

Original Article

Insects associated to ephemeral pools in Huentelauquén (29°S Coquimbo Region, Chile)

Insetos associados a lagoas temporárias em Huentelauquén (29°S Região de Coquimbo, Chile)

J. Pizarro-Araya^{a*} , F.M. Alfaro^{a,b}  and P. De Los Ríos-Escalante^{c,d} 

^a Universidad de La Serena, Departamento de Biología, Laboratorio de Entomología Ecológica, La Serena, Casilla 554, Chile

^b Universidad de La Serena, Instituto de Investigación Multidisciplinar en Ciencia y Tecnología, La Serena, Casilla 554, Chile

^c Universidad Católica de Temuco, Facultad de Recursos Naturales, Departamento de Ciencias Biológicas y Químicas, Temuco, Casilla 15-D, Chile

^d Universidad Católica de Temuco, Núcleo de Estudios Ambientales, Temuco, Chile

Abstract

In northern central Chile, ephemeral pools constitute shallow isolated water bodies with a favourable habitat for fauna adapted to seasonal changes. Based on the limited knowledge about the fauna—particularly insects—associated to these ecosystems, the objective of this study was to characterize the richness, composition, structure and similarity of the insect communities associated with ephemeral pools in Huentelauquén (29° S, Coquimbo Region, Chile). By using pitfall traps, 10,762 individuals were captured, represented by 7 orders, 27 families, and 51 species. Coleoptera and Hymenoptera were the best represented orders, with Neuroptera, Orthoptera and Plecoptera being poorly represented groups. The non-parametric estimators evaluated showed wealth values above those observed for all the studied pools, and their accumulation curves suggest the existence of an incomplete species inventory in the studied community. Additionally, the hierarchical and ordering analysis showed groupings of pools located in the northwest and southeast of Huentelauquén. Preliminarily we found a negative correlation between the area of the pools and the richness (species) and abundance of insects. Additional studies (on other arthropod groups and other seasons of the year) could provide a better understanding of the local processes of extinction and colonization of the species inhabiting these fragile coastal environments.

Keywords: arid zones, coastal desert, coastal wetlands, insect communities, species richness.

Resumo

No norte central do Chile, lagoas efêmeras constituem corpos de água isolados e pouco profundos, com um habitat favorável para a fauna adaptada as mudanças sazonais que as zonas úmidas estão sujeitas. Com relação a estes ecossistemas, sabe-se pouco sobre sua fauna, principalmente a de insetos. O objetivo do presente estudo foi caracterizar a riqueza, composição, estrutura e similaridade das comunidades de insetos que habitam as lagoas temporárias de Huentelauquén (29° S, Região de Coquimbo, Chile). Usando armadilhas de interceptação, se capturou um total de 10.762 indivíduos, pertencentes a 7 ordens, 27 famílias e 51 espécies. Coleoptera e Hymenoptera foram as ordens mais representativas, enquanto Neuroptera, Orthoptera e Plecoptera foram grupos pouco representativos. Os estimadores não paramétricos avaliados mostraram valores de riqueza superiores ao observados para todas as lagoas estudadas, e suas curvas de acumulação parecem indicar que o inventário da comunidade estudada está incompleto. A análise hierárquica e de ordenamento revelou agrupamentos de lagoas correspondentes a zona nordeste e sudeste de Huentelauquén. Preliminarmente encontramos uma correlação negativa entre a área de lagoas efêmeras e a riqueza (espécies) e abundância de insetos. É necessário realizar estudos adicionais (sobre outros grupos de artrópodes e em outras estações do ano) para melhor compreensão dos processos locais de extinção e colonização das espécies que habitam estes frágeis ambientes costeiros estudados.

Palavras-chave: zonas áridas, deserto costeiro, zonas úmidas costeiras, comunidades de insetos, riqueza de espécies.

1. Introduction

The coastal areas of northern Chile have different ecological and geomorphological zones (Abreu and Bannon, 1993; Villagrán, 2001; Smith-Ramírez et al., 2005) that support a wide variety of habitats conditioned by the

maritime influence and aridity (Ormazábal, 1993; Gajardo, 1993). In these areas there have been relict zones with biotic components from the Tertiary period, which have affected species distribution and favoured the emergence

*e-mail: japizarro@userena.cl

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of endemic species (Jerez, 2005; Villagrán and Armesto, 2005; Smith-Ramírez et al., 2005; Arroyo et al., 2006).

These coastal zones are considered important due to their diversity and endemism and, consequently, for biological conservation (Smith-Ramírez et al., 2005), and are included in an important hotspot for Chile (Cowling et al., 1996; Gaston, 2000; Lamoreux et al., 2006). In addition, as a result of its latitudinal position, the coastal area of Central Chile is affected by the ENSO phenomenon (El Niño Southern Oscillation) (Romero and Garrido, 1985; Cepeda-Pizarro et al., 2005a, b), as well as by the potential effects of global climate change (Schlesinger and Mitchell, 1987; Mooney et al., 2001).

