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Community patterns in sandy beaches of Chile: richness, composition, distribution and abundance of species

Patrones comunitarios en playas arenosas de Chile: riqueza, composición, distribución y abundancia de especies

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ABSTRACT

The search for patterns, i.e., statistical arrangement in the data, is a key step to understand the way in which natural systems change in space and time. In order to detect community patterns I analyzed in this study some community traits of forty-five local assemblages of sandy beach invertebrates of Chile. There were identified three main community patterns. (1) Species richness tended to decrease with beach slope (morphodynamic state index), fitting a power model. The variability non-explained by beach slope (about 50%) was independent of grain size and latitude, but a little fraction (9%) was explained by sampling effort. Beach length seemed also to be related with this unexplained variability, but in a non-linear way. (2) The species composition of the local assemblages tended to be a non-random nested subgroup of the species composition of the richer assemblages, i.e., the species composition fitted a nested pattern. (3) The species abundance and distribution were positively correlated, which indicate that wide distributed species tended also to be locally abundant. This is the first time that the "nested species composition pattern" (N° 2) and the "interspecific abundance-distribution pattern" (N° 3) are documented for sandy beach fauna. These three patterns were statistically evident at both regional (~$2x10^2$ km) and geographical (~$2x10^3$ km) scales, suggesting that they are scale-independent along the evaluated range. Much work is still needed to explain how sandy beach communities are structured, in the present study only the first step has been taken, i.e., the detection of patterns, leaving open the question about the underline processes and mechanisms.

Key words: abundance-distribution relationship, Chile, morphodynamic, nestedness, pattern, sandy beaches, spatial scale, species composition, species richness.

RESUMEN

La búsqueda de patrones, i.e., arreglos estadísticos en los datos, constituye un paso clave en el proceso de entendimiento de la variabilidad espacial y temporal de los sistemas naturales. Con el objeto de identificar patrones comunitarios, en este trabajo se analizaron algunos atributos comunitarios de cuarenta y cinco ensambles locales de invertebrados de playas de arena de Chile. Se identificaron tres principales patrones comunitarios. (1) La riqueza de especies tendió a decrecer con la pendiente de la playa (índice del estado morfodinámico), ajustando un modelo potencial. La variabilidad no explicada por la pendiente de la playa (alrededor de 50%) fue independiente del tamaño de grano y latitud, pero una pequeña fracción (9%) fue explicada por el esfuerzo de muestreo. La longitud de la playa también pareció estar asociada con esta variación no explicada, aunque en una forma no lineal. (2) La composición de especies de los ensambles locales tendió a ser un subgrupo anidado, no aleatorio, de la composición de especies de los ensambles más diversos, i.e., la composición de especies siguió un patrón de anidamiento. (3) La distribución y abundancia de las especies se correlacionaron positivamente, lo que indicó que las especies ampliamente distribuidas tendieron además a ser las más abundantes localmente. Esta es la primera vez que se documenta en playas de arena la ocurrencia de "anidamiento en la composición de especies" (patrón N° 2) y de "relación interespecífica positiva entre distribución y abundancia" (patrón N° 3). Estos tres patrones fueron estadísticamente evidentes, tanto a escala regional (~$2x10^2$ km) como geográfica (~$2x10^3$ km), lo que sugiere que son independientes de la escala en el rango evaluado. Aún hace falta mucho trabajo para explicar como se estructuran las comunidades de playas de arena, en el presente trabajo solo se ha dado el primer paso, i.e., la detección de patrones, permaneciendo abierta la interrogante respecto a los procesos y mecanismos subyacentes.

Palabras clave: relación distribución-abundancia, Chile, morfodinámica, anidamiento, patrón, playas de arena, escala espacial, composición de especies, riqueza de especies.

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INTRODUCTION

Ecology deals with the variability of natural systems. The standard scientific approach to explain this variability involve the following steps: (1) identify patterns of variation, (2) infer possible processes and mechanisms capable of generating the patterns detected, (3) propose explicative hypothesis, and finally (4) evaluate the hypothesis. Thus, the search for patterns, i.e., statistical arrangement in the data, is a key step to understand the way in which natural systems change in space and time. Furthermore, as was claimed by Shrader-Frechette & McCoy (1993), in the absence of strict empirical laws the foundations of much of population and community ecology will have to be laid in broad statistical generalizations.

The spatial variability of species richness (e.g. Hutchinson 1959, Ricklefs & Schluter 1993) and composition (e.g. Patterson & Atmar, 1986), and the interspecific variability of abundance (e.g. Preston 1948, 1962) and distribution (e.g. Brown 1984, Hanski 1982), are among the principal topics of community ecology. In this paper, these community attributes were investigated in assemblages of intertidal invertebrates of sandy beaches of Chile, in order to detect patterns of variation. The focus was placed on four main topics: (1) the relationship between local species richness and physical factors, (2) the degree of nestedness in the local species composition, (3) the interspecific relationship between abundance and distribution, and (4) the effect of spatial scale on the detection of community patterns.

