora. The pools are also habitats for uncommon and interesting species, such as the fern allies *Isoetes savatieri* and *Marsilea mollis* and other relatively unstudied species such as *Hydrocotyle cryptocarpa* which has not previously been reported from Chile (L. Constance, pers. com.) At a different scale, the Chilean pools have global significance. The amphitropical plant genus and species distributions are a remarkable example of the linkages that can exist between distant regions. We cannot understand the circumstances that favored their invasion without the preservation of a representative number of natural habitats in Chile. These amphitropical species, along with the unique Chilean elements, provide an excellent opportunity for testing ideas about community assemblage through evolutionary and ecological time. Finally, in California four of the amphitropical genera include endangered species, *Lasthenia*, *Blennosperma*, *Downingia* and *Navarretia*. This is evidence that the Chilean pools are a subset of a community-type that is becoming increasingly rare as human use of the land intensifies.

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