The first reports of aquatic insects inhabiting ephemeral pools in Chile in terms of structure and function were documented in Andean pools of Tambo-Puquios ($29^{\circ}45' S$; Cepeda-Pizarro and Pola, 2013; Cepeda-Pizarro et al., 2006a; Cepeda-Pizarro et al., 2006b; Cepeda-Pizarro et al., 2013; Cepeda-Pizarro et al., 2015a, b; Cepeda-Pizarro et al., 2016), where 14 insects orders were reported in addition to other taxa, such as cladocerans, copepods, and ostracods. In these pools marked seasonal and spatial variation were reported (Cepeda-Pizarro et al., 2016). Currently, there are no studies accounting for the diversity and structure of the arthropod assemblages of ephemeral pools in the coastal desert of Chile. Therefore, the aim of this study is to conduct a first characterization of the insects communities in ephemeral pools of northern Chile, more specifically in the plains of Huentelauquén ($29^{\circ} S$, Coquimbo region), originating from the southern autumn and winter rains (Zuleta and Piñones, 2014; Zuleta and Piñones, 2015; De Los Ríos-Escalante et al., 2019; Sigvardt et al., 2019; Zuleta et al., 2019).

2. Material and Methods

2.1. Study area

The study site encompassed the locality of Huentelauquén in the Coquimbo region, Chile, located in the Choapa river basin, a zone under marine and fluvial influence (Castillo and Robles, 2012). The study was conducted in the semiarid plains of a Ramsar site called "Las Salinas de Huentelauquén", located 40 km north of the town of Los Vilos (Figure 1) and in coastal terrace/plains located near 5 km SE (around of $31^{\circ}35'45''S$, $71^{\circ}30'30''W$). The weather is Mediterranean, with a nine-month dry season with many cloudy days, and an annual average precipitation of 130 mm (Novoa and Villaseca, 1989). This site is inserted in a transition area between steppe shrubs and shrubs and trees (Chang et al., 1989; Gajardo, 1993; Cepeda-Pizarro et al., 2000). The flora species that have been reported for this area include *Echinopsis skottsbergii* (Backb.) H. Friedrich and G.D. Rowley, *Heliotropium stenophyllum* Hook. et Arn., *Senna cumingii* (Hook. et Arn.) Irving et Barneby, *Chuquiraga ulicina* (Hook. et Arn.), *Frankenia chilensis* K. Presl., *Baccharis macraei* (Hook. et Arn.), *Bahia ambrosioides* Lag., *Haplopappus foliosus* DC., and *Marygicarpus pinnatus* (Lam.) Kuntze (Cea and Zuleta, 2016; Cea et al., 2019). The aquatic flora is characterized by

the presence of Poaceae (Cea and Zuleta, 2016), a frequent family in ephemeral pools (Bliss et al., 1998; Álvarez et al., 2012). In this site, we studied a series of ephemeral pools with shallow and variable water levels subject to the rainfall conditions (Table 1, Figure 2). All the studied water pools were georeferenced using a satellite navigator (e-Trex 30, Personal Navigator, Garmin). The data were captured in decimal degrees using DATUM WGS84 and downloaded using MapSource 3.0. Based on this information, a grid was prepared using ArcGIS 9.3 with Add XY Data and projected to UTM 19S DATUM WGS84.

2.2. Data collection, sample processing and identification of insects

The specimens were collected using pitfalls traps following Cepeda-Pizarro et al. (2005a, b). For each site, a grid was installed consisting of 4×5 m sites with 20 traps each. The traps were installed between October 15 and October 18, 2015. The captured material was removed, cleaned and preserved in alcohol (70%) until the moment of processing. For the taxonomic identification at a generic and specific level, specialized literature was used. The collected specimens were deposited in the entomological collection of the Ecological Entomology Laboratory of the University of La Serena (LEULS, La Serena, Chile).

2.3. Statistical analysis

To estimate species richness, the smoothed richness accumulation curves for the non-parametric estimators ACE, Chao 1, Jackknife first order (Jack 1) and Bootstrap were analysed. (Colwell, 2013). ACE is based on the abundances of species with ten or less individuals in the sample, whereas Chao 1 is based on rare species found in the sample. Jack 1 is based on the number of species present in one sampling unit, whereas the bootstrap estimator is based on the proportion of sampling units containing each species. The non-parametric estimators do not require special assumptions as parametric estimators do—calculation is easy and effective (Escalante, 2003). These estimators are universally valid for any species abundance distribution and more robust than parametric estimators based on species abundance (Chao and Chiu, 2016). All of these estimators were calculated using EstimateS version 9.10 (Colwell, 2013). To calculate the structuration grade for each habitat (pool), a similarity join analysis or cluster analysis was done based on the Bray-Curtis index. To analyse the structure of the insect communities associated with the pools, a non-metric multidimensional scaling analysis (NMDS) was done using the similarity Bray-Curtis index. Finally, a correlation matrix was developed using Spearman's rank correlation coefficient (r) to compare the richness and abundance of insects with some physical characteristics of pools (area, altitude, max deep). The similitude, ordering and correlation analysis were performed using RStudio 1.2.5033 (RStudio Team, 2021).

