# **Co-occurrence of lemnids in Argentina: a null model analysis**

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ABSTRACT: Sixteen pleustonic species from northern Argentina were examined for co-occurrence. A set of 156 relevés was used in the null model analysis. Presence-absence date was taken into account. The results suggest that the species combinations found in the sample analyzed may be treated as random. In this respect, pleustonic assemblages from the Argentine correspond to those from Poland.

KEY WORDS: species co-occurrence, lemnids, Argentina, null model analysis

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### INTRODUCTION

In community ecology, null models are useful tools for examining observed community patterns. In this approach, the null hypothesis that the species combinations found are random subsets of a set of potentially available species is tested. To falsify this hypothesis, random species combinations (so-called null communities) are generated by means of computer simulation. Next, the simulated combinations are compared with the observed ones. Different null model algorithms, simulation procedures and co-occurrence indices have been invented to accomplish this task (Gotelli 2000).

Null models were introduced into community ecology over fifty years ago, but their development has progressed rapidly, especially since a paper by Connor and Simberloff (1979). This paper also started a debate on the philosophical basis of null model analysis which has lasted over 20 years, and no end to this controversy in sight (Wołek 1997; Gotelli 2000). In spite of this, more and more ecologists realize the need to confront actual data with null model predictions, as may be observed from year to year in ecological journals.

The present paper deals with the co-occurrence of lemnids or pleustonic plants in northern Argentina. Landolt and Zarzycki (1994) investigated these plants and came to the conclusion that there were some pleustonic associations *sensu* Braun-Blanquet (class *Lemnetea*) having their own characteristic species combinations. Some years ago, Professor Kazimierz Zarzycki egged the senior author on to analyze the Argentinean data for co-occurrence by the null model method. He is very pleased that he can do so now.

### $M {\rm ATERIAL} \ {\rm AND} \ {\rm METHODS}$

Sixteen pleustonic species from the Argentine were examined for co-occurrence (Table 1). A set of  $n_r = 156$  relevés kindly placed at the senior author's disposal by Professor K. Zarzycki was used in the study. The relevés were made by means of the Braun-Blanquet method in all bodies of water in which the species considered were found (K. Zarzycki, pers. comm.). Only presence-absence data were employed. Other plants occurring in the examined relevés were omitted.

**Table 1.** Species and their proportions in the null model pool.  $S_i$  – sum for matrix row i (= species i); p – probability calculations for the null model algorithm (SIMULATION 1); N – matrix total.

No.	Species considered	$S_i$	$p = S_i / 804$
1	Lemna minuscula Herter	101	0.126
2	Azolla caroliniana Willd.	87	0.108
3	Pistia stratiotes L.	73	0.091
4	Wolffiella lingulata (Hegelm.) Hegelm.	67	0.083
5	Salvinia minima Baker	61	0.076
6	Wolffiella oblonga (Phil.) Hegelm.	57	0.071
7	Wolffia columbiana Karsten	52	0.065
8	Lemna gibba L.	50	0.062
9	Ricciocarpus natans (L.) Corda	49	0.061
10	Spirodela intermedia W. Koch	47	0.058
11	Lemna valdiviana Phil.	37	0.046
12	Salvinia herzogii de la Sota	32	0.040
13	Wolffia brasiliensis Weddell	30	0.037
14	Azolla filiculoides Lam.	30	0.037
15	Lemna aequinoctialis Welwitsch	20	0.025
16	Salvinia auriculata Aubl.	11	0.014
Total		N = 804	1.000

All relevés were analyzed for the shared appearance of the species in question. The observed species combinations and their occurrence frequencies or recurrence in the set examined are presented in Table 2. These data became the basis for further investigations.

As a rule, presence-absence data are presented in the form of a presence-absence matrix. In such a matrix, the rows are species and the columns are sites or, in our case, relevés. Using the information contained in the data matrix, nine different null models can be constructed, and it depends only on how the row and column sums are treated – as fixed, equiprobable or proportional (Gotelli 2000). The null model applied in this study was based on the assumption that the rows are proportional and the columns equiprobable. This means, respectively, that (1) the species differ in occurrence and the probabilities of species occurrences are proportional to the observed row sums and (2) the sites do not differ in suitability. A detailed description of the model and simulation procedure is given in Wołek (1997). The proportions or probabilities of the species under consideration are shown in Table 1.