The theme of species richness of sandy beaches has been treated in several studies carried out around the world (e.g. Defeo et al. 1992, Borzone et al. 1996, McLachlan et al. 1996), and also in Chile (e.g. Jaramillo 1978, Jaramillo & Gonzalez 1991, Jaramillo & McLachlan 1993). In these studies, local species richness has been related to physical factors such as sediment type (e.g. McLachlan et al. 1981, Defeo et al. 1992), intertidal slope (e.g. McLachlan et al. 1981, Defeo et al. 1992) and wave exposure (Eleftheriou & Nicholson 1975). Nowadays it is known that beach slope, grain size and exposure are correlated, and they contribute to determine the morphodynamic state of the beach, which explains great part of the local variability of species richness (e.g. McLachlan 1990, McLachlan et al. 1993). However, a considerable amount of variation remains without explanation, justifying therefore the search for new patterns of species richness in sandy beach assemblages. The first aim of this paper was to determine how local species richness is related with beach slope (morphodynamic state index), and then to evaluate how the variation non explained by the slope is affected by others factors, such as sampling effort, latitude, grain size, and beach length.

Nestedness take place when the composition of the poorer assemblages tend to be a non-random nested subgroup of the composition of the richer ones (Patterson & Atmar 1986). Nestedness implies that the distribution of species among localities is predictable, which has important implications from the ecological and management point of view. Although the problem of nestedness has been recently pointed out (eighties), patterns of nestedness have been broadly documented in the literature (e.g. Patterson & Atmar 1986, Wrigth & Reeves 1992, Cook 1995). In sandy beaches assemblages the local variability of species composition has been poorly studied, and it is to date unknown if nestedness occur in such habitats. The second objective of this study was to assess the degree of nestedness in the local species composition of sandy beach assemblages of intertidal invertebrates.

One of the more widely supported generalizations in ecology is that the local abundance and distribution of species tend to be positively related (e.g. Brown 1984, Gaston 1994, Gaston et al. 1997). This pattern has been documented in a variety of taxa, habitats, geographic regions, and spatial scales (for recent revision see Brown 1984, Gaston 1994, 1996). However, the relationship between the abundance and distribution of species has never been studied in sandy beach macrofauna. Thus, the third aim was to evaluate how the distribution and abundance of sandy beach species of invertebrates are related.

The description of patterns is the description of variability, and its quantification depends on the scale of observation (Levin 1992). Consequently, the concepts of pattern and scale are strongly connected, in the sense that different patterns (aspects of the system) could emerge depending on the scale of observation (e.g. Wiens 1989). Thus, the fourth objective was to analyze how the spatial scale employed affect the detection of community patterns. I examined two spatial scale, named geographical (~2x10^3 km) and regional (~2 x10^2km).

In summery, the main objective of the present study was to detect community patterns in sandy beach assemblages, in order to encourage future investigations focused on particular problems. To this end, I analyzed published and unpublished data that include biotic and abiotic information from forty-five sandy beaches of Chile.

METHODS

Database

The database includes biotic and abiotic information from forty-five exposed sandy beaches of Chile (between 20° and 40° S). The information was obtained from published data of thirty three beaches, and from surveys carried out on twelve exposed sandy beaches of central Chile (see Appendix 1). Twelve sandy beaches of central Chile (32°61'-34°40' S) were sampled during low tides of April - May of 1997, following a systematic approach. For the propose of this study, a sandy beach locality is defined as a sandy coastal belt of 100 m in length, where the along-beach variability of physical characteristics is assumed to be relatively low. Along ten transects (10 m apart), five sampling units (SU) per transect were obtained with a core of 0.02 m^2 and 30 cm in depth. The first SU was collected on the drift line (1-3 m above), the second and third were obtained between the drift and effluent lines, and the fourth and fifth were taken under the effluent line. SU's were sieved through 1-mm meshes, and the retained organisms were stored in 10% formalin.

The published information included in the database was also obtained from snapshot surveys, carried out in summer - early autumn, during low tides. In all studies, biological information was obtained taking sampling cores along several transects, and sieving sand through 1-mm meshes. Surface of sampling cores varied between 0.03 and 0.1 m^2, number of transects between 1 and 6, and total sampled area between 0.9 and 4.8 m^2. Retained organisms were stored in 5-10% formalin until sorting in laboratory.

The database contains information classified by beach of the following variables: (1) species richness, (2) species composition, (3) species density, (4) latitude, (5) beach slope (measured following Emery 1961), (6) mean grain size, (7) beach length and (8) sampling effort (total area sampled). The whole database, that includes forty-five localities distributed from Iquique (20° S) to Valdivia (40° S), was used in the geographical scale analysis (~2 x10^3 km). The reduced database, that includes the twelve localities sampled in central Chile (32°61'-34°40' S), was used in the regional scale analysis (~2 x10^2 km).

Statistical analyses

Evaluating sampling effort adequacy:

The number of species that could be found in a given area depends on the sampling effort (e.g. Sanders 1969). Thus, before any analysis with species richness (ideally during pilot sampling), it is important to evaluate if the performed sampling effort (sampled area in benthic communities) was adequate to estimate the number of species occurring in a given area.

To assess the sampling effort adequacy, species-area curves were made for each of the twelve localities surveyed in central Chile. In contrast with the approach followed by Jaramillo *et al.* (1995), the curves were generated by cumulating species by transects, and not by sampling stations. I preferred this alternative procedure because sandy beach species show evident zonation patterns along the intertidal (e.g. Jaramillo & McLachlan 1995, Brazeiro & Defeo 1996), and thus the suitable sampling units, which have biological sense to estimate the species richness of the whole intertidal assemblage is the transect, rather than the station.