A species absence/presence matrix was constructed, with the species in rows and the sites in columns. We calculated the Checkerboard score ("C-score"), which is a quantitative index of occurrence that measures the extent to which species co-occur less frequently than what

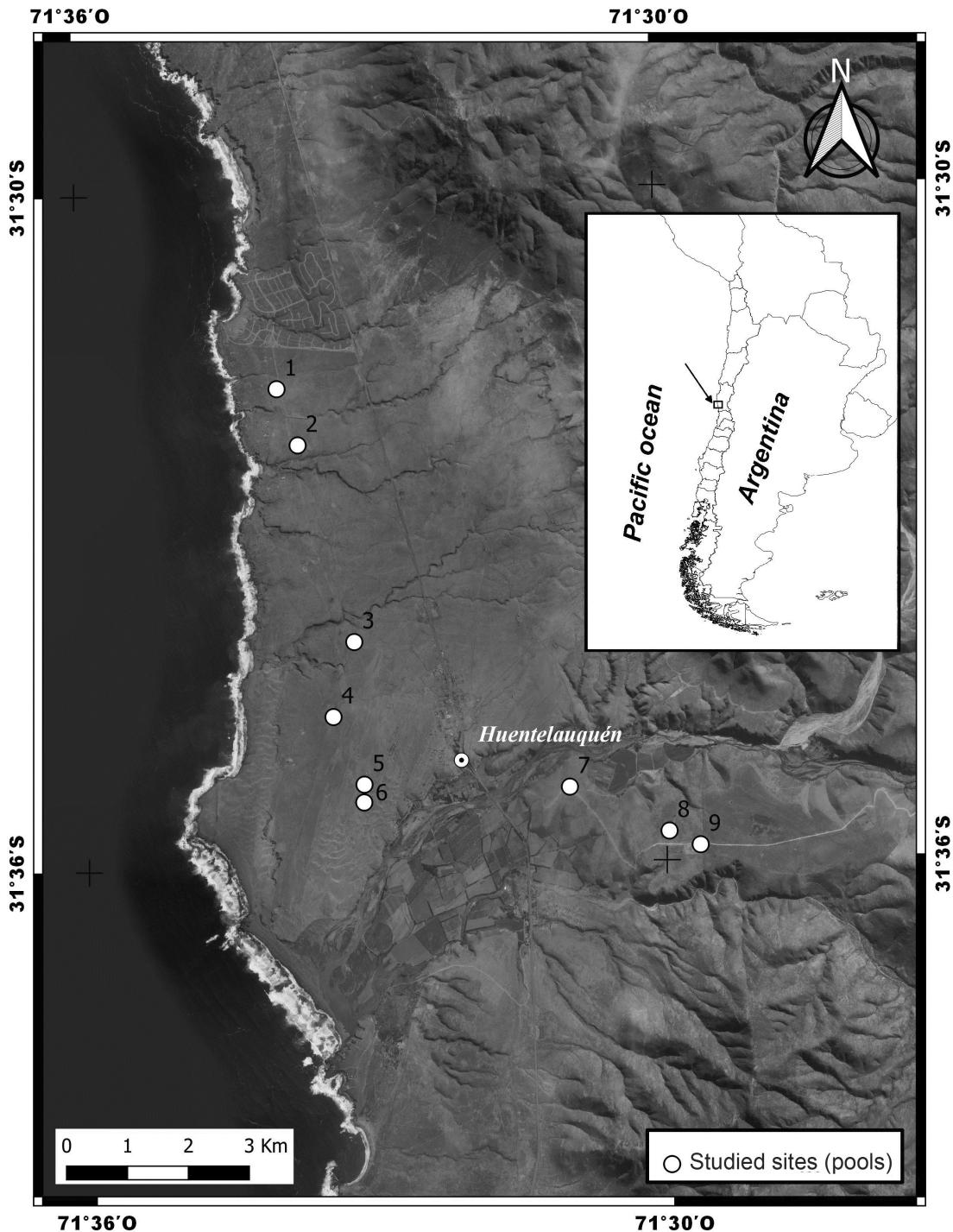


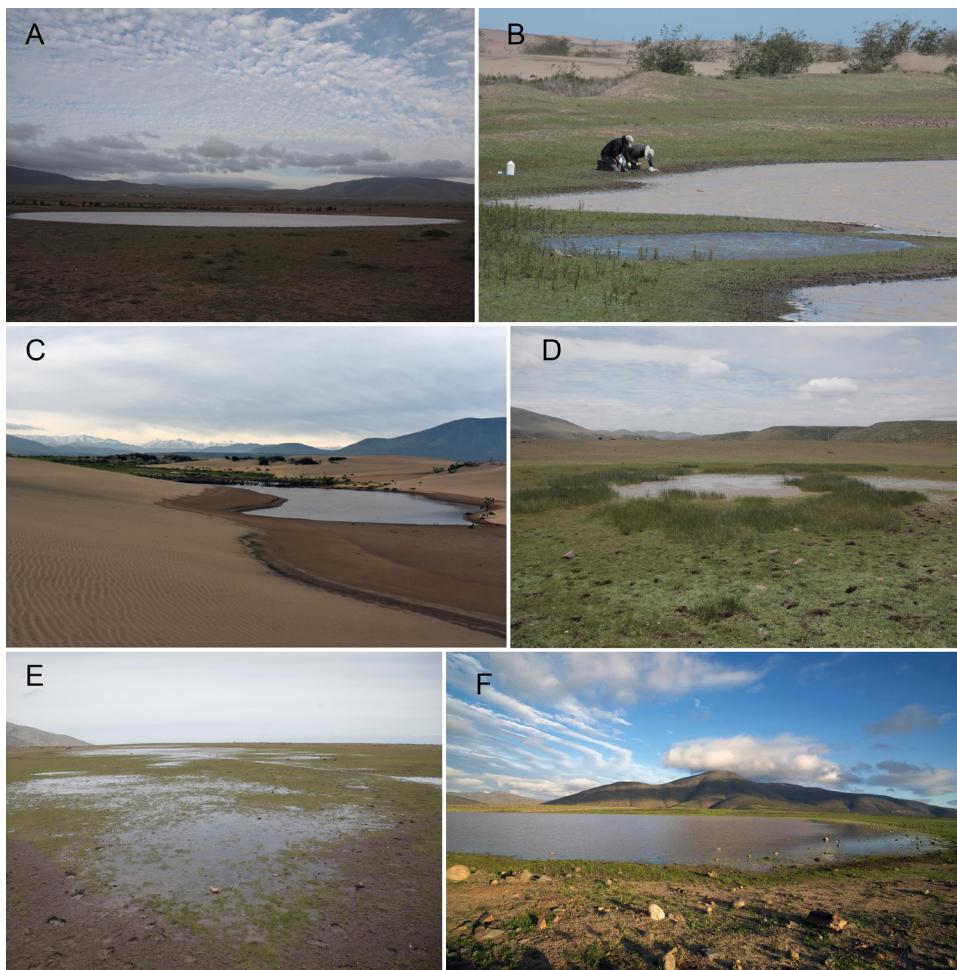
Figure 1. Map showing the geographic location of the ephemeral pools studied in Huentelauquén (Coquimbo Region, Chile). The numbers represent the pools as in Table 1.

is expected by chance (Gotelli, 2000). A community is structured by competition when the C-score is significantly larger than the value expected by chance (Gotelli, 2000; Tondoh, 2006; Tiho and Josens, 2007). In addition, we

compared co-occurrence patterns with null expectations via simulation. Gotelli and Ellison (2013) proposed the fixed-effects model as a statistical null model. In this model, the sums of the rows and columns of the matrix are

Table 1. Geographical location and physical characteristics of the ephemeral pools studied in Huentelauquén (Coquimbo Region, Chile).

Pool	Latitude	Longitude	Altitude (m.a.s.l.)	Area (m ²)	Maximum depth (cm)
1	31°33'44.5"	71°33'56.5"	18	6,500	20
2	31°32'14.7"	71°33'44.2"	27	2,300	14
3	31°34'00.2"	71°33'11.8"	48	5,000	22
4	31°34'39.9"	71°33'25.8"	43	27,700	32
5	31°35'16.3"	71°33'07.5"	46	15,700	20
6	31°35'25.8"	71°33'07.9"	43	3,100	20
7	31°35'19.9"	71°30'59.6"	71	1,000	39
8	31°35'44.5"	71°29'58.2"	158	20,000	17
9	31°35'52.2"	71°29'39.0"	157	40,000	20

