Patterns of endemism in south-eastern Pacific benthic polychaetes of the Chilean coast

Rodrigo A. Moreno[1]*, Cristián E. Hernández[1,2], Marcelo M. Rivadeneira[3], Marcela A. Vidal[4] and Nicolás Rozbaczylo[1]

[1]Departamento de Ecología and Center for Advanced Studies in Ecology & Biodiversity (CASEB), Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, [2]Departamento de Zoología, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Casilla 160-C, Concepción, Chile, [3]Section of Ecology, Behavior and Evolution, Division of Biological Sciences, University of California, San Diego, La Jolla, CA 92093-0116, USA and [4]Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile

ABSTRACT

Aim In this study we evaluate patterns of endemism for benthic polychaete species along the southeastern Pacific coast of Chile. Our goals were (1) to describe latitudinal gradients of endemism and identify areas of high endemism, (2) to evaluate the effect of biogeographical limits on endemism patterns, and (3) to evaluate indirectly the role played by evolutionary dynamics on patterns of endemism.

Location South-eastern Pacific coast of Chile, ranging from Arica (18° S) to Cape Horn (56° S).

Methods We used a list of 178 species of endemic, shallow benthic polychaetes to evaluate patterns of endemism. Parsimony analysis of endemicity (PAE) and the endemism index (EI) were used to evaluate hierarchical relationships of endemism between different latitudinal bands, and to identify areas with high degrees of endemism and differences in endemism. We evaluated the effect of biogeographical limits on endemic polychaete fauna by testing for the existence of geometric constraints (mid-domain effect). The role of evolutionary dynamics on latitudinal patterns of endemism was evaluated with nestedness analysis (NA) using the temperature index.

Results The PAE analysis indicated two large, separate areas of endemism: (1) the northern area between 18° S and 38° S, and (2) the southern area between 39° S and 56° S. The endemism index showed a maximum value (32 species) around 39°–41° S. Species-richness curves of each 3° band of latitude showed a clear mid-domain effect (69%), but the two maximum points of species richness at mid-latitudes (36° S to 38° S and 39° S to 41° S) did not correspond to the mid-domain peak in species richness, presenting a greater number of species than expected by the mid-domain effect. The nestedness analysis showed that the number of genera reaches a maximum of 70 at mid-latitudes (36°–41° S), decreasing towards both the northern and southern areas. The spatial distribution of the entire data set of endemic species showed a nested pattern ($T° = 24.5°$, $P < 0.0001$).

Main conclusions Our results strongly support the existence of a latitudinal gradient of endemism for benthic polychaete species along the Chilean coast. The shape of this gradient is clearly non-linear, with a marked peak of endemism occurring at mid-latitudes (36°–41° S, endemism hotspot), which also corresponds to a peak in species richness. Furthermore, this hotspot is the midpoint separating two distinct areas of endemism to the north and south. We suggest that the observed pattern of endemism for benthic polychaete taxa of the Chilean coast can be explained by a combination of geometric constraints and historical mechanisms, such as the processes that affected the Chilean coast during the Neogene (e.g. ENSO, oxygen minimum zone, glaciations).

*Correspondence: Rodrigo A. Moreno, Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Alameda 340, Casilla 114-D, Santiago 6513667, Chile.
E-mail: romoren@bio.puc.cl

INTRODUCTION

Patterns of endemism have been described for a variety of taxa, in diverse geographical areas (e.g. Cracraft, 1991; Glasby & Alvarez, 1999; Ron, 2000; Bisconti *et al.*, 2001; Aguilar-Aguilar *et al.*, 2003; Porzecanski & Cracraft, 2005). The identification of patterns of endemism has important consequences for conservation plans, since the concurrence of hotspots in endemism and species richness increases the effectiveness of protected areas (e.g. Kerr, 1997; Reid, 1998; Myers *et al.*, 2000). Nevertheless, while many endemism patterns have been identified, the factors generating these patterns are not well studied. Unlike geographical richness patterns, where causal factors are often associated with present-day environmental conditions (Gaston, 2000; Allen *et al.*, 2002), endemism patterns are commonly hypothesized to be associated with historical processes (Brown & Lomolino, 1998). In some cases, endemism hotspots correspond to areas of 'evolutionary novelties', which harbour a high proportion of new genetic and taxonomic forms (Phillips, 2001; Bossuyt *et al.*, 2004). In other cases (such as Quaternary range contractions), endemism patterns may correspond to 'palaeoendemic' forms (Tribsch & Schönswetter, 2003). Understanding which processes give rise to patterns of endemism allows for the identification of factors that maintain biodiversity in specific zones, which can further aid in conservation plans.

Currently there are no studies regarding patterns of endemism in marine organisms on the southeastern Pacific coast. While there are studies on patterns of diversity in marine invertebrates, few of these studies have evaluated the potential processes underlying the observed patterns (see Camus, 2001). Along the Chilean coast (18° S to 56° S), Camus (2001) proposed that historical processes (e.g. intense oceanographic, climatic and geomorphologic changes during the Neogene, *c.* 24 Ma; Martínez-Pardo, 1990) have determined current patterns of biogeography and may also be responsible for shaping patterns of endemism.

Recently, Hernández *et al.* (2005) identified two biogeographical units for marine benthic polychaetes along the southeastern Pacific coast of Chile (i.e. the Peruvian province, 18°–41° S, and the Magellanic province, 42°–56° S). These authors indicated the existence of an ecotone of high species richness located on the Chiloé Archipelago (*c.* 41°–42° S), probably related to the great divergence of the oceanic current system, which limits the geographical ranges of polychaete species. A high proportion of polychaete species with small range sizes in this zone suggests the existence of an endemism hotspot (Hernández *et al.*, 2005), but this hypothesis has not yet been evaluated.

In this study we evaluate patterns of endemism for benthic polychaete species along the southeastern Pacific coast of Chile. Our aims were: (1) to describe latitudinal gradients of endemism and identify areas of high endemism, (2) to evaluate the effect of biogeographical limits on endemism patterns, and (3) to evaluate indirectly the role played by evolutionary dynamics on patterns of endemism.

MATERIALS AND METHODS

Endemic species data base

The data base utilized in this study consists of a list of 178 species of endemic, shallow benthic polychaetes (< 200 m depth, on the continental shelf) from the southeastern Pacific coast. This data base was compiled by Rozbaczylo (1985; unpubl. data), and includes a list of species of polychaete taxa for the entire Chilean coast, ranging from 18° S (Arica) to 56° S (Cape Horn). The data base compiled for this study is the most current and complete data base for this region of the world, and is based on an exhaustive literature search, reviews of museum collections, and field expeditions.