The form of the species-are curves could vary with the cumulating order. Thus, to contemplate this source of variability, for each locality 100 curves generated with random (with reposition) cumulating order were built. The average curves were used to evaluate by aye the degree of saturation.

Detecting patterns:

The search for patterns of species richness was carried out on the basis of regression analysis, exploring linear, exponential and power models. Residuals of the model fitted to the relationship between species richness and beach slope were also examined using (multiple and simple) regression analysis and analysis of variance (ANOVA). The relationship between species density and distribution was assessed by linear regression analysis. The degree of nestedness in local species composition was measured following the procedure described by Atmar & Patterson (1993), which imply the estimation of the "temperature" (index of order) of the matrix of species distribution. Temperature and its statistical significance were calculated using the computational program developed by Patterson & Atmar (1993) (available via Internet).

RESULTS AND DISCUSSION

Species richness

Methodological aspects:

The average species-area curves made by cumulating transect, showed in each of the 12 sandy beach localities evidences of saturation (Fig. 1). Poorer beaches achieved saturation with few transects (1-6), while richer localities needed grater sampling efforts (4-8 transects) (Fig. 1). These results demonstrated that a sampling effort of 8 transects, which corresponded to a total cumulate area of 0.8 m^2, was adequate to estimate the species richness of the local communities surveyed. Furthermore, the same patterns of figure 1 were observed in other seven bimonthly samples (Brazeiro not published).

The present results disagree from the sampling effort of 4 m^2 recommended by Jaramillo et al. (1995). This discrepancy is consequence of the different sampling unit used to generate the species-area curves. The curves of Jaramillo et al. (1995) achieved saturation slowly because they used a unit (i.e, station) that only sampled a little part of the area occupied by the intertidal assemblage, whereas the unit used in this study (i.e., transect) sampled the whole area, and therefore saturation was achieved earlier.

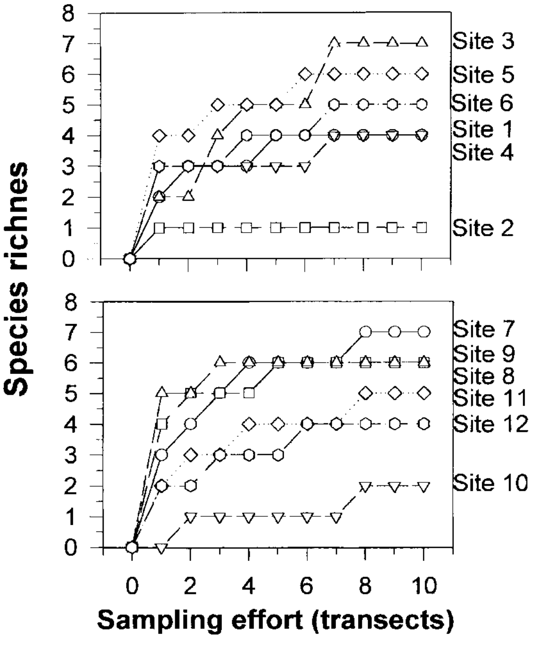

Fig. 1: Species-area curves of the 12 sandy beach localities surveyed in central Chile. Each curve represents the average of 100 curves generated by randomizing the cumulating order.

Curvas especies-área de las 12 localidades de playas arenosas investigadas en Chile central. Cada curva representa el promedio de 100 curvas generadas mediante la aleatorización del orden the acumulación.

Patterns of species richness:

At regional and geographical scales the species richness of sandy intertidal assemblages decreased significantly with intertidal slope, following in both cases a similar power model (Fig. 2). It is important to point out that beach slope is an index of beach morphodynamic state. Beaches with flat slopes tend to be in the dissipative extremity of the morphodynamic gradient, while steepest beaches tend to be in the reflective margin (Wright & Short 1983). Therefore, the "richness-slope pattern" detected in this study imply a "richness-morphodynamic pattern". The scale independence of this relationship was also suggested by others regional (e.g. Jaramillo & Gonzalez 1991, Defeo et al. 1992, Jaramillo 1994, Borzone et al. 1996) and geographical studies (McLachlan et al. 1981, McLachlan et al. 1996). Thus, it is categorically demonstrated that the richness-slope relationship is the most conspicuous and relevant community pattern in sandy beach habitats.

Although the "richness-slope pattern" has been well documented (see also McLachlan et al. 1993, Jaramillo & McLachlan 1993, Jaramillo et al. 1993), the processes and mechanisms responsible of its generation remain unknown, but some hypotheses have been proposed. McLachlan et al. (1993) suggested that an increasing number of species is excluded from the beach as swash climate (see McArdle & McLachlan 1991, 1992) become harsher as beach slope become steeper. It was also suggested that, because of it type of coastal circulation (i.e., circulation cells), primary productivity is higher in flat beaches (i.e., dissipatives), allowing therefore that many species were capable to sustain viable populations in this type of beach (McLachlan 1990). These hypotheses have not been properly tested yet.