**Figure 2.** Panoramic views of the Huentelauquén ephemeral pools (Coquimbo Region, Chile). (A) pool 3 located in the north of Huentelauquén; (B) installation of pitfall traps in pool 5; (C) pool 6 in a coastal dune; (D) pool 7 located in the southeast of Huentelauquén; (E) pool 8 located in the southeast of Huentelauquén; (F) pool 9 located in the southeast of Huentelauquén.

preserved such that each random community contains the same number of species as the original community (fixed column) and each species occurs with the same frequency as in the original community (fixed row).

Niche overlap and separation in the insect communities were analyzed using a null model based on Pianka's overlap index with retained niche breadth and reshuffled zero states. The null model analyses were performed using

RStudio 1.2.5033 (RStudio Team, 2021) and the package EcosimR version 7.0 (Gotelli and Ellison, 2013; Carvajal-Quintero et al., 2015). The EcosimR program also determines whether the measured overlap values differ from what would be expected in a random sampling of the species data. EcosimR performs Monte Carlo randomisations to create pseudo-communities and then statistically compares the patterns of these randomised communities with those in the real data matrix (Gotelli and Ellison, 2013). In our analysis, all the values in the general matrix were randomised 1,000 times and the niche breadth was retained for each species; in this way, the algorithm retained the total amount of specialization for each species (Gotelli and Ellison, 2013; Carvajal-Quintero et al., 2015). Finally, an analysis was conducted based on the unified neutral theory of biodiversity (Hubbell, 2001) using the R package UNTB (Hankin, 2018). For this analysis, we used the θ estimator and conducted a Preston analysis.