Maps of species distributions were created using data with a spatial resolution of 1° of latitude, and ranges were assumed to be continuous between points. To describe latitudinal patterns and compare distributions of endemic species with the biogeographical units described by Hernández *et al.* (2005), we categorized species distribution ranges into three groups: (1) species recorded only within 1° of latitude; (2) species with medium–small ranges of distribution from 2° to 14° of latitude; and (3) species with medium–large distributions ranging from 15° to 33° of latitude. To evaluate latitudinal patterns in the distributions of endemic benthic polychaete taxa, we divided the coast of Chile into 3° bands of latitude, registering the presence or absence of each taxon in each 3° segment of the coast.

Parsimony analysis of endemicity

To evaluate hierarchical relationships of endemism between different latitudinal bands, and to identify areas with high degrees of endemism, we utilized the parsimony analysis of endemicity (PAE). This analysis is analogous to the cladistic methods used in phylogenetic analysis; this approach classifies areas (analogous to taxa) by their shared endemic taxa (analogous to characters), according to the most parsimonious

cladogram (see Rosen, 1988; Cracraft, 1991; Morrone, 1994; Posadas & Miranda-Esquivel, 1999; Morrone & Escalante, 2002; Rovito *et al.*, 2004). PAE data consist of area × taxa matrices, and the resulting cladograms represent nested sets of areas (Morrone & Crisci, 1995), where the terminal branches of the area cladogram represent a single band of endemism (Morrone, 1994). The matrix for this study was prepared by coding taxa as absent (0) or present (1) in each area. The cladogram was rooted using a hypothetical area that was coded with all zeros (see Lundberg, 1973; Lambshead & Paterson, 1986; Rosen & Smith, 1988; Morrone, 1994). We use this hypothetical area as an outgroup, considering that Lambshead & Paterson (1986) suggest that 'for synecological analysis if species are to be used as characters to derive cladograms then species presence must be regarded as derived and species absence as primitive'. Hypotheses of area relationships were generated using Camin & Sokal (1965) parsimony in PAUP* software (Swofford, 2002). This algorithm searches for the tree that minimizes the number of changes from ancestral to derived states (Legendre, 1986). In our study this corresponds to the number of endemic species gained along the lineages (i.e. branches of the tree) resulting from ecological processes of immigration and/or evolutionary processes of speciation. To find the most parsimonious area cladogram we implemented a 'Branch and Bound' algorithm search in the tree space (Hendy & Penny, 1982; Felsenstein, 2004).

It should be noted that many studies have utilized PAE to establish relationships among biogeographical units of diverse taxa; however, as far as we know none of these studies utilizes all of the valuable information (e.g. branch length) that can be obtained from analyses based on the reconstruction of cladograms by parsimony. In our study we utilize the length of terminal branches, which could be considered a measure of the number of endemic species in each zone or study unit, which in the cladistic perspective corresponds to autapomorphies (e.g. Wiley *et al.*, 1991) and in PAE could be called 'autapospecies'. Furthermore, internal branch lengths could be considered a measure of the number of shared species that are endemic to two or more zones or study units, which in cladistics would correspond to shared derived traits, or synapomorphies, and in PAE could be called 'synapospecies' (see Morrone, 1994). We suggest that, by using this information in PAE, researchers can obtain quantitative and comparative measures of the degree of endemism in different geographical zones of the world, which would aid in the identification of biodiversity hotspots.

Endemism index

To evaluate differences in endemism along the southeastern Pacific coast of Chile we calculated the index of endemism proposed by Usher (1986) (see Kerr, 1997) for each 3° latitudinal band as follows:

$$\text{Endemism} = \sum_{i=1}^{s} Q^{-1},$$

where S is the total number of species in the taxon under consideration, and Q is the total number of 3° latitudinal bands included within each species' range. Thus, areas containing many species with small ranges of distribution have higher indices of endemism, and areas in which all species occur only in one band will receive a score of 1.0 in the endemism index. A species with a large range of distribution will contribute relatively little to the overall endemism score of each latitudinal band in which it occurs, whereas a species with a small range of distribution will contribute more to the index of endemism, but for fewer bands. This index is useful for distinguishing between bands with similar values of species richness, but different degrees of endemism.

The effect of biogeographical limits

We evaluated the effect of biogeographical limits on the endemic polychaete fauna of the Chilean coast by testing for the existence of geometric constraints using the Monte Carlo simulation program Mid-Domain Null (McCain, 2003, 2004), implemented in Microsoft® Excel software (Microsoft Corporation 1985–2001). Species richness data (i.e. the number of endemic benthic polychaete species) for each 3° latitudinal band were compared with null model predictions using a Monte Carlo simulation of species richness curves. Simulated curves were based on empirical range sizes within a bounded domain, using the analytical stochastic models of Colwell & Hurtt (1994) and Colwell (2005). We used 50,000 Monte Carlo simulations of empirical range sizes sampled with replacement (i.e. the bootstrap method) and without replacement (i.e. the randomization procedure) to calculate the amplitude of the 95% confidence simulation prediction curves (Manly, 1997; McCain, 2004). As stated by Manly (1997), in randomization procedures 'the hypothesis under investigation suggests that there will be a tendency for a certain type of pattern to appear in data, whereas the null hypothesis says that if this pattern is present then this is a purely chance effect of observations in a random order'. This randomization procedure corresponds precisely to the Mid-Domain and Geometric Constraints Model (McCain, 2004; see Hernández *et al.*, 2005).