Although beach slope explained a considerable fraction of the variance of species richness at geographical scale (52% see Fig. 2), a significant proportion remains without explanation. This remained variability was analyzed in relation to sam-

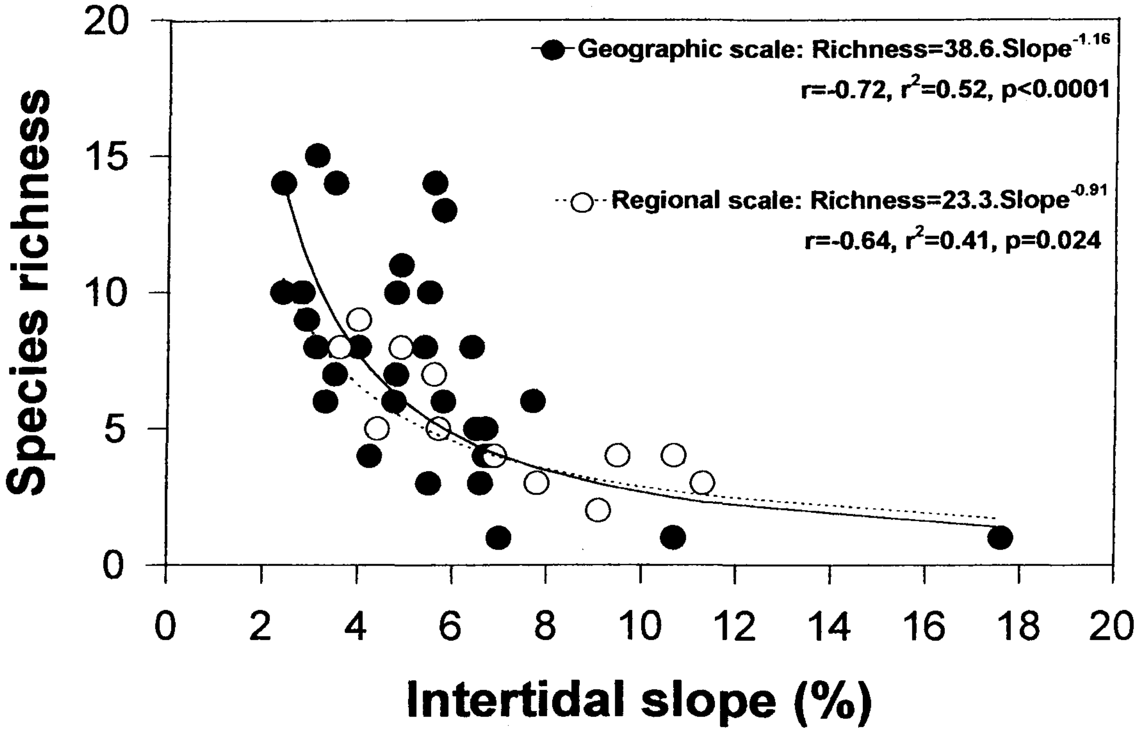

Fig. 2: Relationship between species richness and beach slope at both goegraphic and regional scales. The fitted models are shown in the upper right hand of the graph.

Relación entre la riqueza de especies y la pendiente de la playa a escala geográfica y regional. Los modelos ajustados se muestran en la parte superior derecha del gráfico.

pling effort, grain size, latitude and beach length. In a multiple regression analysis (forward stepwise method), only sampling effort had a positive and significant effect on species richness residuals, explaining a small fraction of the total variability (r^2=0.09, P=0.04). Simple regression analyses corroborate the same results, i.e. none of the ecological factors studied were correlated with species richness (but see beach length below), whereas sampling effects were detected. At regional scale, the varia-