3. Results

A total of 10,762 individuals were captured, belonging to 7 orders, 26 families, and 51 species (Table 2). The highest species richness was found in the two and seven pool, both with 24 species, whereas the lowest value was observed in the fifth pool, with 13 species (Figure 3). The exclusive species number was different for each ephemeral pool studied and three species (i.e., *Bembidion (Notaphus)* sp., *Pachymorphus* sp. and Plecoptera sp. larva) were present at all sites (Table 2).

Among the insect groups, the orders with the highest number of taxa were Coleoptera (17 families, 37 genus, and 39 species) and Hymenoptera (2 families, 4 genus, and 4 species), whereas those with the lowest were Neuroptera, Orthoptera, and Plecoptera (Table 2). Within Coleoptera, the families with the highest number of species were, in decreasing order, Tenebrionidae, Carabidae, and Curculionidae. Families with only one species included

Anthicidae, Coccinellidae, Cryptophagidae, Dytiscidae, Erotylidae, Heteroceridae, Hidrophylidae, Hydraenidae, Latridiidae, Scarabaeidae, and Trogossitidae (Table 2).

The non-parametric estimators produced estimated total richness values higher than the values observed (Figure 4). For example, the estimator Chao 1 estimated a high number of rare species (singletons and doubletons) for the set of pools under study (see Figure 4); these species belonged mainly to Coleoptera (see Table 2).

The most abundant species were Collembola sp. 1 (26.2% of total captured), Plecoptera sp. (larvae) (16.2%), and *Arthrobrachus limbatus* Solier, 1849 (15.7%) (Table 2). Overall, the highest relative abundances occurred in the second (20.5% of total captured), the seventh (17.3%), the third pool (13.8%), and the eighth pool (13.6%) (Table 2). Although the second pool does not have a large surface area, it shows a high richness and abundance in comparison to the ninth pool, which has the largest surface area (see Table 1).

The cluster analysis showed high similarity between the first and fourth pools, and the seventh to ninth pools (more than 60% similarity) (Figure 5). The first group is located in the north of Huentelauquén and was characterized by the dominance of *A. limbatus* and Collembola sp. 2, whereas the second group is located in the south-east of this locality and was characterized by the almost exclusive dominance of Collembola sp. 1 (see Table 2). The non-metric multidimensional scaling analysis showed relative correspondence between the similarities identified in the cluster analysis. Nevertheless, the most notable similarity was observed in pools located southeast of Huentelauquén (seventh to ninth pool) (Figure 6), which are the habitats with the largest surface area included in the present study (see Figure 1).

Only richness (species) ($r = -0.66$, $p = 0.02$) and abundance ($r = -0.44$, $p = 0.02$) were negatively correlated with the area of the pools. No significant correlations were observed when analyzing the altitude and maximum depth of the pools (Figure 7).

The co-occurrence species and niche-sharing analysis revealed that the species associations reported were not structured, which means the absence of patterns between

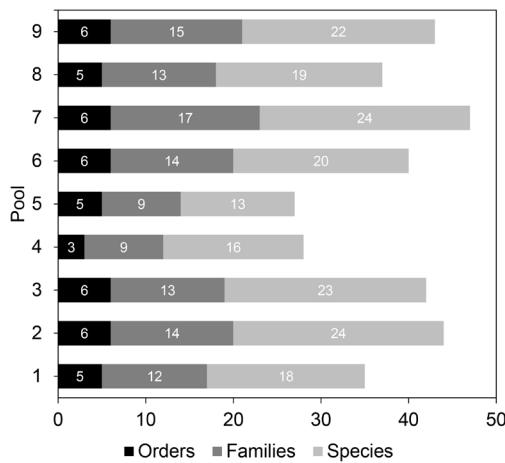


Figure 3. Number of species, families and orders of insects associated with ephemeral pools in Huentelauquén (Coquimbo Region, Chile).

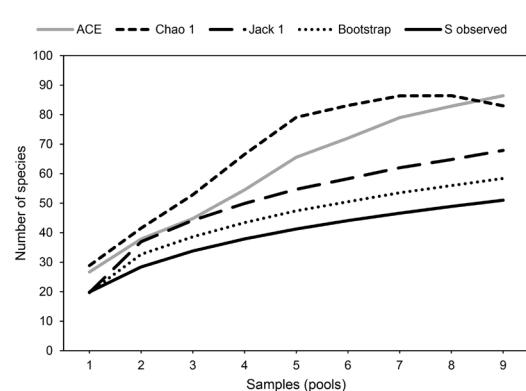


Figure 4. Smoothed richness accumulation curves for the non-parametric estimators ACE, Chao 1, Jack 1, and Bootstrap, for insects associated with ephemeral pools in Huentelauquén.

Table 2. Taxonomic composition and abundance (n) of insects for the ephemeral pools studied in Huentelauquén (Coquimbo Region, Chile).