The role of evolutionary dynamics on latitudinal patterns of endemism

In practice, the role of evolutionary dynamics in generating endemism patterns can only be evaluated using indirect tests, because of poor fossil records and/or a lack of information regarding the genetic composition of biotas. In particular, the fossil record is extremely poor for annelids, and there are no genetic analyses of polychaete species inhabiting the Chilean coast. Therefore, in order to assess indirectly the possible role of evolutionary processes on the observed latitudinal gradient of polychaete species richness, we performed two different analyses. First, we contrasted the

latitudinal gradient of generic richness with predicted values generated from a null model. For the observed species richness in each latitudinal band, we compared the respective observed number of genera with the expected number recorded from a random sampling (1000 iterations) of the entire data set of endemic species. Observed values above or below the 95% and 5% percentiles, respectively, were considered to be significant. Latitudinal bands with high values of generic richness (i.e. a richness value different from that expected from a simple random process) indicate zones of high evolutionary rates, with an unusually high number of 'evolutionary novelties'. Second, we analysed the relative degree of order of the distribution of species (Atmar & Patterson, 1993) by performing an analysis of nestedness on the original species presence–absence matrix (Nested Calculator Software, Atmar & Patterson, 1995). Briefly, the method analyses the degree of disorder in the system as estimated by the 'temperature' (T) of the matrix, where $T = 0°$ indicates perfect nestedness, and $T = 100°$ indicates complete randomness. The existence of a particular array of species within the latitudinal gradient, where the set of species found at poorer sites are nested subsets of the set of species found at the richest sites (instead of a random sample of the entire biota), may shed light on the possible processes generating latitudinal patterns of endemism (e.g. extinction/colonization dynamics; Patterson & Atmar, 2000). Analyses were re-done for each endemism region defined by the PAE, in order to test whether nestedness degree (i.e. temperature) varied, hence revealing possible differences in the structuring forces.

RESULTS

Latitudinal patterns of endemic species distributions

Of the 178 species analysed in this study, 76 (42.7% of the total) were recorded only within 1° of latitude; 53 of these were distributed in the Peruvian province (PP), and 23 in the Magellanic province (MP) (Fig. 1a). Of the 73 species (41%) presenting medium–small ranges of distribution, 36 species were restricted to the PP and 16 to the MP (Fig. 1b). The rest of the species with medium–small ranges ($n = 21$) overlapped both provinces. The species group with medium–large ranges included 29 species (16.3%) (Fig. 1c), of which 7 species were restricted to the PP, and 22 overlapped the two provinces.

The latitudinal pattern of species richness indicated two clear zones corresponding to latitudinal bands with the greatest number of endemic species along the Chilean coast (Fig. 2); these are: (1) the area between 36° and 38° S (80 species, 44.9% of total species richness), and (2) the latitudinal band between 39° and 41° S (82 species, 46.1% of total richness). Furthermore, we identified the two zones with the lowest numbers of endemic species. Both of these zones are located on the southern Chilean coast: (1) the latitudinal band corresponding to 48°–50° S (16 species, 9%), and (2) the area between 54° and 56° S (9 species, 5.1%) (Fig. 2). The endemism index showed a maximum value of 32 species around 39°–41° S (Fig. 3), with decreasing values of endemism towards the northern and southern areas (3 to 8 species), with the exception of the 51°–53° S band, where endemism increased.
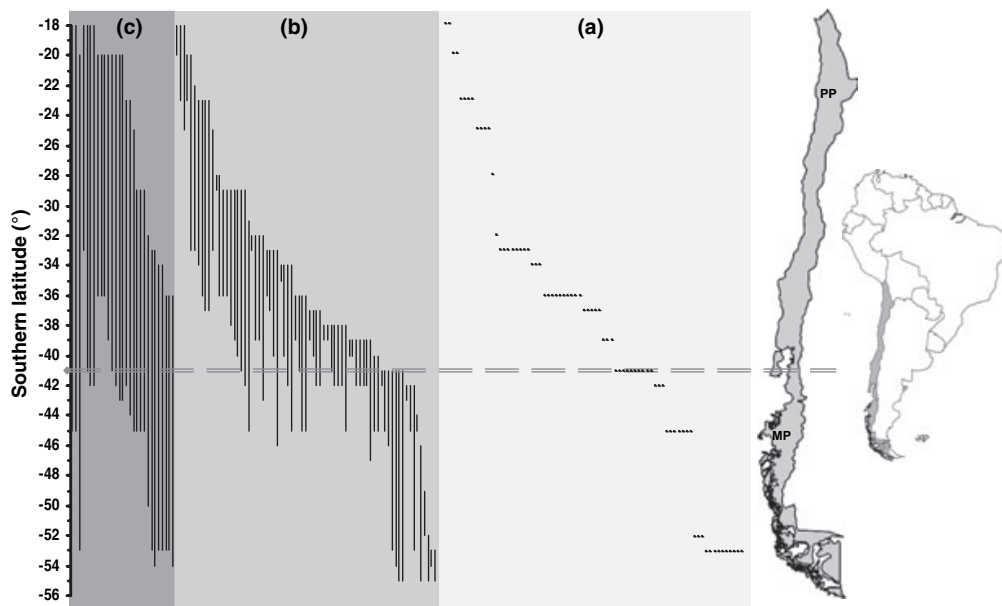

Figure 1 The latitudinal extent of 178 endemic benthic polychaete species distributions from the southeastern Pacific coast of Chile. (a) 76 species recorded within only 1° of latitude; (b) 73 species with medium-small ranges of distribution from 2° to 14° of latitude; (c) 29 species with medium-large distributions ranging from 15° to 33° of latitude. Each vertical bar represents the distribution of a single species. The horizontal grey line shows the limits of the two major biogeographical units described by Hernández *et al.* (2005): the Peruvian province (PP) and the Magellanic province (MP).
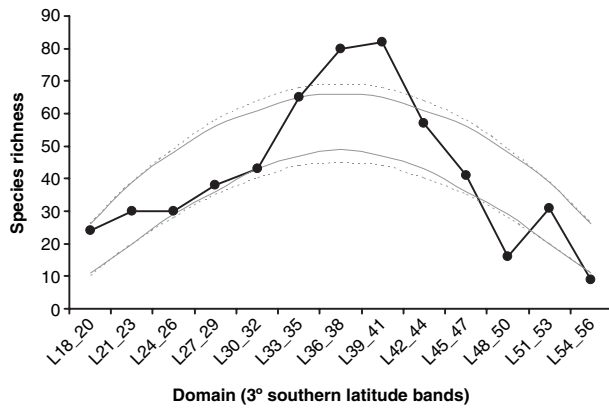
Figure 2 Total number of endemic benthic polychaete species found along the Chilean coast in each 3° band of latitude (black lines with data points). The grey lines show the 95% prediction curves sampled without replacement (solid grey lines) and with replacement (dotted grey lines) using the program 'Mid-Domain Null' (50,000 simulations).
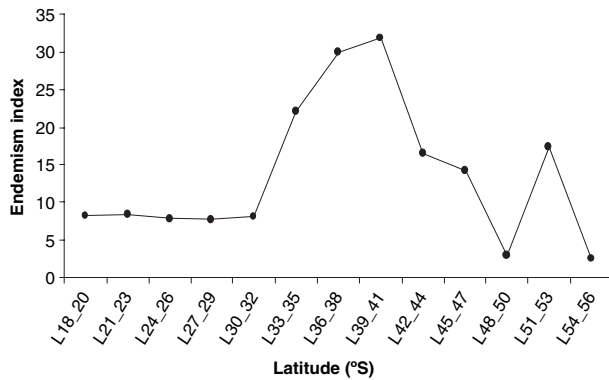

Figure 3 Endemism index values (calculated following Usher, 1986: see text) for benthic polychaete species found along the Chilean coast in each 3° band of latitude (black line with data points).