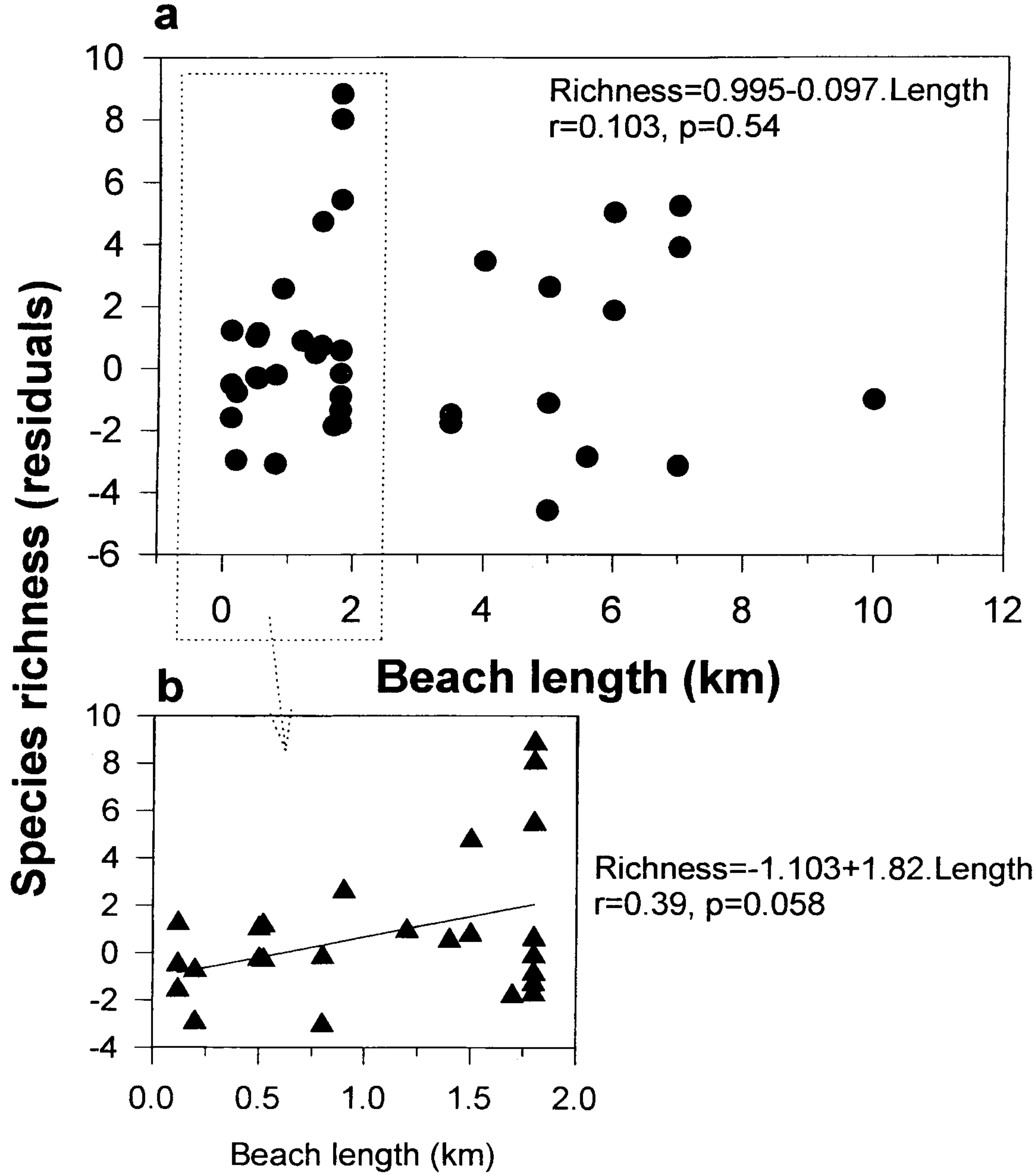

Fig. 3: a) Relationship between the species richness variation, that was not explained by the intertidal slope (i.e., residuals of the power model fitted, see Fig. 2, and the length of the beach. The fitted lineal model is shown in the upper right hand of the graph. b) Zoom of the indicated part of the graph of Fig. 3a (0.2-2 km range of length). The fitted model is shown outside the graph box.

a) Relación entre la variación de la riqueza de especies que no fue explicada por la pendiente de la playa (i.e., residuos del modelo potencial ajustado, ver Fig. 2, y la longitud de la playa. El modelo ajustado se muestra en la parte superior derecha del gráfico. b) Ampliación de la parte indicada en el gráfico de la Fig. 3a (rango de longitud 0,2-2 km). El modelo ajustado se muestra fuera del cuadro del gráfico.

tion of species richness non-explained by beach slope was also independent of beach length and grain size.

The absence of correlation between beach length and species richness residuals was an unexpected result. It is widely known that islands support fewer species than continental areas of similar surface (MacArthur & Wilson 1967). Likewise, several studies on landscape ecology have found that patches located in continuos large areas tend to sustain more species than patches of comparable area located in small fragments of habitat (e.g. Thomas et al.1992). The "rescue effect" (i.e., immigration reduce extinction rate, Brown & Kodric-Brown 1981) has been evoked as the responsible process. Thus, it had been suspected before the analysis that local assemblages immersed in longer beaches could maintain higher diversity, but simple linear regression analysis did not show any significant trend (r=0.1, P=0.54) (Fig. 3a). But when the relation was separately analyzed along the range 0.2-2 km of length, species richness residuals tended to increase with beach length (r=0.39, P=0.058 (Fig. 3b). This suggests that species richness and beach length could be related, but not in an obvious way. This relationship seemed to be non-linear and scale dependent, but is still needed much work to determine how beach length affect species richness.

Another unexpected result was the fate that sandy beach macrofauna did not present the general trend of diversity increase towards low latitudes (e.g. Brown & Gibson 1983, Rosenzweig 1992, 1995). This result agree with observations carried out by McLachlan et al. (1996), who stated that latitude is a negligible factor in determining local species richness in sandy beaches of Australia. Sandy beach macrofauna seems to be another exception of the general latitudinal pattern of species richness (e.g. Santelices 1980).

Nested species composition

The local species composition in insular systems and fragmented habitats (e.g. lakes, patch forest, mountain tips) tend in many cases to be nested, i.e., the species assemblages of poorer localities tend to be a nested, non-random subgroup of the species assemblages of the richer ones (Patterson & Atmar 1986). Examples of nested species composition have been broadly reported in the recent ecological literature (e.g. Soulé et al. 1992, Patterson 1990, Wrigth & Reeves 1992, Doak & Mills 1994), but there are not published antecedents of this pattern in sandy beach fauna.

