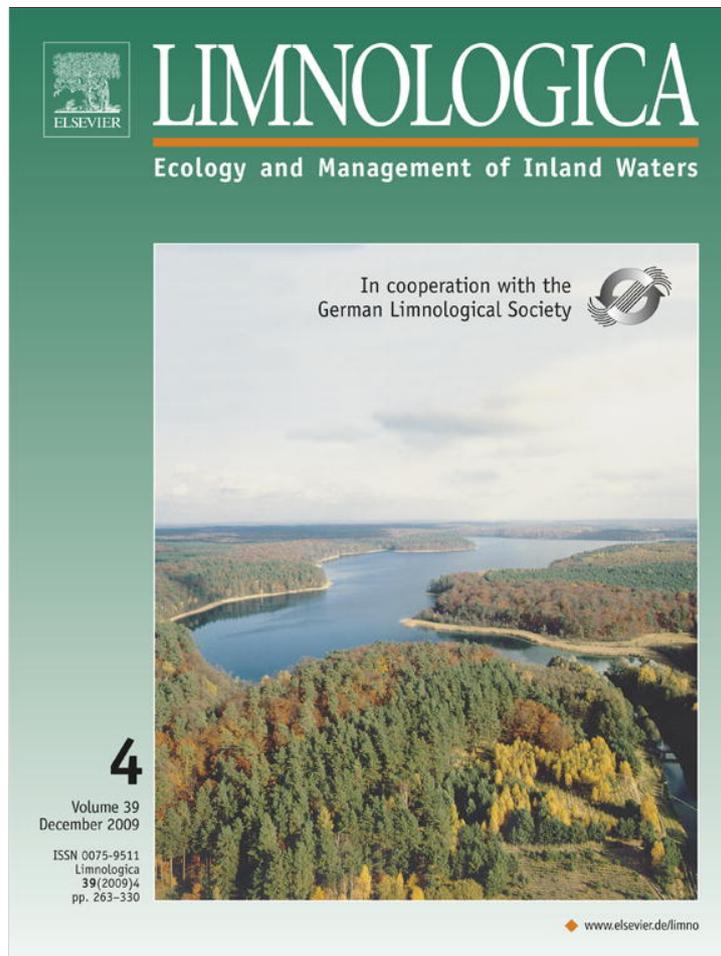


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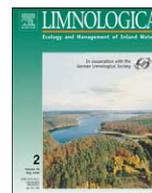
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Nested structure of plankton communities from Chilean freshwaters

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ABSTRACT

1. Nestedness has been recognized as a characteristic pattern of community organization. In a nested metacommunity, species-poor sites are proper subsets of relatively richer sites, implying that the conservation of many poor habitats can be ineffective.
2. Here we compiled the last 30 years of published limnological research on Chilean lakes, in order to determine whether or not species distribution of freshwater plankton communities exhibit a nested structure, and which habitat features best explain the observed biogeographic order.
3. We built presence–absence matrices for diatoms, green algae, blue-green algae, cladocerans, copepods, rotifers, as well as for the grouped phytoplankton and zooplankton. For each matrix, we calculated their degree of nestedness and tested whether or not they differ from matrices assembled according to two alternative null models. From nestedness results, we identified a minimal set of lakes that contain 75% of the regional species pool. After that, we evaluated whether nestedness is maintained when the community structure is organized according to latitude, altitude, area and isolation of lakes.
4. Our analyses reveal that total phytoplankton, total zooplankton, as well as diatom, cladoceran, copepod, and rotifer assemblages of Chilean lakes are not randomly assembled but highly nested. Conversely, green and blue-green algae did not show a clear nested structure. A few sites (3–5) ranked by nestedness for each taxonomic group, covered 75% of the species pool. Finally, we found that surface area and isolation of lakes were the two variables more likely to affect nestedness.

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Introduction

Chilean plankton has been studied over several decades, mainly as part of more inclusive limnological characterizations of water bodies. In spite of a good – albeit dispersed – record of species occurrence across many lakes, up to date we have been unsuccessful in uncovering patterns of species distribution and metacommunity organization of Chilean freshwater biota, and plankton particularly.

It has been recognized that one of the most common biogeographic patterns is nestedness of species assemblages (Fig. 1), where species inhabiting sites with lower species richness tend to be proper subsets of the biotas of richer sites (Patterson and Atmar 1987). Thus, the nested-subset hypothesis has been proposed to account for the observed non-random structure of species composition in metacommunities (Cutler 1991). On the other hand, nestedness has profound implications

for the conservation of species assemblages since the few species present on poor sites can be found everywhere, whereas only richer sites will support uncommon species in need of preservation (Patterson 1987). Therefore, diversity maintenance in nested communities may rest on the conservation of a few rich habitats that contain the full set of species, since a large collection of species-poor sites will hardly contain the entire regional biota.