Parsimony analysis of endemicity

The two most parsimonious area cladograms (CI = 0.68, tree length = 263) were obtained from cladistic analysis of the distribution of 178 endemic benthic polychaete taxa from the southeastern Pacific coast of Chile (Fig. 4). The two trees have similar topologies and branch lengths, with the greatest differences occurring in the clade formed by the latitudinal bands 27°–29° S and 30°–32° S. The cladograms indicate two large areas of endemism: (1) the northern area between 18° S and 38° S, and (2) the southern area between 39° S and 56° S (Fig. 4). Within the northern area the band with the greatest number of endemic species, or 'autapospecies', was found in the extreme south (latitudinal band 36°–38° S, branch length = 33), and in the southern area, the band with the greatest number of 'autapospecies' was found in the extreme north (latitudinal band 39°–41° S, branch length = 32). Furthermore, the internal branch lengths of the cladograms

showed an increase in shared endemic species, or 'synapospecies', towards the central zone between the Peruvian and Magellanic provinces (between 36° S and 41° S).

The effect of biogeographical limits

The species-richness curves of each 3° band of latitude showed a clear mid-domain effect (Fig. 2). A comparison of the empirical data with the prediction curves from the 95% simulation performed without replacement (i.e. randomization procedure) and with replacement (i.e. bootstrap method) showed that 69% of empirical diversity points (9 of 13 points) occurred within the predicted range of the analytical stochastic null model (Fig. 2). However, the two maximum points of species richness at mid-latitudes (36° S to 38° S and 39° S to 41° S) did not agree with the mid-domain peak in species richness, presenting a greater number of species than expected by the mid-domain effect.

The role of evolutionary dynamics on latitudinal patterns of endemism

The number of genera reached a maximum of 70 at mid-latitudes (36°–41° S), decreasing towards both northern and southern areas (Fig. 5). Minimum values were found at the southern tip of the continent, where endemic species comprise only nine genera. In general, the observed latitudinal gradient of generic richness was not different from that expected by the null model, except in the three richest bands, located between 36° S and 44° S, where there were more genera present than expected by a simple random process.

The spatial distribution of the entire data set of endemic species showed a nested pattern ($T° = 24.5°$, $P < 0.0001$). In addition, each of the separate endemism areas identified by PAE (i.e. northern and southern areas) also showed a high degree of order, and were significantly nested in both cases ($P < 0.0001$), although the southern area exhibited a lower temperature (15.4°) than the northern area (27.3°).

DISCUSSION

Our results strongly support the existence of a marked latitudinal gradient of endemism for benthic polychaete species along the Chilean coast. The shape of this gradient is clearly non-linear, with a peak of endemism occurring at mid-latitudes (36°–41° S). Furthermore, these bands represent the midpoint separating two larger areas of endemism. The existence of this endemism hotspot (between 36° S and 41° S) has previously been suggested for all benthic polychaete taxa (39°–41° S) (Hernández *et al.*, 2005) and for benthic invertebrates in general (Brattström & Johanssen, 1983), based on the presence of species with restricted latitudinal ranges. The presence of two endemism areas and an endemism hotspot is strongly coupled with the biogeographical limit between the Peruvian and Magellanic provinces, which has

Figure 4 The two most parsimonious trees (T1 and T2) were obtained from cladistic analysis of the distribution of 178 endemic benthic polychaete taxa from the southeastern Pacific coast of Chile in each 3° band of latitude. The black lines indicate the midpoints of latitudinal bands analysed. The grey lines show the two areas of endemicity (the northern area, between 18° S and 38° S, and the southern area, between 39° S and 56° S) recognized in this study, which coincide with the two major biogeographical units reported by Hernández *et al.* (2005) (PP: Peruvian province, and MP: Magellanic province). The area within the grey ellipse indicates the hotspot area suggested by PAE.
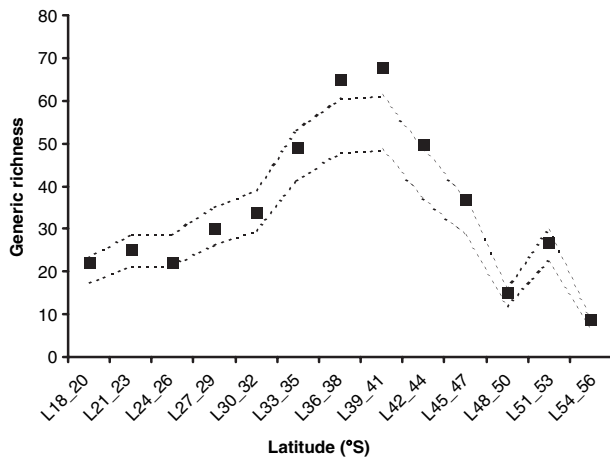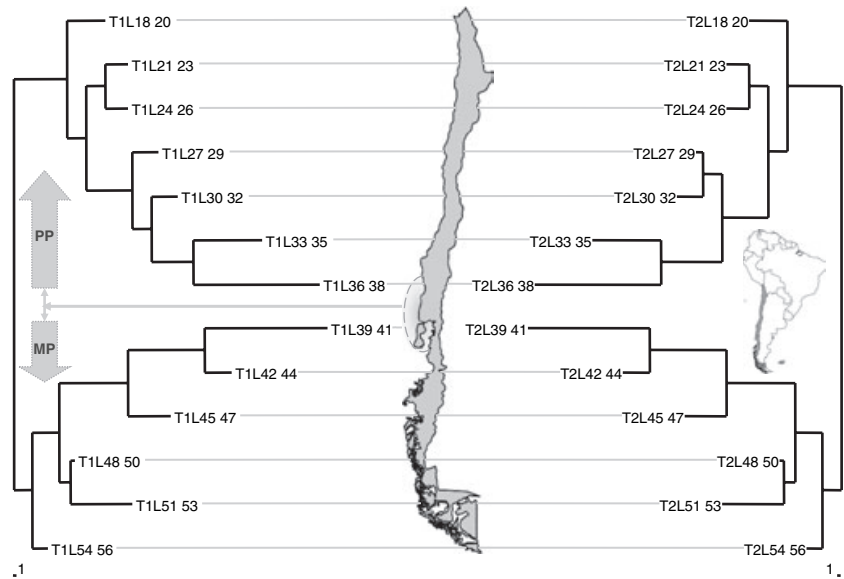

Figure 5 Latitudinal gradient in the number of genera of endemic polychaete species along the Chilean coast. Dotted lines show the upper and lower limits of 95% confidence intervals of 1000 simulations of a null model of generic richness.

been reported for several taxa of marine organisms around 40°–42° S (Brattström & Johanssen, 1983; Moyano, 1991; Ojeda *et al.*, 2000; Santelices & Meneses, 2000; Camus, 2001; Hernández *et al.*, 2005), suggesting that endemism patterns reflect large-scale and historical processes shaping the composition of entire biotas along the Chilean coast.