**Table 2.** Frequencies of occurrence of the unique k-species combinations observed ( $f_u$ ), found in the set of  $n_r = 156$  relevés, and null ( $f_u^*$ ), generated during SIMULATION 1 (1) and SIMULATION 2 (2). Only the null combinations identical with the observed ones are presented. The numbers 1, 2, 3, ..., 16 represent the species examined as in Table 1. In SIMULATIONS 1 and 2, mean values ( $f_u^*$ ) were calculated over 10 iterations of the simulation algorithm. Any significant deviation of the frequencies observed from the expected by chance are marked \*. For SIMULATION 3, only the simulated species combinations identical to the observed ones are presented and marked ×. For 2-species combinations (18 relevés) 45 iterations of the algorithm were run, and for 3-species combinations (25 relevés) 38 iterations. In this way, 810 and 950 null combinations were simulated, respectively.

Combinations	No							S	Speci	es no	).							fu		fu*	
(relevés)	110.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	ju	1	2	3
	1	1																2	5.0*	3.1	
1-species	2		2															6		6.2	
	3								8									2		3.0	
	1	1	2	 														2	1.0*	2.0	×
	2	1		 3														2	2.6	1.6	×
	3	1		 					8									4	1.0*	4.2	×
	4		2	 												15		2			×
<b>a</b> i	5			 3	4													2		1.8	×
2-species	6			 3			6											1	2.0		×
	7			 		5										15		1			×
	8			 					8		10							1			×
	9			 					8			11						1			×
	10			 					8						14			1			×
	11										10					15		1			×
	1	1	2	 3														2		2.2	×
	2	1	2	 					8									1			×
	3	1	2	 									12					1			
	4	1		 3							10							1	1.0	1.0	×
	5	1		 		5									14			1			×
	6	1		 			6	7										1		2.0	×
	7	1		 				7						13				1			=
	8	1		 					8						14			3		1.8	×
3-species	9		2	 3	4													1			=
o species	10		2	 3												15		2			×
	11		2	 		5		7										1			×
	12		2	 		5				9								1	1.0		
	13		2	 		5					10							1			×
	14		2	 						9						15		1			
	15			 3					8						14			1			×
	16			 3							10					15		2			×
	17			 		5	6					11						1			
	18			 				7	8						14			2			×
	19								8					13	14			1			
	1	1	2	 3		5												1			=
	2	1	2	 3									12					1			=
4 .	3	1	2	 	4					9								1			=
4-species	4	1	2	 2				7						13				1		1.0	
	5	1		 3				7							14			1		1.0	=
	6	1		 	4			-		9					1.4	15		1			=
	7	1						7	8						14			1			

(cont.)