An added value of nestedness analysis is that it also promotes the generation of new working hypotheses to be tested independently. Ultimately, the main causal forces of a nested distribution of species across sites are differential rates of local colonization and extinction (Lomolino 1996). Therefore, through evaluating nestedness with respect to environmental surrogates of colonization and extinction it becomes possible to postulate causes of the observed distributional pattern, which is helpful for understanding the structuring process of metacommunities.

Although nestedness analysis was initially developed for species distribution on islands and well-delimited land patches (Patterson and Atmar 1987), lake biota is specially well-suited to be studied through this approach given the strong similarities between insular and lentic habitats.

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		A					B				
		1	2	3	4	5	4	1	3	5	2
a	a	1	0	0	1	0	1	1	1	1	1
	b	1	1	1	1	1	1	1	1	0	0
	c	0	0	0	1	0	1	1	0	0	0
	d	1	0	1	1	0	1	0	0	0	0

Fig. 1. Species composition of a perfectly nested metacommunity. Numbered columns represent species and rows represent sites. Presences and absences of a species in a given site are denoted by 1 and 0, respectively: (A) species and sites sorted in an arbitrary order and (B) packed matrix, where nestedness is made evident after reordering species and sites by decreasing incidence and richness, respectively.

After reviewing the primary literature dealing with species composition of Chilean pelagic biota, in this work we use the tools of nested-subset theory (Fleishman et al. 2007; Ulrich and Gotelli 2007) for testing whether or not species distribution of plankton communities in Chilean lakes exhibit a nested structure that differs significantly from randomly assembled units. We also evaluate the usefulness of nestedness analysis for identifying key communities for species protection. Lastly, we test hypotheses about causal association between observed biogeographic nestedness and habitat variables. Particularly, we test whether or not gradients of latitude, altitude, lake surface area, and isolation, constitute possible structuring forces of the observed species distribution pattern.

Methods

Data

We reviewed the published literature from 1973 to 2007 containing reliable information about presence of phytoplankton and zooplankton species in Chilean freshwater lakes. From this database, we extracted for analysis the zone where information was most complete. This zone locates between 33.02° and 46.5° S latitude and comprise 45 lakes (Table 1).

From the distributional data we constructed presence–absence matrices with sites as rows and species as columns. Matrix elements are either ones or zeroes, denoting, respectively, presences and absences of species in sites. A matrix was constructed for each of the following groups: Bacillariophyceae, Chlorophyceae, Cyanophyceae, total phytoplankton, Cladocera, Copepoda, Rotifera, and total zooplankton. Other taxa were ignored because of scarcity of data. From the matrices with total zooplankton and total phytoplankton we deleted sites with species richness below percentile 10, in order to avoid purely anecdotal records.

For each lake we recorded its latitude, altitude, surface area, and isolation. Most data of latitude, altitude and area were obtained either from published information or from the official website of the Dirección General de Aguas de la República de Chile (<http://www.dga.cl>). For a few lakes for which data were unavailable, we measured latitude, altitude and area from georeferenced digital images. Isolation of each lake was measured on the images, as the minimal distance between the focal lake and the nearest large “mainland” lake. The largest 20% of lakes (in surface area), or equivalently those lakes larger than 100 km², were considered to be “mainland” lakes. Ten such lakes fell within this category (Table 1).

Analyses

For each presence–absence matrix we first measured their degree of nestedness by means of the discrepancy index (Brualdi and Sanderson 1999), here represented as d . The index is a counting of the number of discrepancies (absences or presences) that should be erased for obtaining a perfectly nested matrix. This index was preferred because its good statistical properties, such as insensitivity to matrix size, shape, and fill (Ulrich and Gotelli 2007). Nestedness d was calculated after packing the matrix for maximal nestedness. We used two packing algorithms. The first one utilizes a genetic algorithm in order to minimize the matrix disorder or temperature. This algorithm is implemented in the software Binmatnest (Rodríguez-Gironés and Santamaría 2006). The second packing algorithm sorts the matrix by descending row and column totals. This algorithm is implemented in the software Nestedness (Ulrich and Gotelli 2007).