Our results show that a large part of endemic species richness along the Chilean coast is affected by the mid-domain effect (MDE) (see Colwell & Lees, 2000; Colwell *et al.*, 2004; Romdal *et al.*, 2005), as a result of geometric constraints (i.e. a geographical characteristic that limits the geographical range of the species, acting as a barrier to dispersal; *sensu* Grytnes, 2003), which results in the classic humped curve of species richness. Our study indicates a greater MDE than that reported by Hernández *et al.* (2005) for the entire (i.e. both endemic and non-endemic species) assemblage of benthic polychaete

fauna of the Chilean coast. This demonstrates that geometric constraints can have differential effects on endemic vs. non-endemic fauna of a given geographical area. This suggests the need for more studies that compare endemic and non-endemic fauna, which, according to Colwell *et al.* (2004) 'may well turn up interesting surprises'. Our results support the presence of an MDE on endemic polychaetes of the Chilean coast, as previously suggested by Hernández *et al.* (2005). This effect is probably the result of two hard boundaries at both extremes of the coast, which limit the geographical ranges of the species: (1) the northern boundary (18° S), which is the result of mixing between the cold Humboldt Current and the warm Peru Counter-Current; and (2) the southern boundary (56° S), which is formed by the end of the Cape Horn Current and the edge of continental shelf. Given that, in the absence of environmental gradients, species' distributions may form patterns that depend on geometric constraints (e.g. Colwell & Hurtt, 1994; Colwell & Lees, 2000; Grytnes, 2003), we suggest that the distributional patterns of endemic polychaete fauna on the Chilean coast do not undergo great changes due to latitudinal and seasonal variations in the water masses that they inhabit. Nevertheless, the results of the MDE analyses show that at middle latitudes (36° to 41° S) endemic species richness values are greater than expected under the geometric constraints model, which indicates that there are other causes that are not related to current environmental gradients, which produce the high levels of endemism in this zone. In this respect, we agree with the proposal by Hernández *et al.* (2005) that geometric constraints, together with geomorphology and historical characteristics of the Chilean coast, explain the biogeographical patterns of benthic polychaete taxa in Chile.

The geographical patterns of endemism observed here are probably generated by macroevolutionary dynamics affecting polychaete taxa, rather than by present-day environmental conditions. Although fossil-record and phylogenetic information is lacking, two indirect lines of evidence support this idea:

(1) increased generic richness in the hotspot area, and (2) the existence of nested assemblages in both endemism areas. Elevated generic richness (i.e. higher richness than expected by the null model) may reflect macroevolutionary dynamics, indicating that hotspot areas may correspond to areas of either 'evolutionary novelties' or 'palaeoendemic forms' (Roy *et al.*, 1996). Furthermore, the existence of nested assemblages in both endemism areas implies active extinction–colonization dynamics occurring on evolutionary time-scales. We hypothesize that intense oceanographic, climatic and geomorphological changes occurred along the Chilean coast during the Neogene (Brattström & Johanssen, 1983; Martínez-Pardo, 1990; Camus, 2001; Tsuchi, 2002), which promoted intense extinction-colonization dynamics that has shaped geographical patterns of endemism. The only prior study regarding biogeographical patterns of Austral polychaetes (i.e. Gondwanic forms; Glasby & Alvarez, 1999) involved much larger geographical scales than in the analysis presented here, and therefore very different historical processes shaping endemism patterns, which cannot be applied to our data set.

Modern marine benthic assemblages in the Magellanic province (south of 42° S) have been shaped by the intense glaciations that affected the entire area during the Pleistocene (Clapperton, 1994), perhaps since the onset of western Antarctic glaciation at around 6 Ma (Zachos *et al.*, 2001). The advance of glacial ice over the coastal shelf probably devastated benthic biotas, as is observed in modern Antarctic benthic assemblages (Arntz *et al.*, 1994; Barnes, 1999; Gutt, 2001; for reviews see Poulin *et al.*, 2002; Gutt & Piepenburg, 2003; Thatje *et al.*, 2005). An ongoing study (Rivadeneira, 2005) shows that mollusc richness has decreased during the last 23 Myr in the Magellanic province, supporting the idea that extinctions have affected the generic richness of benthic polychaete taxa. Recolonization probably occurred only during the last *c.* 8 Kyr, following the full retreat of glacial ice and the return of the sea-level reaches to modern levels (Gordillo, 1999), so the elapsed time has not been enough to allow a full recovery of the system. In this sense, many eurybathic polychaete species distributions recorded from the Magellanic province (N. Rozbaczylo & R.A. Moreno, unpubl. data) are in accordance with the distribution patterns of subantarctic and Antarctic polychaetes (Knox, 1977; Knox & Lowry, 1977; Glasby & Alvarez, 1999). These distribution patterns support the hypothesis that the advance and retreat of glaciers has been a major driving force, promoting intense extinction-colonization dynamics of polychaete fauna over evolutionary time-scales, principally in the southern area.

At least two oceanographic and climatic forcing mechanisms operated strongly north of 36° S (see Escribano *et al.*, 2004), potentially controlling the species richness of benthic polychaete taxa: (1) the Neogene development of a shallow oxygen minimum zone (OMZ) (Martínez-Pardo, 1990), and (2) the onset of the El Niño-Southern Oscillation (ENSO) during the mid-Holocene (see Moy *et al.*, 2002). The upper boundary of the persistent OMZ (< 0.5 mL L^{-1} dissolved O$_2$) observed on the Peruvian and northern Chilean coasts is located at less than 50 m depth (see Morales *et al.*, 1999; Escribano *et al.*, 2004; Helly & Levin, 2004), and imposes a strong influence on the distribution and diversity of benthic marine species (Levin *et al.*, 2002). Around the world, OMZs are often associated with coastal upwelling areas (Levin, 2003), and therefore the Mio-Pliocene onset of the Humboldt upwelling system (Tsuchi, 2002) would have generated the OMZ. Preliminary fossil records show the existence of massive mollusc extinctions (up to 70% of species) during the late Pliocene in the Peruvian province (Herm, 1969; DeVries, 2001). These mass extinction events are probably associated with the onset of OMZ (Rivadeneira, 2005). We propose that a similar mechanism might have operated in polychaetes of the southeastern Pacific coast, producing the observed patterns of endemism.