Combinations	No							S	Speci	ies no	0.							fu		fu*	
(relevés)	10.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	ju	1	2	3
	8	1							8	9					14			1			
	9		2					7	8						14			1			=
	10			3	4		6					11						1			=
4-species	11			3	4			7				11						1			=
	12			3		5		7		9								1			
	13				4	5						11	12	10				1			
	14							.7	8		10			13	14			2			=
	15	1	2	2	4	5				9	10			13	14			1			
	1	1	2	3	4	Э			0		10							1			=
	2	1	2	3	4			7	0		10		12					1			
	4	1	2		4					9			12	13				1			
	5	1		3	4	5	6			· · · · ·				15				1	1.0		
5-species	6	1		3	4	5	6				10							1	1.0		
	7	1		5	4	5	0				10			13			16	1			=
	8		2	3	4	5	6											1		1.0	
	9		2			5	6					11	12					1			
	10			3	4	5			8								16	1			=
	1	1	2	3	4	5	6											1		2.0	
	2	1	2	3	4		6	7										1			
	3	1	2	3	4			7		9								1			
	4	1	2	3	4				8			11						1			
	5	1	2	3	4					9	10							1			
	6	1	2	3		5					10		12					2			
	7	1	2	3		5					10			13				1			
	8	1	2	3			6	7	8									1			
	9	1	2	3			6			9					14			1			
	10	1	2		4	5	6					11						1			
	11	1	2		4	5		7					12					1			
6-species	12	1	2		4			7						13		15		1			
	13	1	2		4					9				13			16	1			
	14	1	2			5	6				10	11						1			
	15	1	2			5	6				10		12					1			
	16	1	2				6		8				12		14			1			
	17	1		3	4					9	10	11						1			
	18	1				5	6	7				11	12					1			
	19	1						7	8	9	10							1			
	20		2	3		5	6					11	12					1			
	21		2	3			6	7				11				15		1			
	22		2		4	5	6					11	12					1			
	23			3	4	5	6	7				11						1			
	24				4		6			9		11		13			16	1			
	1	1	2	3	4	5	6			9								1			
7-species	2	1	2	3	4	5	6						12					1			
/-species	3	1	2	3	4		6		8			11						1			
	4	1	2		4		6	7	8					13				1			

Table 2. Continued.

Table 2. Continued.		
Species no.	£,	fu*

Combinations	No.							S	Speci	es no	).							fu		fu*	
(relevés)		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	J	1	2	3
	5	1		3	4	5	6	7	8									1			
	6	1		3	4	5		7			10					15		1			
	7	1		3	4	5		7			10						16	1			
	8	1		3	4	5				9	10		12					1			
7-species	9	1		3	4	5				9		11	12					1			
	10	1			4			7	8	9				13	14			1			
	11	1					6	7	8			11		13	14			1			
	12		2	3		5	6		8	9						15		1			
	13		2		4	5	6			9		11		13				1			
	1	1	2	3	4	5	6			9		11						1			
	2	1	2	3	4	5		7			10		12					1			
	3	1	2	3	4	5				9	10		12					1			
	4	1	2	3	4		6	7	8				12					1			
	5	1	2	3	4			7	8			11				15		1			
	6	1	2	3	4					9	10					15		1			
	7	1	2	3			6	7	8			11		13				1			
	8	1	2		4	5	6	7	8			11						1			
	9	1	2		4	5	6			9	10		12					1			
	10	1	- 2		. 4	5		7		9	10						16	2			
8-species	11	1	2		4	5				9	10		12			15	16	- 1			
	12	1		3	4	5	6	7	8		10		12		14	10	10	1			
	13	1		3	4		6	7	8				12		14			1			
	14	1		3		5	6	7	0	0	10		12	13	14			1			
	15	1		5		5	6	' 7	Q	0	10			13	14			1			
	15	1					6		0	2	10	11		12	14			1			
	10	1	2	2			6		0	9	10	11		13	14			1			
	1/		2	2	4	~	0	/	0	0	10	11	10	15				1			
	18		2	3		د ح	6			9	10	11	12	10				1			
	19		2		4	2	6			9	10	11	10	13				1			
	20		2		4	5	6			9		11	12	13				1			
	21		2		4		6			9		11		13		15	16	1			
	1	1	2	3	4	5	6			9	10	11						1			
	2	1	2	3	4	5	6			9	10		12					1			
	3	1	2	3	4	5	6				10	11	12					1			
	4	1	2	3	4	5		7		9	10	11						1			
	5	1	2	3	4	5		7		9	10					15		1			
9-species	6	1	2	3	4	5		7			10		12				16	1			
L.	7	1	2	3	4		6	7	8				12	13				1			
	8	1	2	3		5	6	7	8	9	10							1			=
	9	1	2	3			6			9		11	12	13		15		1			
	10	1	2			5	6		8	9	10	11			14			1			
	11	1		3	4	5		7		9	10	11	12					1			
	12	1				5	6		8	9	10	11		13	14			1			
10	1	1	2	3	4	5	6	7		9	10		12					1			
10-species	2	1	2	3	4	5		7		9	10		12				16	1			

The null hypothesis ( $H_0$ ) that the observed frequency of a k-species combination is random was tested. Null combinations were generated with the help of a stochastic null model and then the observed frequency of a given species combination was compared with the random one. If the frequencies compared were in agreement, the null hypothesis was accepted. Otherwise it was rejected in favor of the alternative hypothesis that the tested species combination is nonrandom.