Order	Family	Species	Pool									Total	
			1	2	3	4	5	6	7	8	9		
		n	n	n	n	n	n	n	n	n	n	%	
Coleoptera	Anthicidae	<i>Ischyropalpus</i> sp.	0	0	0	0	0	0	0	0	1	0.01	
	Carabidae	<i>Bembidion</i> (<i>Notaphthus</i>) sp.	211	10	16	66	69	10	43	55	33	513	4.77
		<i>Calosoma vagans</i> Dejean, 1831	2	19	2	0	0	0	0	0	0	23	0.21
	Carabidae sp.	(larva)	37	13	5	10	1	0	31	27	2	126	1.17
	Carabidae	<i>sp. 1</i>	3	0	2	2	0	8	2	9	3	29	0.27
	Carabidae	<i>sp. 2</i>	0	0	0	0	0	0	1	0	0	1	0.01
		<i>Incagonium</i> sp.	0	0	0	0	1	2	7	3	7	20	0.19
		<i>Pachymorphus</i> sp.	38	18	33	33	7	5	87	45	34	300	2.79
	Trirannatus	<i>striatula</i> (Fabricius, 1775)	0	1	0	0	0	0	0	0	1	2	0.02
	Chrysomelidae	<i>Chrysomelidae</i> sp.	0	0	0	0	0	0	0	1	0	1	0.01
		<i>Phaedon cyanopterum</i> Guérin-Méneville, 1844	0	0	0	0	2	0	0	0	0	2	0.02
	Coccinellidae	<i>Eriopis connexa</i> (Germar, 1823)	0	0	0	0	0	0	0	0	1	1	0.01
		<i>Cryptophagidae</i> sp.	0	0	0	0	0	0	1	0	1	1	0.01
	Curculionidae	<i>Chneoeculus</i> sp.	0	0	0	0	1	0	0	0	0	1	0.01
		<i>Curculionidae</i> sp. 1	81	4	32	70	0	0	505	97	2	791	7.35
		<i>Curculionidae</i> sp. 2	1	56	12	169	9	0	0	0	1	248	2.30

Table 2. Continued...

Order	Family	Species	Pool									Total	
			1	2	3	4	5	6	7	8	9		
n	n	n	n	n	n	n	n	n	n	n	n	%	
		Curculionidae	0	3	6	26	0	0	0	0	0	35	0.33
		<i>sp. 3</i>											
		Curculionidae	0	0	0	0	0	0	0	0	4	4	0.04
		<i>sp. 4</i>											
	Dytiscidae	<i>Dytiscidae sp.</i>	0	1	0	0	0	0	0	1	2	0.02	
	Erotylidae	<i>Erotylidae sp.</i>	0	0	0	0	0	1	0	0	1	0.01	
	Heteroceridae	<i>Heterocerus sp.</i>	0	1	0	2	11	3	2	6	1	26	0.24
	Hydrophilidae	<i>Tropisternus</i> (<i>Pristotermus</i>)	1	0	0	0	0	0	1	0	0	2	0.02
		<i>setiger</i> (Germar, 1824)											
	Hydraenidae	<i>Gymnochthebius</i> <i>af. plesiohypus</i>	0	0	2	3	5	1	4	0	1	16	0.15
		Perkins, 1980											
	Latridiidae	<i>Latridiidae sp.</i>	0	0	0	0	0	0	1	0	0	1	0.01
	Melyridae	<i>Arthrobrachus</i> <i>limbatus</i> Solier, 1849	129	449	707	381	0	0	5	13	5	1,689	15.69
	Melyriidae	<i>Melyriidae sp.</i>	0	0	0	1	0	0	0	0	0	1	0.01
		<i>Lichnia gallardoi</i> Gutiérrez, 1943	0	20	7	0	0	0	1	0	0	28	0.26
	Scarabaeidae	<i>Staphylininae</i> sp. 1	1	0	0	0	0	0	2	1	0	4	0.04
		<i>Staphylininae</i> sp. 2	0	12	1	10	0	4	1	186	200	414	3.85
	Tenebrionidae	<i>Alphitobius</i> <i>diaperinus</i> Panzer, 1797	0	1	12	0	0	0	0	2	15	0.14	

Table 2. Continued...