Following the origin of ENSO activity during the last *c.* 7 Kyr (Moy *et al.*, 2002), the southeastern Pacific biota has continued to experience this disturbing influence, and ENSO now constitutes a critical component for defining the current biogeography of this area (Fernández *et al.*, 2000; Camus, 2001). Hernández *et al.* (2005) hypothesize that the low diversity of the northern area has two causes: (1) a high extinction rate caused by ENSO, and (2) a low speciation rate, owing to the small differentiation of niches observed in this area, with respect to the southern area (south of 41° S). Our results support these hypotheses, in which high extinction and low speciation rates would function as biological mechanisms determining local-scale diversity (see Shmida & Wilson, 1985), resulting in low endemism and species richness of benthic polychaetes taxa in the northern area.

The forcing mechanisms of the northern and southern areas would not have operated strongly between 36° S and 41° S, which corresponds to the endemism hotspot area. First, glacial ice did not reach coastal areas north of 42° S (Clapperton, 1994). Secondly, a less intense OMZ (> 0.5 mL L^{-1} dissolved O$_2$) is located in deeper waters (between 50 and 300 m), south of 36° S (Escribano *et al.*, 2004; Helly & Levin, 2004), where ENSO effects are also much weaker (see Escribano *et al.*, 2004). Therefore, we suggest that the endemism hotspot area might correspond to a palaeo-refugium, where species escaped from the severe extinction events that occurred in the northern and southern areas. The re-colonization process probably occurs from this area towards northern and southern latitudes, which could explain the humped curve of endemic species richness, the existence of a mid-domain effect, the two distinct endemism areas, and the existence of nested assemblages. Similar endemism patterns for other invertebrate taxa (Brattström & Johanssen, 1983) suggest that these processes operate over the entire benthic biota, but the generality of this statement needs to be tested.

CONCLUDING REMARKS

An understanding of patterns of endemism is important for determining criteria for conservation planning. Our results provide strong evidence that endemism depicts a clear hump-shaped latitudinal pattern of variation along the Chilean coast

in the southeastern Pacific. A marked peak of endemism (i.e. endemism hotspot) is observed at 36°–41° S, corresponding to a peak in species richness. Our results imply that conservation efforts should be focussed primarily on this hotspot area, which would ensure the protection of most polychaete species (including both endemic and non-endemic species). We suggest that this hotspot has been a historical refuge for species, acting as a source from which taxa have dispersed towards more impoverished northern and southern areas.

ACKNOWLEDGEMENTS

REFERENCES

Aguilar-Aguilar, R., Contreras-Medina, R. & Salgado-Maldonado, G. (2003) Parsimony Analysis of Endemicity (PAE) of Mexican hydrological basins based on helminth parasites of freshwater fishes. *Journal of Biogeography*, **30**, 1861–1872.

Allen, A., Brown, J.H & Gillooly, J.F. (2002) Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science*, **297**, 1545–1548.

Arntz, W.E., Brey, T. & Gallardo, V.A. (1994) Antarctic zoobenthos. *Oceanography and Marine Biology: an Annual Review*, **32**, 241–304.

Atmar, W. & Patterson, B.D. (1993) The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia*, **96**, 373–382.

Atmar, W. & Patterson, B.D. (1995) *The nestedness temperature calculator: a Visual Basic program, including 294 presence-absence matrices*. AICS Res., Inc., University Park, NM, and the Field Museum, Chicago, IL.

Barnes, D.K.A. (1999) The influence of ice on polar nearshore benthos. *Journal of the Marine Biological Association of the United Kingdom*, **79**, 401–407.

Bisconti, M., Landini, W., Bianucci, G., Cantalamessa, G., Carnevale, G., Ragaini, L. & Valleri, G. (2001) Biogeographic relationships of the Galapagos terrestrial biota: Parsimony Analyses of Endemicity based on reptiles, land birds and *Scalesia* land plants. *Journal of Biogeography*, **28**, 495–510.

Bossuyt, F., Meegaskumbura, M., Beenaerts, N., Gower, D.J., Pethiyagoda, R., Roelants, K., Mannaert, A., Wilkinson, M., Bahir, M.M., Manamendra-Arachchi, K., Ng, P.K.L.,

Schneider, C.J., Oomen, O.V. & Milinkovitch, M.C. (2004) Local endemism within the Western Ghats-Sri Lanka biodiversity hotspot. *Science*, **306**, 479–481.

Brattström, H. & Johanssen, A. (1983) Ecological and regional zoogeography of marine benthic fauna of Chile. *Sarsia*, **68**, 289–339.

Brown, J.H. & Lomolino, M.V. (1998) *Biogeography*, 2nd edn. Sinauer Associates, Sunderland, MA.

Camin, J.H. & Sokal, R.R. (1965) A method for deducing branching sequences in phylogeny. *Evolution*, **19**, 311–326.

Camus, P.A. (2001) Biogeografía marina de Chile continental. *Revista Chilena de Historia Natural*, **74**, 587–617.

Clapperton, C.M. (1994) The quaternary glaciation of Chile: a review. *Revista Chilena de Historia Natural*, **67**, 369–383.

Colwell, R.K. (2005) *RangeModel: a Monte Carlo simulation tool for assessing geometric constraints on species richness*, Ver. 4. User's guide and application published at http://viceroy.eeb.uconn.edu/RangeModel.

Colwell, R.K. & Hurtt, G.C. (1994) Nonbiological gradients in species richness and a spurious Rapoport effect. *The American Naturalist*, **144**, 570–595.

Colwell, R.K. & Lees, D.C. (2000) The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology and Evolution*, **15**, 70–76.

Colwell, R.K., Rahbek, C. & Gotelli, N. (2004) The mid-domain effect and species richness patterns: what have we learned so far? *The American Naturalist*, **163**, E1–E23.