Significance of nestedness was determined through comparing the observed d index value with that of random matrices obtained by two different null models (Bascompte et al. 2003). Null model I is the least conservative one and assumes equiprobability of site occupancy by every species, maintaining the total number of occurrences. In null model II the probability of each site being occupied by a species is proportional to both the site's richness and the species' incidence over sites.

After testing for nestedness, we calculated the cumulative fraction of the regional species pool that occurs over sites ordered according to their rank in the maximally packed matrix. This procedure gives a hierarchy of sites that enclose increasing proportions of the species pool. For testing if this algorithm renders the shortest possible list of sites that include a threshold fraction (75%) of the species, we repeated this calculation for 10,000 random matrices whose lakes were randomly shuffled. The number of lakes containing 75% of the species (L_{75}) was calculated for each of the random matrices and, from this empirical distribution, the fraction of random matrices giving an L_{75} value smaller than that obtained from the packed one (i.e. the significance level) was obtained. These calculations were performed in Matlab 7.3.0.

For causality analyses of nestedness we followed the methods of Lomolino (1996). For this step, we calculated the nestedness index d for each matrix whose sites were previously ordered by decreasing area, increasing isolation, increasing latitude, and increasing altitude. Richness of sites tends to decrease after ordering them in this way. Significance was tested by comparing the observed d value against a distribution of d values calculated for null matrices whose sites were randomly ordered. These analyses were performed with a Matlab code.

Table 1
Names and main characteristics of the sites used for analyses.

	Lake	Latitude (deg S)	Altitude (m.a.s.l.)	Area (km ²)	Isolation (km)	P	Z
1	Rungue	33.016	698	0.48	134.53		23
2	El Plateado	33.077	340	0.02	117.74	113	23
3	Peñuelas	33.167	347	19	106.69	5	52
4	Lo Orozco	33.216	284	0.565	99.58		17
5	Huechun	33.24	577	2.64	134.47		3
6	El Peral	33.504	20	0.158	70.68		14
7	De Aculeo	33.85	350	11.527	57.68	53	8
8	Rapel	34.372	240	137	0	23	25
9	Grande de San Pedro	36.816	18	1.665	275.65	19	
10	Chica de San Pedro	36.841	5	0.82	274.8	118	3
11	Lo Mendez	36.867	80	0.101	272.03	30	3
12	La Posada	36.926	20	0.644	269.41	65	
13	Lanahue	37.916	23	31.9	173.35		19
14	Lleu-lleu	38.159	15	41.442	159.14		11
15	Icalma	38.8	1350	9.901	78.12		5
16	Galletue	38.903	1140	13.075	88.52		5
17	Huilipilun	39.133	335	11.328	8.09		10
18	Caburgua	39.133	505	52.274	22.43	33	13
19	Pichilafquen	39.224	320	0.4	1.3		42
20	Villarrica	39.25	230	175.971	0	45	60
21	Calafquen	39.516	203	120.6	0		25
22	Quillehue	39.566	1200	1.38	40.84		15
23	Pellaifa	39.6	209	7.677	3.97		35
24	Panguipulli	39.716	140	117	0		20
25	Neltume	39.783	186	10	11.94		8
26	Rinihue	39.833	117	77.5	10.37	38	32
27	Pirehueico	39.95	586	30	24.99		10
28	Ranco	40.233	69	443	0	106	25
29	Puyehue	40.666	184	165	0	74	28
30	Rupanco	40.816	118	236	0	84	20
31	Bonita	40.883	290	2.036	2.4		20
32	Todos los santos	41.1	189	178.5	0		22
33	Llanquihue	41.133	51	870	0	52	41
34	Chapo	41.45	241	45	26.94		3
35	Cucao	42.633	10	10.6	178.72	6	9
36	Huillinco	42.653	13	19.1	175.65	7	12
37	Tarahuin	42.725	66	7.7	175.18	9	14
38	Tepuhueico	42.775	25	14.3	188.24	5	14
39	Natri	42.78	39	7.8	186.16	8	12
40	Riesco	45.5	15	15.041	117.28		2
41	Polux	45.666	679	8.453	80.91		4
42	Atravesado	45.7	290	9.113	79.77		4
43	Elizalde	45.766	225	24.829	75.63		4
44	Chiguay	45.986	969	0.09	47.21		3
45	General carrera	46.5	215	1892	0		5

P and Z represent number of species of phytoplankton and zooplankton, respectively. Lakes in boldface are the largest ones (> 100 km²), considered as mainlands.