Order	Family	Species	Pool									Total	
			1	2	3	4	5	6	7	8	9		
n	n	n	n	n	n	n	n	n	n	n	n	%	
		<i>Geoborus nigripennis</i> (Solier, 1851)	0	0	0	1	0	0	0	0	0	1	0.01
		<i>Grammicus mahunkai</i> Kaszab, 1969	0	0	1	0	0	0	0	0	0	1	0.01
		<i>Gyriosomus foreopunctatus</i> <td>0</td> <td>1</td> <td>0</td> <td>0</td> <td>0</td> <td>0</td> <td>0</td> <td>0</td> <td>0</td> <td>1</td> <td>0.01</td>	0	1	0	0	0	0	0	0	0	1	0.01
		<i>Nycterinus</i> sp.	0	0	0	0	0	1	0	0	0	1	0.01
		<i>Praocis (Praocis) bicentenario</i> Flores and Pizarro-Araya, 2012	0	0	0	0	1	0	0	0	0	1	0.01
		<i>Praocis (Praocis) subaenea</i> Erichson, 1834	0	0	3	1	0	0	0	0	0	4	0.04
		<i>Thinobatis arenaria</i> Peña, 1974	0	2	3	0	6	0	0	0	0	11	0.10
		<i>Thinobatis rufipes</i> Solier, 1835	0	0	0	0	2	205	0	0	0	207	1.92
	Trogossitidae	<i>Diontolobus</i> sp.	0	0	0	0	0	0	1	0	0	1	0.01
Collembola	Colembola	<i>Collembola</i> sp. 1	360	184	0	0	0	1	960	320	2,824	26.24	
		<i>Collembola</i> sp. 2	0	986	0	0	47	5	0	31	1,069	9.93	
Hemiptera	Cicadellidae	<i>Cicadellidae</i> sp.	10	1	0	0	0	10	2	0	0	23	0.21
	Lygaeidae	<i>Lygaeidae</i> sp.	5	0	0	0	5	1	5	3	1	20	0.19
	Saldidae	<i>Saldula coxalis</i> (Stål, 1873)	44	7	0	0	0	6	2	0	0	59	0.55

Table 2. Continued...

Order	Family	Species	Pool						Total	
			1	2	3	4	5	6	7	
Hymenoptera	Formicidae	<i>Camponotus morosus</i> Smith, 1858	8	0	0	0	0	0	0	8
		<i>Dorymyrmex pogonius</i> (Snelling, 1975)	54	45	7	1	0	0	0	0.07
		<i>Solenopsis gayi</i> Spinola, 1851	99	127	47	0	1	5	14	343
	Mutillidae	Mutillidae sp.	0	0	6	0	0	0	1	0.07
	Neuroptera	Neuroptera sp. (larva)	8	1	1	0	1	1	16	30
	Orthoptera	Gryllidae sp.	0	0	1	0	0	0	0	0.28
	Plecoptera	Plecoptera sp. (larva)	134	68	399	211	240	397	139	1,745
	Total (abundance)		866	2,206	1,489	987	358	711	1,864	1,461
	Exclusive species		1	1	2	2	0	5	3	2
										100
										10,762

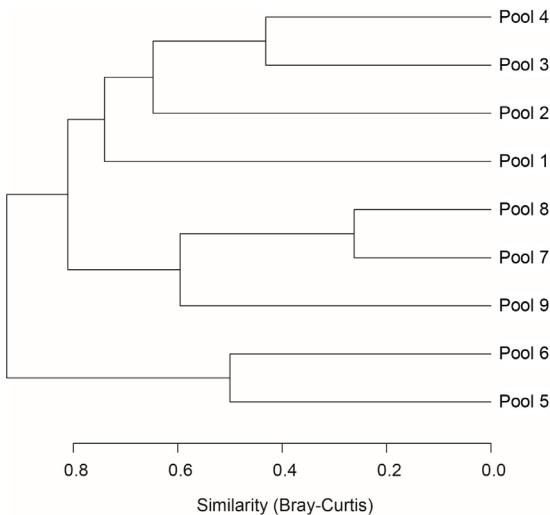


Figure 5. Dendrogram of cluster analysis based on Bray-Curtis similarity for the ephemeral pools of Huentelauquén.

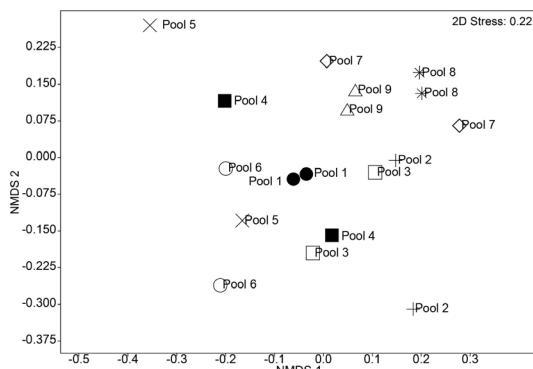


Figure 6. Non-metric multidimensional scaling analysis (NMDS) using the similarity Bray-Curtis index for the ephemeral pools of Huentelauquén.

species associations and niche overlapping (Table 3). The results of the analyses based on unified neutral theory of biodiversity revealed low species number, with an optimal θ of 6.581, respectively, and a singletons number of 16.

4. Discussion

The insect assemblage associated to ephemeral pools included native species that are widely distributed in the Chilean coastal desert, such as *Camponotus morosus* (Formicidae), a native species with wide distribution in sclerophyllous shrubs in central Chile and generalist feeding behaviour (Snelling and Hunt, 1975; Grez et al., 1986); and *Gyriosomus foveopunctatus* (Tenebrionidae), a darkling beetle typical from inner steppe shrubs (Pizarro-Araya and Jerez, 2004). The shared species of Carabidae (see Table 2) have a wide distribution in continental Chile (Roig-Juñent and Domínguez, 2001).