Agreement between the simulated and observed frequencies for a given individual species combination was estimated according to Wołek (1988). Practically, all simulated frequencies were contained within a range of  $\pm 3\sigma$  around the arithmetic mean, so  $H_0$  was accepted if the frequency of an actual species combination was within this range; if it was outside the range,  $H_0$  was rejected. This means that  $H_0$  was accepted or rejected at significance level  $\alpha = 0.0027$  (two-tailed test). Tenfold simulation was used because for our purposes it seemed quite sufficient to assess the differences between the generated and observed frequencies.

Actual data were also analyzed for co-occurrence with the help of the null model procedures and co-occurrence indices outlined by Gotelli (2000). All four co-occurrence indices were applied: (1) number of species pairs forming perfect checkerboard distributions, coded here as CHECKER (Diamond 1975); (2) checkerboard score, coded as C-score (Stone & Roberts 1990); (3) variance ratio, coded as V-ratio (Robson 1972; Schulter 1984); (4) number of unique species combinations, coded as COMBO (Pielou & Pielou 1968). Two null model algorithms were used: SIM2 (row sums fixed, columns equiprobable), recommended by Gotelli (2000) for analyzing "sample lists" or incomplete lists of species; and SIM4 (row sums fixed, columns proportional). SIM2 is not to prone to Type I error; it behaves very well with all four co-occurrence indices. In this respect, SIM4 behaves well for indices V-ratio and COMBO. SIM7 (rows proportional, columns equiprobable) was used because this procedure was based on the same restrictions as the senior author's null model algorithm. All analyses employed EcoSim, an application of null model software (Gotelli & Entsminger 1999).

The definitions of the terms used in this paper are given below. They follow Wołek (1997).

*Co-occurrence*: this term means that the species examined occur together in a relevé.

*Null or random combination:* a combination assembled randomly from potentially available species following a given null model algorithm.

**Species combination**: the species composition of a pleustonic assemblage registered in a given relevé. According to the theory of combination, any subset consisting of k-species drawn in any sequence from the *n*-species set is a k-species combination from the set of *n*-species  $(n \ge k)$ . In this context, the term "unique or different species combinations" means combinations that differ from the other ones in at least one of the species under study. The species combination is interpreted as a pleustonic assemblage.

### RESULTS AND DISCUSSION

#### Null model analysis by the senior author's method

The species combinations found in the relevés are presented in Table 2. It may be seen from the table that 130 of the 156 observed combinations were different. It is also evident that the combinations consist of no more than 10 pleustonic species. Neither 11-, 12-, ..., nor 16-species combinations were found in the set of relevés.

SIMULATION 1. This simulation was done with the model assuming that species disperse randomly and independently of one another and that the species compositions and occurrence frequencies of the observed combinations depend only on the occurrence proportions of the potentially available species in the pool (Model 1). The proportions of the species are shown in Table 1.

		SIMUL	ATION 1		
<i>k</i> ( <i>n</i> = 16)	$f_k$	$f_k^*$	F <sub>u</sub>	$F_u^*$	F <sub>id</sub>
1	10	15.7	3	6.7	1
2	18	23.3	11	17.8	4
3	25	24.9	19	24.9	2
4	16	24.4	15	24.2	0
5	10	25.2	10	24.6	1
6	25	20.9	24	19.0	0
7	13	8.8	13	8.8	0
8	25	5.9	21	5.9	0
9	12	2.9	12	2.9	0
10	2	3.4	2	3.4	0
11	0	0.6	0	0.6	0
Total	156	156.0	130	138.8	8

**Table 3.** SIMULATION 1: number of null *k*-species combinations falling in each category of *k*, compared with the number of observed ones.