The results obtained in the present study demonstrated that sandy beach macrofauna is not an exception. At both geographical and regional scale, the distribution of species among localities tended to be nested. The temperatures of the geographical and regional matrices were 10.97° and 11.09° respectively, and its probabilities, calculated by 500 montecarlo-randomization, were 4.4×10^{-36} and 2.7×10^{-6} respectively (Fig. 4). These results constitute the first evidence of nested species composition in sandy beach macrofauna.

Three major hypotheses capable to explain the pattern of nestedness have been proposed. (1) The local extinction probabilities of the species of the regional pool are nested (e.g. Patterson & Atmar 1986, Patterson 1990, Worthen & Rohde 1996). (2) The species probabilities of local colonization are nested (e.g. Patterson & Atmar 1986, Worthen & Rohde 1996). (3) The environmental tolerances of species are nested (e.g. Patterson & Brown 1991). Given the importance that beach morphodynamic have to species richness (see Fig. 2), the interspecific variability in the tolerance to the environmental conditions generated by different morphodynamic states, could play an important role in the generation of the pattern of nestedness. Therefore, I suggest that the distribution of the sandy beach macrofauna of Chile follow a nested pattern because the species capability to live throughout the morphodynamic gradient is nested.

Interspecific abundance and range of distribution

The range of distribution (i.e., number of localities occupied) and the average lineal

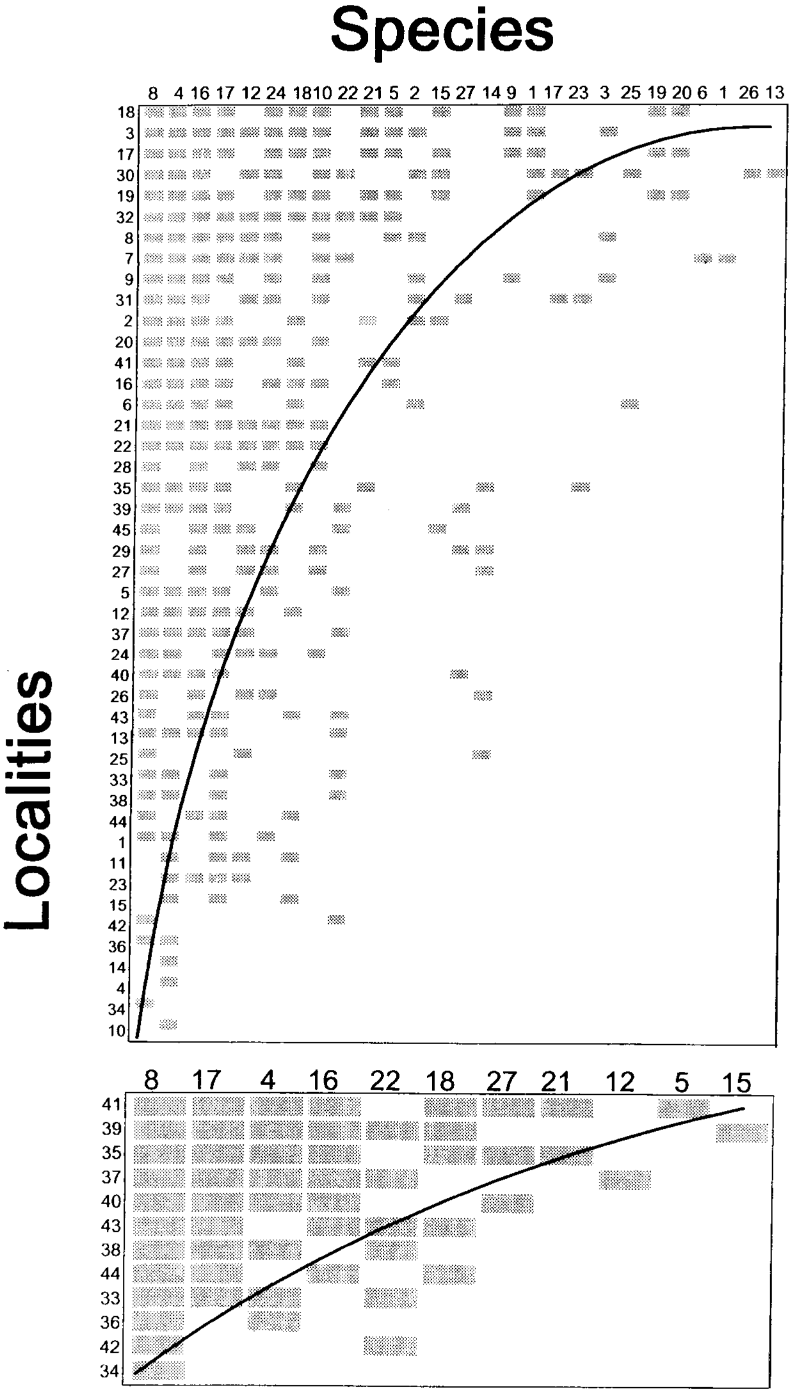

Fig. 4: Geographical (upper) and regional (below) analysis of nestedness in the sandy beach macrofauna of Chile. The "temperature" method (Atmar & Patterson 1993) was employed (see text for details). Species presence is marked with a black square, absence with white. The lines of perfect order (minimum temperature) are indicated in each matrix. The names of the localities and species are given in Annexes 1 and 2 respectively.