Even though several insect groups characteristic of the coastal scrub were recorded, the species accumulation curves did not reach a defined asymptote, which suggests that the species inventory of the studied communities is incomplete (Escalante, 2003; Alfaro and Pizarro-Araya, 2017).

Preliminarily we found a negative correlation between the area of the pools and the richness (species) and abundance of insects. These observations are in stark contrast with the increase in the number of species resulting from increased habitat size, a very common phenomenon observed in ecology (Rosenzweig, 1995). Even though coastal shrub-type vegetation dominates all the studied sites, it is likely that the presence of insect species is conditioned by the characteristics of the microhabitat around the area of the pools. Nevertheless, additional samplings in other seasons are necessary to test these ecological hypotheses at a local level, as well as it is also necessary to evaluate how the structure of the habitat, floristic richness and the connectivity between pools could

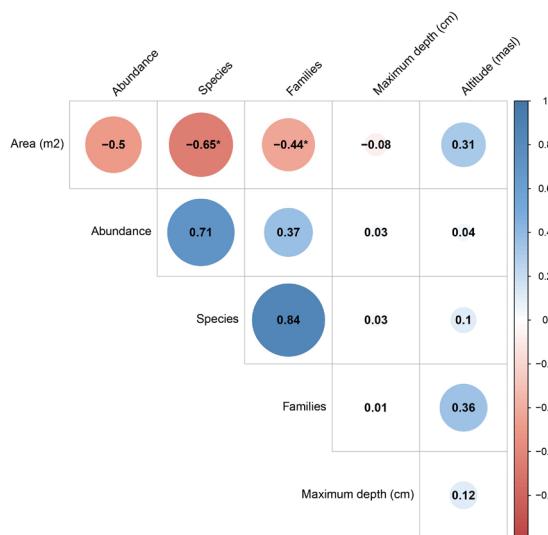


Figure 7. Spearman's correlation matrix. Values (r) show the positive or negative correlation between richness (species and families) and abundance of insects and some physical characteristics of pools (area, altitude, maximum depth). *Significant at 0.05.

Table 3. Results of the null model of species co-occurrence and niche sharing for the species and sites included in the present study.

	Observed index	Mean index	Standard effect size	Variance	P
Species co-occurrence	1.698	1.965	0.176	< 0.001	0.435
Niche sharing	0.217	0.219	-0.287	< 0.001	0.564

explain the structure of the insect community in these environments (Tornero et al., 2016; Heino et al., 2017).

Some groups, such as Collembola (see Table 2), require wet edaphic conditions to complete their biological cycles (Cepeda-Pizarro and Pola, 2013), and their diversity and abundance patterns in arid environments may be determined by soil humidity (Cepeda-Pizarro and Whitford, 1989). The dominance of some Collembola species in these pools could be explained by the higher humidity conditions observed in the surrounding microhabitat of these water bodies, however it was not a general pattern for all the pools studied (see Table 2). Although pitfall traps are directed to walking insects (Cepeda-Pizarro et al., 2005a, b), and these have been used for studying tenebrionids (Coleoptera) in arid zones (Cepeda-Pizarro, 1989; Alfaro et al., 2009, 2016), they can also be used to capture flying and phytophage insects (Pietruszka, 1980). In all studied pools a high number of Plecoptera (stoneflies) with this sampling method was observed. Although little is known about the biology of these groups in Chile, the aquatic nymphs of these species are dominant components in trophic networks of temperate freshwater ecosystems (Stewart, 2009) and in some cases both their larvae and eggs can survive desiccation as survival strategy in habitats with intermittent conditions (McRoberts and Grubbs, 2021).

In spite of the differences in the number of species reported, the random associations found between species is a result of the presence of many repeated species in the studied sites (Tondoh, 2006; Tiho and Josens, 2007), which is a very frequent phenomenon in the analysis of inland water communities in Chile. The present study is relevant because it is the first to include terrestrial insects, additional to a previous study on aquatic crustaceans (De Los Ríos-Escalante et al., 2019), because both groups probably would have potential interactions that would regulate the presence and absence of the species in each habitat (Vega et al., 2020). However, more detailed studies would be necessary to assess trophic interactions and interspecific competition in these coastal ecosystems.

The analysis based on unified neutral theory of biodiversity showed a number of species so high that each species would virtually be represented by a single individual (Hubbell, 2001; Hankin, 2018). The trend observed in the results is similar to that observed in zooplankton metacommunities in shallow water bodies (Sokol et al., 2015), and to the existence of many repeated species in the studied sites (Rosindell et al., 2015; Overcast et al., 2019).

In conclusion, the results suggest the existence of habitats with high species richness at the contour of ephemeral pools, where the studied pools represent metacommunities with their respective metapopulations. Considering the seasonality of these habitats, the

presence and abundance of species is likely determined by colonization and microhabitat structure around the pools. To better understand the processes and factors influencing on the species inhabiting the studied sites, additional studies including absolute abundances of other invertebrates, such as crustaceans, as well as seasonal studies in other years are needed.

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