Cracraft, J. (1991) Patterns of diversification within continental biotas: hierarchical congruence among the areas of endemism of Australian vertebrates. *Australian Systematic Botany*, **4**, 211–227.

DeVries, T.J. (2001) Contrasting patterns of Pliocene and Pleistocene extinctions of marine mollusks in western North and South America. *Geological Society of America, Abstract with Programs*, **33**, A-35.

Escribano, R., Daneri, G., Farías, L., Gallardo, V.A., González, H.E., Gutiérrrez, D., Lange, C.B., Morales, C.E., Pizarro, O., Ulloa, O. & Braun, M. (2004) Biological and chemical consequences of the 1997–1998 El Niño in the Chilean coast upwelling system: a synthesis. *Deep-Sea Research II*, **51**, 2389–2411.

Felsenstein, J. (2004) *Inferring phylogenies*. Sinauer Associates, Sunderland, MA.

Fernández, M., Jaramillo, E., Marquet, P.A., Moreno, C.A., Navarrete, S.A., Ojeda, F.P., Valdovinos, C. & Vásquez, J. (2000) Diversity, dynamics and biogeography of Chilean benthic nearshore ecosystems: an overview and guidelines for conservation. *Revista Chilena de Historia Natural*, **73**, 797–830.

Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220–227.

Glasby, C.H. & Alvarez, B. (1999) Distribution patterns and biogeographic analysis of Austral polychaeta (Annelida). *Journal of Biogeography*, **26**, 507–533.

Gordillo, S. (1999) Holocene molluscan assemblages in the Magellan region. *Scientia Marina*, **63**, 15–22.

Grytnes, J.A. (2003) Ecological interpretations of the mid-domain effect. *Ecology Letters*, **6**, 883–888.

Gutt, J. (2001) On the direct impact of ice on marine benthic communities, a review. *Polar Biology*, **24**, 553–564.

Gutt, J. & Piepenburg, D. (2003) Scale-dependent impact on diversity of Antarctic benthos caused by grounding of icebergs. *Marine Ecology Progress Series*, **253**, 77–83.

Helly, J.J. & Levin, L.A. (2004) Global distribution of naturally occurring marine hypoxia on continental margins. *Deep-Sea Research I*, **51**, 1159–1168.

Hendy, M.D. & Penny, D. (1982) Branch and bound algorithms to determine minimal evolutionary trees. *Mathematical Bioscience*, **59**, 277–290.

Herm, D. (1969) Marines Pliozän und Pleistozän in Nord und Mittel Chile unter besonderer Berücksichtigung der Entwicklung der Mollusken-Faunen. *Zitteliana*, **2**, 1–159.

Hernández, C.E., Moreno, R.A. & Rozbaczylo, N. (2005) Biogeographical patterns and Rapoport's rule in southeastern Pacific benthic polychaetes of the Chilean coast. *Ecography*, **28**, 363–373.

Kerr, J.T. (1997) Species richness, endemism, and the choice of areas for conservation. *Conservation Biology*, **11**, 1094–1100.

Knox, G.A. (1977) The Antarctic polychaete fauna: its characteristics, distribution patterns, and evolution. *Adaptations within Antarctic ecosystems* (ed. by G.A. Llano), pp. 1111–1127. Smithsonian Institution, Washington, DC.

Knox, G.A. & Lowry, J.K. (1977) A comparison between the benthos of the Southern Ocean and the North Polar Ocean with special reference to the Amphipoda and the Polychaeta. *Polar oceans. Proceedings of the SCOR/SCAR Polar Oceans Conference* (ed. by M.J. Dunbar), pp. 423–462. Arctic Institute of North America, Calgary.

Lambshead, P.J.D. & Paterson, G.L.G. (1986) Ecological cladistics. An investigation of numerical cladistics as a method for analysing ecological data. *Journal of Natural History*, **20**, 895–909.

Legendre, P. (1986) Reconstructing biogeographic history using phylogenetic-tree analysis of community structure. *Systematic Zoology*, **35**, 68–80.

Levin, L.A. (2003) Oxygen Minimum Zone benthos: adaptation and community response to hypoxia. *Oceanography and Marine Biology: an Annual Review*, **41**, 1–45.

Levin, L.A., Gutiérrez, D., Rathburn, A., Neira, C., Sellanes, J., Muñoz, P., Gallardo, V.A. & Salamanca, M. (2002) Benthic processes on the Peru margin: a transect across the oxygen minimum zone during the 1997–98 El Niño. *Progress in Oceanography*, **53**, 1–27.

Lundberg, J.G. (1973) More on primitiveness, higher level phylogenies and ontogenetic transformations. *Systematic Zoology*, **22**, 327–329.

Manly, B.F.J. (1997) *Randomization, bootstrap and Monte Carlo methods in biology*. Chapman & Hall, London.

Martínez-Pardo, R. (1990) Major Neogene events of the Southeastern Pacific: the Chilean and Peruvian record. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **77**, 263–278.

McCain, C. (2003) North American desert rodents: a test of the mid-domain effect in species richness. *Journal of Mammalogy*, **84**, 967–980.

McCain, C. (2004) The mid-domain effect applied to elevational gradients: species richness of small mammals in Costa Rica. *Journal of Biogeography*, **31**, 19–31.

Morales, C., Hormazábal, S. & Blanco, J. (1999) Interannual variability in the mesoscale distribution of the depth of the upper boundary of the oxygen minimum layer off northern Chile (18–24° S): implication for the pelagic system and biogeochemical cycling. *Journal of Marine Research*, **57**, 909–932.

Morrone, J.J. (1994) On identification of areas of endemism. *Systematic Biology*, **43**, 438–441.

Morrone, J.J. & Crisci, J.V. (1995) Historical biogeography: introduction to methods. *Annual Review of Ecology and Systematics*, **26**, 373–401.

Morrone, J.J. & Escalante, T. (2002) Parsimony Analysis of Endemicity (PAE) of Mexican terrestrial mammals at different area units: when size matters. *Journal of Biogeography*, **29**, 1095–1104.

Moy, C.M., Seltzer, G.O., Rodbell, D.T. & Anderson, D.M. (2002) Variability of El Niño/Southern Oscillation activity at millennial timescales during the Holocene epoch. *Nature*, **420**, 162–165.

Moyano, H.I. (1991) Bryozoa marinos chilenos VIII: una sintesis zoogeográfica con consideraciones sistemáticas y la descripción de diez especies y dos géneros nuevos. *Gayana Zoología*, **55**, 305–389.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.