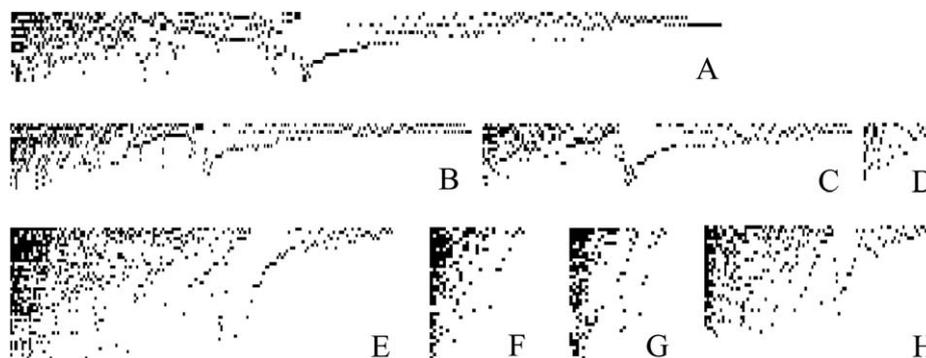


Fig. 2. Presence-absence matrices for the plankton groups studied here, packed with Binmatnest algorithm: (A) total phytoplankton, (B) Bacillariophyceae, (C) Chlorophyceae, (D) Cyanophyceae, (E) total zooplankton, (F) Cladocera, (G) Copepoda, and (H) Rotifera. Columns and rows contain species and lakes, respectively; filled cells represent presences.

Results

The presence-absence matrices of the analyzed groups are shown in Fig. 2, with sites as rows and species as columns. The shown

matrices were previously packed to maximal nestedness by the Binmatnest's algorithm (Rodríguez-Gironés and Santamaría 2006).

In general terms, zooplankton groups were found to be highly nested, whereas the structure of phytoplankton communities was

less definite. Total phytoplankton and diatoms show a highly significant ($P < 0.001$) nested structure under the two null models and the two packing algorithms used here (Table 2). On the other hand, green algae showed a clear nested structure only in comparison with the null model I, but marginally significant under null model II. Blue-green algae showed to be weakly nested since presented a marginally significant nestedness only under the least conservative null model I.

The analysis of zooplankton groups showed a highly significant nestedness structure ($P < 0.001$) in all groups, under both null models and packing algorithms (Table 2).

Overall, zooplankton groups as well as diatoms show consistent evidence of being highly nested, while green and blue-green algae tend to exhibit nestedness only under the most liberal null model I.

In Table 3A, we show the list of sites ranked by nestedness that enclose increasing proportions of the regional phytoplankton species pool, up to overcome a threshold of 75%. When total phytoplankton was analyzed, it was found that five lakes contained 79% of the phytoplankton species. For diatoms, 80% of the species pool was found into three lakes. Five lakes contained 78% of green algae species and five lakes covered 76% of blue-green algae species. Although nestedness was far to be perfect in the tested phytoplankton communities, the hierarchy of lakes obtained from the maximally nested matrices offered a shorter list of lakes covering 75% of the regional species pool, compared with null matrices whose sites were randomly ordered ($P < 0.01$).

For total zooplankton, a group of five lakes hosted 77% of the regional species pool (Table 3B). Only three lakes included 79% of cladoceran species, five lakes contain 81% of copepod species, and four lakes covered 76% of rotifer species.

Causality analyses of nestedness revealed that both isolation and lake area were the variables that best explained the observed nestedness pattern of total phytoplankton, green algae, rotifers, and cladocerans ($P < 0.05$) and even more markedly for total zooplankton and copepods ($P < 0.01$) (Table 4). Latitude and altitude did not contribute to explain nestedness, with the

Table 2
Basic matrix description and nestedness d testing for phytoplankton and zooplankton.

Phytoplankton				
	Total phytoplankton	Diatoms	Green algae	Blue-green algae
Species	482	271	151	29
Sites	19	19	18	16
% Fill	10.35	10.84	10.23	11.64
d (A)	613	324	177	34
I	***	***	***	*
II	***	***	*	
d (B)	603	325	209	33
I	***	***	*	*
II	***	***		
Zooplankton				
	Total zooplankton	Rotifers	Cladocerans	Copepods
Species	164	104	29	31
Sites	42	31	39	39
% Fill	10.47	11.01	16.27	15.05
d (A)	368	188	69	85
I	***	***	***	***
II	***	***	***	***
d (B)	351	184	58	72
I	***	***	***	***
II	***	***	***	***

A indicates the results obtained from the matrices packed by the Binmatnest's algorithm, while B indicates the results from the matrices packed by the Nestedness' algorithm (see text for details). Significance level was calculated using 2000 random matrices (see text for details). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 3
First Lakes ranked by their position in the maximally packed matrices, and the cumulative fraction of the regional phytoplankton (A) and zooplankton (B) species pool they contain (up to 75%).