Análisis de anidamiento geográfico (arriba) y regional (abajo) en la macrofauna de playas de arena de Chile. El método de la "tempertaura" (Atmar & Patterson 1993) fue empleado (ver texto por detalles). La presencia de especies es marcada con cuadrados negros, la ausencia con blancos. Las líneas de perfecto orden (mínima temperatura) se indican en cada matriz. Los nombres de las localidades y las especies se dan en los Anexos 1 y 2 respectivamente.

density (regarding only the occupied localities) of the sandy beach macrofauna of Chile were directly correlated, both at regional ($r=0.63$, $P=0.038$) and geographical ($r=0.76$, $P<<0.01$) scales (Fig. 5). In the regional-scale analysis all species followed the general trend, but in the geographical analysis, two outliers species were observed, the amphipod Tylos spinulosus and the polychaete Nephtys lamelibranchiata. When extensive study areas were analyzed, like in the geographical-scale analysis, it is probable that the species pool include species whose geographical ranges overlap only a little part of the study are. In such cases, the distribution would be underestimated, but not the abundance. Thus, abundant but poor distributed species, that generate noise in the relationship, could appear simple by methodological fails.

But in general, the species with the widest range of distribution tended also to be the most abundant locally, regardless the spatial scale of analysis (Fig. 5). This pattern is known as the "interspecific abundance-range relationship" (Gaston et al. 1997), and has been widely documented in the ecological literature (e.g. Hanski 1982, Brown 1984, Gaston & Lawton 1990, Warren & Gaston 1997), becoming one of the most general pattern in ecology (Gaston et al. 1997). The interspecific relationship between abundance and distribution has never been investigated before in sandy beaches, indeed, this the first time the "interspecific abundance-range relationship" is documented in this system.

Following the nomenclature introduced by Hanski (1983), the species of wide distribution and high abundance are named "core species", whereas the species of restricted distribution and low abundance are known as "satellite species". In both regional and geographical-scale analyses there were detected the same four "core species", being them *Emerita analoga*, *Orchestoidea tuberculata*, *Excirolana hirsuticauda* and *E. braziliensis* (Fig. 5). This indicates that the consistence between the regional and geographical pattern was not only in the general trend (i.e, positive relationship between abundance and distribution), but also in the identity of the common and rare species.

Many hypotheses have been proposed to explain the "interspecific abundance-range relationship". These involve different mechanisms, such as sampling artifact, geographical distribution, niche breadth, resource availability, metapopulation dynamics, density dependent habitat selection, and vital rates (see Gaston 1994 and Gaston et al. 1997 for revisions). Although the most plausible mechanisms have already been identified, none of the hypotheses have irrefutable evidences (e.g. Gaston

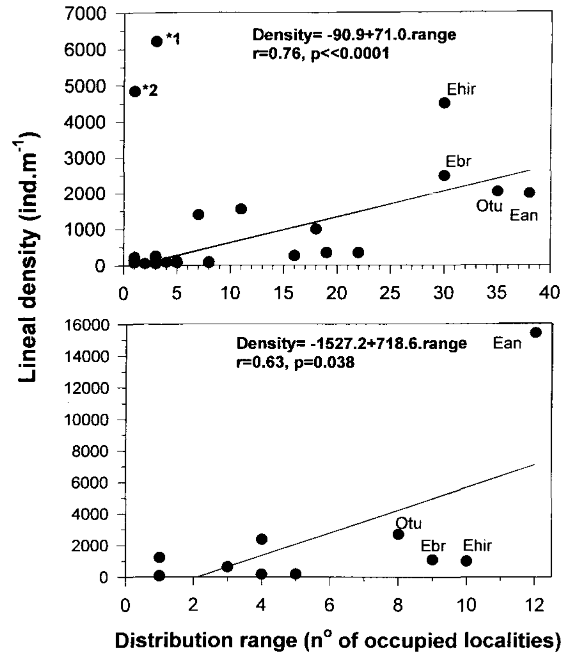

Fig. 5: Interspecific relation between lineal density and range of distribution in sandy beach macrofauna of Chile, at both geographical (upper) and regional (below) scales. The species indicated by an asterisk (1: *Tylos spinulosus* and 2: *Nephtys lamelibranchiata*) were considered outliers and were not included in the lineal regression analysis at geographical scale. The linear models fitted are shown in the upper right hand of the graphs. Ehir: *Excirolana hirsuticada*, Ebr: *E. braziliensis*, Otu: *Orchestoidea tuberculata* and Ean: *Emerita analoga*.

Relación interespecífica entre la densidad lineal y el rango de distribución en la macrofauna de playas de arena de Chile, a escala geográfica (arriba) y regional (abajo). Las especies indicadas con un asterisco (1: *Tylos spinulosus* y 2: *Nephtys lamelibranchiata*) fueron consideradas "outliers", y no fueron incluídas en el análisis de regresión lineal a escala goegráfico. Los modelos lineales ajustados se muestran en la parte superior derecha del los gráficos.

et al. 1997, Warren & Gaston 1997). In relation with sandy beach macrofauna, I believe that the abundance and distribution of species could be related with theirs capacity to live in different ranges of morphodynamic conditions. Accordingly with the general hypothesis of niche breadth (Brown 1982), I suggest that species capable to tolerate wider ranges of morphodynamic conditions (i.e, generalist species) could achieve broad distribution and high abundance, whereas intolerant ones (i.e., specialist species) could only sustain low abundance and restricted distribution.