k – number of species occurring in a relevé (= combination), where k = 1, 2, ..., n species;

n – maximum possible number of species in a relevé;

 $f_k$  – frequency of k-species relevés (= observed combinations), where k = 1, 2, ..., n species per relevé;

 $f_k^*$  – frequency of simulated k-species combinations (means calculated over ten iterations of the simulation algorithm);  $F_\mu$  – number of observed unique k-species relevés;

 $F_{u}^{*}$  – number of simulated unique k-species combinations (means calculated over ten iterations of the simulation algorithm);

 $F_{id}$  – number of simulated null combinations identical to observed ones with respect to species composition, found in the sample of random species combinations generated during ten iterations of the simulation algorithm.

The null model algorithm was run 10 times, with 156 null combinations generated per program run, yielding a total of 1560 random combinations. These results are summarized in Tables 2 and 3. The results may be interpreted as follows.

In the group of null simulated combinations there were only 8 combinations identical to the observed ones in respect of species composition (Table 3). The occurrence frequencies of these identical combinations, null and observed, are in disagreement (Table 2).

The expected frequencies of k-species combinations  $(f_k^*)$  are in disagreement with the observed ones  $(f_k)$  [one-sample chi-square test;  $\chi^2 = 87.3 > \chi^2$  (0.001; 8)]. There was also a distinct difference between the number of different combinations observed  $(F_u)$  and simulated  $(F_u^*)$  in individual categories of k (Table 3).

From the formal point of view, the results warrant rejection of the null hypothesis in favor of the alternative one stating that the observed frequencies of species combinations are nonrandom. This means that the species in question are not independent of each other: some species combinations may be rarer and some more frequent than expected by chance. Before we accept such a conclusion, however, may the analyzed set really be treated as a representative sample?



**Fig.1**. Frequency of k-species relevés (= observed combinations), where k = 1, 2, 3, ..., 16 species per relevé, found in the set of  $n_r = 156$  relevés.

The proportions of relevés with k = 1, 2, ..., n lemnid species are presented in Figure 1. Two important conclusions may be inferred from this figure.

(1) The frequency distribution of the relevés is approximately symmetric. This finding contrasts with Wołek's (1997) observations: in the field, the frequency pattern of the number of Polish lemnid species per relevé (= combination) was consistently right-skewed.

(2) The shape of the distribution of observed proportions of the relevés is irregular to an extent than cannot be explained by statistical fluctuation. If one assumes that the frequency distribution of the number of lemnid species per relevé reflects the actual frequency pattern in lemnid communities in Argentina, it must be concluded that the three-, six- and eight-species communities are the most frequent, whereas the one- and five-species communities are the rarest.

It is hard to believe that (*i*) Argentinean lemnids reflect quite a different pattern of frequency distributions of *k*-species combinations from the Polish ones, and that (*ii*) certain ecological forces eliminate 5-species combinations in particular, in favor of 6-, 7-, 8- and even 9-species ones. As seen from Table 2, 5-species combinations are composed of the same species as the combinations mentioned above. Another explanation seems rather more probable. It is suggested here that although K. Zarzycki and E. Landolt endeavored to compile a statistically reliable sample of relevés (see Material and Methods), it is biased and thus cannot be treated as a representative in terms of the statistical population of combinations of Argentinean lemnids. It is very probable that some species are absent from some *k*-species categories – see, for example, the class of 1-species combinations. There are one-species combinations of *Lemna minuscula*, *L. gibba* and *Azolla caroliniana* in the class, but the other 13 species are absent from it. Because these circumstances arose from selective sampling, such additional information

should be incorporated into the null model. It is not our intention to assert that none of these 13 species can form 1-species assemblages in the field. We only want to say that 1-species assemblages (= combinations) of these species were not found in the sample analyzed. That is why such information must be taken into account.