A. Phytoplankton							
Total phytopl.**	Diatoms***		Green algae**		Blue-green algae**		
El Plateado	0.25	C. de San Pedro	0.39	La Posada	0.29	Rupanco	0.28
C. de San Pedro	0.48	El Plateado	0.64	El Plateado	0.50	Puyehue	0.45
Ranco	0.64	Ranco	0.80	Rupanco	0.64	Ranco	0.55
Rupanco	0.72			Llanquihue	0.72	Llanquihue	0.62
La Posada	0.79			Ranco	0.78	La Posada	0.76
B. Zooplankton							
Total zoopl.***	Cladocerans***		Copepods**		Rotifers***		
Villarrica	0.37	Peñuelas	0.45	Villarrica	0.58	Peñuelas	0.34
Peñuelas	0.59	El Plateado	0.66	Puyehue	0.68	Villarrica	0.59
Llanquihue	0.65	Pichilafquén	0.79	Llanquihue	0.71	Llanquihue	0.68
Pichilafquén	0.73			Pellaifa	0.74	Pichilafquén	0.76
Pellaifa	0.77			Rapel	0.81		

Significance level of the L75 (number of lakes containing 75% of the species) obtained from maximally nested matrices (Binmatnest's algorithm) was calculated using 10000 random matrices (see text for details). ** $p < 0.01$, *** $p < 0.001$.

exception of cladocerans respect to latitude. On the other hand, diatoms and blue-green algae did not exhibit nestedness under any site ordering tested here.

Discussion

Our results support that most – albeit not all – groups tested here showed strong evidence of possessing a nested distributional structure.

Nested species incidences have been reported widely for terrestrial patchy habitats such as fragmented forests and archipelagos (Wright et al. 1998; Honnay et al. 1999). Nevertheless, analyses on freshwater plankton communities are relatively scarce and often show that nestedness is weaker. In fact, the extensive study of Wright et al. (1998) indicated that small aquatic organisms exhibit a lower degree of nestedness than other taxa. Likewise, Boecklen (1997) show that only two out of four analyzed zooplankton assemblages exhibit a nested-subset structure, and Fontaneto et al. (2005) found that the occurrence of nestedness in stream rotifers depends on the spatial scale of observation. On the other hand, nestedness in entire freshwater communities has also been reported (Srinivasan et al. 2007).

Here we show that species distribution of some groups of freshwater phytoplankton, particularly diatoms, exhibits a significantly nested structure. Conversely, green and blue-green algae do not exhibit a nested distribution under the more conservative null model II. On the other hand, our results show that zooplankton exhibit a marked nested distribution in Chilean freshwaters.

A nested distributional pattern implies that poorer sites are proper subsets of richer sites and therefore, conservation practices should focus on a few rich lakes in order to protect plankton communities (De Meester et al. 2005). The protection of non-nested groups, on the other hand, requires preserving a larger set of smaller areas that include the bulk of species.

In perfectly nested metacommunities, the richest site contains the complete set of species. In contrast, real imperfectly nested metacommunities could contain poor sites with particular species

Table 4
Nestedness d after ordering sites by the tested variable (area, isolation, latitude, and altitude).

	Total phytoplankton	Diatoms	Green	Bluegreen	Total zooplankton	Rotifers	Cladocerans	Copepods
Area	678*	397	199*	38	442*	223*	94*	92**
Isolation	679*	396	198*	39	443*	224*	95*	93**
Latitude	709	390	216	44	494	250	94*	111
Altitude	773	421	257	45	512	275	113	106

Significance was calculated using 2000 runs (see the text for details), and symbols represent: * $P < 0.05$, ** $P < 0.01$.

compositions, that combined with the species set of other sites could encompass a large fraction of the regional pool. Therefore, it is not self-evident that in real systems, the hierarchy of sites obtained from maximally nested matrices informs about the minimal number of sites needed to be conserved in order to protect the entire or a large fraction of the species pool. Here we tested this assumption through comparing the cumulative distribution of species across sites ordered by their nestedness rank, versus sites ordered at random. Our results revealed that the observed nested structure is informative respect to which sites are sufficient for including 75% of the species. The number of critical sites spanned from three to five in every group (Table 3), with a total of 12 lakes identified as core habitats for the groups analyzed here. Although not accurately tested, our results suggest that nestedness ranking could provide an acceptable solution to the minimum area problem (Cabeza and Moilanen 2001) directed towards site selection for reserve networks design (Pressey et al. 1993; Margules and Pressey 2000; Cabeza and Moilanen 2001). It is interesting to highlight that only one out of the 12 core lakes (Peñuelas) is located within a protected area.