CONCLUSION

The present study confirmed that beach slope (morphodynamic state index) occupy the main place among the factors explaining the spatial variability of species richness in sandy beaches. About 50% of the variation of species richness were explained by beach slope. The remaining variability was independent of grain size and latitude, but a little fraction (9%) was explained by sampling effort. Species richness residuals seemed also to be associated with beach length, but not in a simple way. There were documented, for first time in sandy beach macrofuana, the occurrence of two general community-patterns: the "nested species composition" and the "interspecific abundance-distribution relationship". These patterns, jointly with the species richness-beach slope relationship, were statistically evident at both regional and geographical scales, suggesting that they are scale-independent along the evaluated range. This result provides useful information to infer the degree of generality of the patterns, and also suggest that the generating processes are the same along the spatial scales evaluated. Much work is still needed to explain how sandy beach communities are structured, in the present study only the first step has been taken, i.e., the detection of patterns, leaving open the question about the underline processes and mechanisms.

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APPENDIX 1

The forty-five Chilean sandy beaches considered in this study. The source of information, latitude and year of sampling of each one was given in the table

Las cuarenta y cinco playas chilenas consideradas en este estudio. La fuente de información, latitud y año de muestreo de cada una se presenta en esta tabla

Code	Locality	Latitude	Year	Information source
1	Los Molinos 1	39.51	1991	Jaramillo (1994)
2	Curiñaco	39.51	1991	"
3	Ronca	39.24	1991	"
4	Maiquillahue	39.27	1991	"
5	Los Molinos 2	39.51	1991	Jaramillo McLachlan & Coetzee (1993)
6	San Ignacio	39.50	1991	"
7	Matias	39.26	1991	"
8	Queule	39.22	1991	"
9	Mehuin	39.26	1991	"
10	Codihue	39.51	1991	"
11	Agua de las niñas	39.21	1990	Jaramillo & Gonzalez (1991)
12	Mehuin	39.26	1990	"
13	Matias	39.26	1990	"
14	Maiquillahue	39.27	1990	"
15	Mehuin 1	39.26	1975	Jaramillo (1978)
16	Mehuin 2	39.26	1975	"
17	Mehuin 3	39.26	1975	"
18	Universitaria 1	39.25	1975	"
19	Universitaria 2	39.25	1975	"
20	Punta Choros	29.14	1980	Jaramillo (1987)
21	Ronca	39.23	1977	"
22	Mehuin	39.26	1977	"
23	Niebla	39.52	1977	
24	Muicolpue	40.34	1977	"
25	Colorado	20.11	1977	"
26	Cavancha	20.14	1977	"
27	Huaiquique	20.17	1977	"
28	Aguila	20.84	1977	"
29	Guanillo	21.12	1977	"
30	Morrillos 1	30.08	1974	Sánchez, Castilla & Mena (1982)
31	Morrillos 2	30.08	1975	"
32	Los Molles	32.25	1975	Castilla, Sanchez & Mena (1977)
33	Quintay	33.09	1997	This study
34	Mirasol	33.02	1997	"
35	El Tabito	33.29	1997	"
36	Laguna Verde	33.08	1997	"
37	Aguas Blancas	32.37	1997	"
38	Cau Cau	32.43	1997	"
39	Cachagua	32.37	1997	"
40	Matanzas	33.57	1997	"
41	Playa Hermosa	34.24	1997	"
42	Yali	33.45	1997	"
43	Santo Domingo	33.38	1997	"
44	Infiernillo	34.29	1997	"
45	San Carlos	33.30	1996	Brazeiro, Rozbaczylo & Fariña (1998)

APPENDIX 2

The geographical pool of sandy beach species of Chile

El ensamble geográfico de especies de playas arenosas de Chile

Code	Species	Code	Species
1	*Ampelisca* sp (amphipod)	15	*Chaetilia paucidens* (isopod)
2	*Bathyporeiapus magallanicus* (amphipod)	16	*Excirolana braziliensis* (isopod)
3	*Hurape* sp (amphipod)	17	*Excirolana hirsuticuada* (isopod)
4	*Orchestoidea tuberculata* (amphipod)	18	*Excirolana monodi* (isopod)
5	*Phoxocephalopsis mehuinensis* (amphipod)	19	*Macrochiridotea aff lilianae* (isopod)
6	*Tryphosella schelenbergi* (amphipod)	20	*Macrochiridotea mehuinensis* (isopod)
7	*Tylos spinulosus* (amphipod)	21	*Macrochiridotea setifer* (isopod)
8	*Emerita analoga* (decapod)	22	*Euzonus heterocirrus* (polychaete)
9	*Lepidopa chilensis* (decapod)	23	*Hemipodus* sp (polychaete)
10	*Mesodesma donacium* (bivalve)	24	*Nephtys impressa* (polychaete)
11	*Bellia picta* (decapod)	25	*Nephtys monilibranchiata* (polychaete)
12	*Phalerisidia maculata* (insect)	26	*Polydora* sp (polychaete)
13	*Candancia* sp (copepod)	27	*Scolelepis chilensis* (polychaete)
14	*Ocypode gaudichaudii* (decapod)		