Irregularities similar to the 1-species combinations were found in the other categories of k-species combinations. In none of them were all species observed to be potentially available in the pool (see Table 2). It was therefore necessary to estimate the probability of occurrence of each species in each class of 1-, 2-, ..., and 10–species combinations and incorporate this additional information into the null model algorithm. In this way the second version of the model was constructed and a second simulation was run, in which null combinations were generated for each k-species combination category individually.

SIMULATION 2. The random and observed combinations are presented in Table 4. It shows that a distinct progression was obtained, compared with the earlier simulation (Table 3). The random frequency distribution ( $f_k^*$ ) was in close agreement with the observed one ( $f_k$ ) [one-sample chi-square test;  $\chi^2 = 5.63 < \chi^2$  (0.05; 8)] and the number of different null combinations ( $F_u^*$ ) falling in each category of *k* corresponds to the number of observed combinations ( $F_u$ ) (Table 4). Agreement between the frequencies of occurrence of identical combinations, null and observed, was also closer (Table 2), but the number of identical combinations was still small, although some new identical combinations appeared.

How should this result be interpreted? We arrive at two inferences: (1) the observed frequencies of different k-species combinations are nonrandom and were likely due to ecological factors; (2) the small number of random combinations identical to the observed ones means that the observed combinations were determined by biotic factors, probably by interspecific competition.

		Simui	LATION 2		
<i>k</i> ( <i>n</i> = 16)	$f_k$	$f_k^*$	$F_u$	$F_u^*$	F <sub>id</sub>
1	10	12.3	3	3.0	3
2	18	24.8	11	10.4	4
3	25	21.0	19	11.0	4
4	16	18.1	15	13.2	1
5	10	10.5	10	8.3	1
6	25	25.8	24	13.9	1
7	13	11.7	13	8.6	0
8	25	21.9	21	12.4	0
9	12	9.9	12	8.3	0
10	2	0.0	2	0.0	0
Total	156	156.0	130	89.1	14

**Table 4.** SIMULATION 2: number of null *k*-species combinations, falling in each category of *k*, compared with the number of observed ones. For detailed explanations see Table 3.

Before we accept such explanations of the floristic structure recorded in those relevés, let us calculate how many different combinations consisting of 1, 2, ..., 16 species may be obtained from the pool of the 16 potentially available species. The results of these calculations are presented in Table 5. As can be seen, the theoretical numbers are gigantic even though only 16 species are considered. The outcome of SIMULATION 2 suggests that the numbers of k-species combinations and their frequencies may be due to chance. As to the identical combinations, we should consider the huge number of different theoretically possible k-species combinations (see Table 5) and the small sample of the total number of random combinations simulated,  $n_s = 1560$ . In this context it is not hard to understand why it is so difficult to hit a given combination, especially a multispecies one. Realization of certain observed species combinations randomly will be difficult for reasons resulting from the theory of probability itself. It seems evident, therefore, that the small number of identical species combinations, observed and expected, results from (1) the small number of null combinations simulated; (2) the low probability of random realization of some combinations; and (3) the great number of different theoretically possible species combinations. The more the species combinations simulated, the greater the number of null species combinations identical to the observed ones.

SIMULATION 3. To confirm this supposition, the third simulation was performed using the second version of the null model. By way of example, the simulation was carried out for the 2- and 3-species combinations only. For 2-species combinations the number of potentially available species in the pool was 11 (some species were absent from the

combination, wl	here $k = 1, 2,,$	, <i>n</i> species; $n - \max$	um possible number of	species in a combination	on; $p_k$ – probability of
occurrence of a	subset of k-spe	cies combinations; pse	election - probability of	occurrence of any com	vination belonging to
given category of	of k-species con	ibinations, e.g., the pro	bability of any 1-speci	es combination equals	1/16 = 0.0625.
	1.	"Ch			