Ojeda, F.P., Labra, F.A. & Muñoz, A.A. (2000) Biogeographic patterns of Chilean littoral fishes. *Revista Chilena de Historia Natural*, **73**, 625–641.

Patterson, B.D. & Atmar, W. (2000) Analyzing species composition in fragments. *Isolated vertebrate communities in the tropics* (ed. by G. Rheinwald), pp. 9–24. Bonner Zoologische Monographen 46, Bonn.

Phillips, J.A. (2001) Marine macroalgal biodiversity hotspots: why is there high species richness and endemism in southern Australia marine benthic flora? *Biodiversity and Conservation*, **10**, 1555–1575.

Porzecanski, A.L. & Cracraft, J. (2005) Cladistic analysis of distribution and endemism (CADE): using raw distribution of birds to unravel the biogeography of the South American aridlands. *Journal of Biogeography*, **32**, 261–275.

Posadas, P. & Miranda-Esquivel, D.R. (1999) El PAE (Parsimony Analysis of Endemicity) como una herramienta en la evaluación de la biodiversidad. *Revista Chilena de Historia Natural*, **72**, 539–546.

Poulin, E., Palma, A.T. & Féral, J.P. (2002) Evolutionary versus ecological success in Antarctic benthic invertebrates. *Trends in Ecology and Evolution*, **17**, 218–222.

Reid, W.V. (1998) Biodiversity hotspots. *Trends in Ecology and Evolution*, **13**, 275–280.

Rivadeneira, M.M. (2005) Macroecología evolutiva de bivalvos marinos de la costa Pacífica de Sudamérica. PhD Thesis, Pontificia Universidad Católica de Chile, Santiago.

Romdal, T.S., Colwell, R.K. & Rahbek, C. (2005) The influence of band sum area, domain extent, and range sizes on the latitudinal Mid-Domain Effect. *Ecology*, **86**, 235–244.

Ron, S. (2000) Biogeographic area relationships of lowland Neotropical rainforest based on raw distributions of vertebrate groups. *Biological Journal of the Linnean Society*, **71**, 379–402.

Rosen, B.R. (1988) From fossils to earth history: applied historical biogeography. *Analytical biogeography. An integrated approach to the study of animal and plant distributions* (ed. by A.A. Myers and P.S. Giller), pp. 437–481. Chapman & Hall, London.

Rosen, B.R. & Smith, A.B. (1988) Tectonics from fossils? Analysis of reef-coral and sea-urchin distributions from late Cretaceous to Recent, using a new method. *Gondwana and Thethys* (ed. by M.G. Audley-Charles and A. Hallam), pp. 275–301. Oxford University Press, Oxford.

Rovito, S., Arroyo, M.T.K. & Pliscoff, P. (2004) Distributional modelling and Parsimony Analysis of Endemicity of *Senecio* in the Mediterranean-type climate area of Central Chile. *Journal of Biogeography*, **31**, 1623–1636.

Roy, K., Jablonski, D. & Valentine, J.W. (1996) Higher taxa in biodiversity studies: insights from Eastern Pacific marine mollusks. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, **351**, 1605–1613.

Rozbaczylo, N. (1985) Los anélidos poliquetos de Chile. Indice sinonímico y distribución geográfica de especies. *Pontificia Universidad Católica de Chile, Serie Monografías Biológicas*, **3**, 1–284.

Santelices, B. & Meneses, I. (2000) A reassessment of the phytogeographic characterization of Temperate Pacific South America. *Revista Chilena de Historia Natural*, **73**, 605–614.

Shmida, A. & Wilson, M.V. (1985) Biological determinants of species diversity. *Journal of Biogeography*, **12**, 1–20.

Swofford, D.L. (2002) *PAUP*: phylogenetic analysis using parsimony (and other methods)*, 4.0 beta. Sinauer Associates, Sunderland, MA.

Thatje, S., Hillenbrand, C.D. & Larter, R. (2005) On the origin of Antarctic marine benthic community structure. *Trends in Ecology and Evolution*, **20**, 530–540.

Tribsch, A. & Schönswetter, P. (2003) Patterns of endemism and comparative phylogeography confirm paleo-environmental evidence for Pleistocene refugia in the Eastern Alps. *Taxon*, **52**, 477–497.

Tsuchi, R. (2002) Neogene evolution of surface marine climate in the Pacific and notes on related events. *Revista Mexicana de Ciencias Geológicas*, **19**, 260–270.

Usher, M.B. (1986) *Wildlife conservation evaluation*. Chapman & Hall, London.

Wiley, E.O., Siegel-Causey, D., Brooks, D.R. & Funk, V.A. (1991) *The Compleat Cladist, a primer of phylogenetic procedures*. Special Publication No. 19. The University of Kansas, Museum of Natural History, ????.

Zachos, J.C., Pagani, M., Sloan, L., Thomas, E. & Billups, K. (2001) Trends, rhythms, and aberrations in global climate 65 Ma to Present. *Science*, **292**, 686–693.

BIOSKETCHES

Rodrigo A. Moreno is an associate researcher in the Departamento de Ecología at the Pontificia Universidad Católica de Chile and research scientist in the EU project CENSOR, supported by Alfred Weneger Institute for Polar and Marine Research (AWI), Bremerhaven, Germany. His research currently focuses on establishing latitudinal patterns of diversity in marine benthic polychaete species along the eastern Pacific coast, using a macroecological approach. He is also interested in the ecology and evolution of benthic marine assemblages on the southeastern Pacific coast, especially within the oxygen minimum zone and Magellanic Fjords.

Cristián E. Hernández is an assistant professor in the Zoology Department of the Universidad de Concepción (Chile) and a post-doctoral researcher at the Center for Advanced Studies in Ecology & Biodiversity (CASEB) at the P. Universidad Católica de Chile. His lines of research are within the framework of evolutionary ecology and macroecology, looking at the evolutive component of macroecological patterns. His research is based on the utilization of models of ecological and morphological trait evolution in a phylogenetic context.

Marcelo M. Rivadeneira has a PhD in ecology from the Departamento de Ecología, P. Universidad Católica de Chile. He is interested in macroecology, macroevolution, biogeography, palaeoecology, and marine conservation.

Marcela A. Vidal is a PhD candidate at the Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile. Her work focuses mainly on the historical biogeography of Chilean biota.

Nicolás Rozbaczylo is a professor at the Departamento de Ecología, P. Universidad Católica de Chile, in charge of the courses on invertebrate zoology and animal biology. His research interests focus on the taxonomy and ecology of marine polychaetes and benthic marine ecology.