It is seldom possible to know the exact mechanism driving the observed distributional pattern from mere presence-absence data. Nested-subset patterns should ultimately result from selective extinctions, selective colonization, or both (Wright et al. 1998). Based on plausible associations between some landscape attributes and colonization/extinction rates, we could advance towards unmasking causal mechanisms of nestedness through identifying one or more environmental variables likely to affect the observed biogeographic order.

Our analyses revealed that surface area and the degree of geographic isolation of lakes are both good candidates for explaining the observed nested structure of plankton communities. Nevertheless, the strong nested pattern exhibited by diatoms remained unassociated to any possible cause (Table 4).

Given that area and isolation are correlated (Spearman rank correlation, $p < 0.05$), they should be treated as a single variable. Thus, our results indicate that smaller, more isolated lakes tend to contain a subset of the species found in larger, more connected lakes. On the other hand, since latitude (as a surrogate of climate) did not show to exert any effect on nestedness, the mechanisms behind the observed distributional pattern for nested groups are more likely to be differential colonization success and differential local persistence. Dispersal ability, defined by the biology of each group, and geographic constraints such as isolation are main components of colonization success. On the other hand, ecological factors such as resource or nutrient limitation and predation pressure constitute main biotic determinants of population abundance and persistence in freshwaters (Lampert 1987). A nested pattern was observed in plankton communities by Declerck et al. (2007), who found that high-productivity systems contained fewer species which were subsets of larger species pools from lower productivity communities. Decreased richness at high productivity was suggested to be a product of the dominance of *Daphnia*, which excluded phytoplankton species through consumption and outcompeted other herbivores.

While isolation was associated to nestedness according to our analyses, it is likely that plankton distribution across Chilean lentic systems be structured through differential colonization. On the other hand, area is positively correlated with depth in Chilean lakes (Spearman rank correlation, $p < 0.05$ from data of Table 1 in Geller 1992). Larger lakes offer a variety of habitats since, besides the horizontal gradient, there often exist a strong vertical structuring where physical and chemical clines could support plankton diversity through permitting habitat and resource partitioning, as well as avoidance of predators (Keller and Conlon 1994; O'Brien et al. 2004). Thus, other things being equal, larger lakes should contain richer species sets through decreased extinction, whereas less isolated lakes should also contain richer species sets but through increased colonization success. Our analyses, nevertheless, were unable to discriminate which specific mechanisms are responsible for the emergence of nestedness in our study system.

A number of geological, chemical, physical, and biological variables could not be presently tested as possible drivers of plankton metacommunity nestedness due to the lack of consistent data. Among those variables, it is worth mentioning the age of the water body. There is evidence that older lakes present a poorer pelagic biota due to slow elimination of supernumerary species (Dumont 1994). The set of lakes considered in this work include both natural and man-made water bodies of different age, although it is still unknown for most of them their date of origin. A rough view to our nestedness results indicates that relatively younger lakes such as El Plateado and C. de San Pedro present a richer phytoplankton biota, whereas older lakes such as Villarrica, Puyehue and Llanquihue present higher zooplankton richness. No evident association can be outlined between nestedness and age with the available data, although a closer look at the taxon-specific relationship between lake age and plankton diversity would shed light on the historical determinants of community structure. Revealing the importance of this structuring force for the emergence of the nested pattern observed in Chilean lakes, as well as the role of productivity, chemical features, and human perturbations, are challenging avenues for future research.

A possible limitation of this work relies on the uncertain quality of data. Some records are likely to be incomplete and taxon-biased. Nevertheless, we have intended to minimize this source of error through considering only the geographic range for which the most complete and continuous record of species' distribution was possible to compile from the scientific literature. Moreover, the number of specialists that authored the compiled articles is relatively reduced, and this also favored homogeneity of species identification effort.

After revealing a non-random, nested structure of species distribution of zooplankton and some groups of phytoplankton, as well as through presenting some consequences of nestedness for reserve selection together with possible mechanisms behind the structure, we expect that this work will serve as starting point for future empirically oriented studies, as well as a guide for regional freshwater conservation planning.

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