Table 5. Number of different theoretically possible k-species combinations calculated for n = 16. k – number of species per

k	nCk	$\mathbf{p}_k$	$p_{selection}$
1	16	0.00024	0.062500
2	120	0.00183	0.008333
3	560	0.00854	0.001786
4	1820	0.02777	0.000549
5	4368	0.06665	0.000229
6	8008	0.12219	0.000125
7	11440	0.17456	0.000087
8	12870	0.19638	0.000078
9	11440	0.17456	0.000087
10	8008	0.12219	0.000125
11	4368	0.06665	0.000229
12	1820	0.02777	0.000549
13	560	0.00854	0.001786
14	120	0.00183	0.008333
15	16	0.00024	0.062500
16	1	0.00002	1.000000
Total	65535	1.00000	#

combination category), and the number of unique, theoretically possible combinations was 55. For 3-species combinations these numbers were 15 and 455, respectively. The number of iterations was increased so that the total number of null 2- and 3-species combinations expected by chance amounted to 810 and 950, respectively. As seen from Table 2, the results obtained support the hypothesis stated above: the greater the total number of null combinations simulated, the greater the total number of different null species combinations simulated, and, as a result, the greater the number of different null species combinations identical with the observed ones,  $F_{id}$ .

In the context of the results of all the simulations, we conclude that - within the individual *k*-species combinations category - the species combinations found in the set of relevés analyzed may be treated as random.

## Null analysis by means of EcoSim null model software

Table 6 illustrates the results of testing the original Argentinean lemnid co-occurrence matrix against three simulation algorithms and four co-occurrence indices. As seen from the table, for simulation procedures SIM2 and SIM7, CHECKER was not statistically significant in comparison to chance, and the *V*-ratio was not statistically significant for SIM4. For nine combinations of indices and algorithms the species co-occurrence patterns were nonrandom. It is worth noting here that for SIM7 all four expected co-occurrence indices were nearly the same as those for SIM2. Therefore, for both simulation procedures the results of null analyses were congruent (Table 6).

Overall the results of testing the Argentinean data against 12 combinations of three algorithms and four indices showed statistically significant nonrandom species co-occurrence patterns in 9 of the 12 combinations. In five cases the observed indices were greater (*C*-score, CHECKER) or less (COMBO) than expected by chance, and these findings seem consistent with the hypothesis that the observed pattern was structured competitively (negative covariance). In two cases the observed *V*-ratio index was significantly greater than expected by chance, suggesting positive covariance between pairs (algorithms SIM2 and SIM7). For the same procedures the observed *C*-score index was significantly less than expected by chance; such a result seems to indicate positive covariance between pairs (for a competitively structured community this index should be greater than the expected one).

## Conclusion

The results obtained for various combinations of simulation procedures and co-occurrence indices differ because, although all the indices measure species co-occurrence, they reveal different aspects of the co-occurrence pattern, so the results they yield are not always congruent (Gotelli 2000).

With these limitations in mind, we conclude that the pattern observed in the Argentinean co-occurrence data generally is nonrandom (irrespective of which ecological factors determine the pattern). We should remember, however, that the analyzed sample Table 6. Summary output from null model analysis for Argentinean lemnid co-occurrence (n= 156 relevés) with different simulation procedures and indices from EcoSim (Gotelli & Entsminger 1999). Null hypothesis that the pattern observed is random was tested. Mean of simulated indices was calculated over 1000 iterations of the simulation algorithm.

Species co- occurrence pattern		nonrandom	random	nonrandom	nonrandom	nonrandom	nonrandom	nonrandom	random	nonrandom	random	nonrandom	nonrandom
Actual tail probability	$(1 > 0.00)$ , $1 \approx 0^{-1} \approx 10^{-1}$	$p(\text{obs}\leq \exp) = 0.000$ $p(\text{obs}\geq \exp) = 1.000$	$p(\text{obs}\leq\text{exp}) = 0.984$ $p(\text{obs}\geq\text{exp}) = 0.110$	$p(obs \le exp) = 0.000$ $p(obs \ge exp) = 1.000$	$p(\text{obs}\leq\text{exp}) = 1.000$ $p(\text{obs}\geq\text{exp}) = 0.000$	$p(\text{obs}\leq\text{exp}) = 0.987$ $p(\text{obs}\geq\text{exp}) = 0.013$	$p(\text{obs}\leq\text{exp}) = 0.995$ $p(\text{obs}\geq\text{exp}) = 0.042$	$p(\text{obs}\leq\text{exp}) = 0.000$ $p(\text{obs}\geq\text{exp}) = 1.000$	$p(\text{obs}\leq\text{exp}) = 0.125$ $p(\text{obs}\geq\text{exp}) = 0.875$	$p(obs \le exp) = 0.000$ $p(obs \ge exp) = 1.000$	$p(\text{obs}\leq\text{exp}) = 0.983$ $p(\text{obs}\geq\text{exp}) = 0.070$	$p(obs \le exp) = 0.000$ $p(obs \ge exp) = 1.000$	$p(\text{obs}\leq\text{exp}) = 1.000$ $p(\text{obs}\geq\text{exp}) = 0.000$
ndex value	max.	988.9	4.0	156.0	1.158	844.3	4.0	154.0	2.436	1075.2	8.0	156.0	1.127
Simulated in	min.	880.5	0.0	147.0	0.480	693.5	0.0	138.0	1.246	912.0	0.0	148.0	0.547
Mean of simulated	indices	936.3	0.622	153.0	0.817	764.5	0.334	146.6	1.76	994.8	0.399	153.7	0.807
Observed co- occurrence	index	818.1	2.0	130.0	1.56	818.1	2.0	130.0	1.56	818.1	2.0	130.0	1.56
Co-ocurrence	TITUCA	C-score	CHECKER	COMBO	V-ratio	C-score	CHECKER	COMBO	V-ratio	C-score	CHECKER	COMBO	V-ratio
the simulation edure	column sums column sums equiprobable							ргорогнона			والمطمعينيين	eduiptonante	
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Simulation procedure SIM 2					7 PULS	+ IMIC			L MIS	/ INTE			

solely by the marginal totals of the data matrix. If the species are distributed independently and the sites are equiprobable, V-ratio = 1.0. If this index is > 1.0, it indicates positive structured community, the observed C-score index should be significantly larger than expected by chance. CHECKER - the number of checkerboard species pairs. This index measures the number of species pairs that never co-occur in any site. In a competitively structured community, the observed CHECKER index should be significantly larger than expected by chance. COMBO - the number of unique species combinations. In a competitively structured community, the observed COMBO index should be significantly smaller than expected by chance. V-ratio – the ratio of the variance of the column sums to the sums of the row variances. Unlike the above indices, the V-ratio is determined covariance between pairs. If it is < 1.0, it indicates negative covariance. In a competitively structured community, the observed V-ratio index should be significantly smaller than expected by chance. cannot be treated as representative. In the case of a sample list, as in phytosociological records, this has a decisive effect on the outcome of any statistical analysis and must be taken into account, otherwise a biased outcome will result. This is what we think happened in the null model analysis by EcoSim.

The frequency distribution of k-species combinations in Polish lemnids has been found to be positively skewed as a rule (Wołek 1997). This pattern was observed in data sets obtained by the objective sampling procedure Wołek suggested. In a sample of relevés taken by the standard method the frequency pattern was always quite different. Usually the frequency distribution of k-species combinations was more or less symmetrical, rectangular, often irregular. It seems unlikely that in Argentinean lemnids the frequency distribution follows a different pattern than in Polish ones. One should rather suppose that there is no difference between groups of lemnids regardless of their origin, but this cannot be verified without further investigation.

Landolt and Zarzycki (1994) stated that the distribution patterns of lemnids in northern Argentina are influenced by climatic factors (i.e., summer and winter temperatures) and as by nitrogen and magnesium content in the water. Beside these factors, interspecific interactions, especially competition, determine the co-occurrence of the lemnids.

In spite of the limits of the data sampling method, our results suggest that another factor, that is, random and independent dispersion of plants, should included as an important agent controlling the co-occurrence patterns of Argentinean lemnids. The outcome corresponds with that obtained earlier for data coming from Poland (Wołek 1997), but reliable results can come only from an unbiased sample of data. Until such a condition is met, all considerations as to whether or not the observed vegetational structure is random will be speculative.

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