Evolutionary drivers of the hump-shaped latitudinal gradient of benthic polychaete species richness along the Southeastern Pacific coast

Rodrigo A. Moreno[1,2], Fabio A. Labra[1,2], Darko D. Cotoras[3], Patricio A. Camus[4,5], Dimitri Gutiérrez[6], Luis Aguirre[7], Nicolás Rozbaczylo[8], Elie Poulin[9], Nelson A. Lagos[1,2], Daniel Zamorano[2,10] and Marcelo M. Rivadeneira[11,12,13]

[1] Facultad de Ciencias, Universidad Santo Tomás, Santiago, Chile
[2] Centro de Investigación e Innovación para el Cambio Climático (CiiCC), Universidad Santo Tomás, Santiago, Chile
[3] Entomology Department, California Academy of Sciences, San Francisco, California, United States
[4] Departamento de Ecología, Facultad de Ciencias, Universidad Católica de la Santísima Concepción, Concepción, Chile
[5] Centro de Investigación en Biodiversidad y Ambientes Sustentables (CIBAS), Universidad Católica de la Santísima Concepción, Concepción, Chile
[6] Dirección de Investigaciones Oceanográficas y de Cambio Climático, Instituto del Mar del Perú (IMARPE), Callao, Perú
[7] Laboratorio de Biología y Sistemática de Invertebrados Marinos (LaBSIM), Facultad de Ciencias Biológicas, Universidad Nacional Mayor de San Marcos, Lima, Perú
[8] FAUNAMAR Ltda. Consultorías Medio Ambientales e Investigación Marina, Santiago, Chile
[9] Instituto Milenio de Ecología y Biodiversidad (IEB), Facultad de Ciencias, Universidad de Chile, Santiago, Chile
[10] Department of Zoology, University of Otago, Dunedin, New Zealand
[11] Laboratorio de Paleobiología, Centro de Estudios Avanzados en Zonas Aridas (CEAZA), Coquimbo, Chile
[12] Departamento de Biología Marina, Facultad de Ciencias del Mar, Universidad Católica del Norte, Coquimbo, Chile
[13] Departamento de Biología, Universidad de La Serena, La Serena, Chile

ABSTRACT

Latitudinal diversity gradients (LDG) and their explanatory factors are among the most challenging topics in macroecology and biogeography. Despite of its apparent generality, a growing body of evidence shows that 'anomalous' LDG (*i.e.*, inverse or hump-shaped trends) are common among marine organisms along the Southeastern Pacific (SEP) coast. Here, we evaluate the shape of the LDG of marine benthic polychaetes and its underlying causes using a dataset of 643 species inhabiting the continental shelf (<200 m depth), using latitudinal bands with a spatial resolution of 0.5°, along the SEP (3–56° S). The explanatory value of six oceanographic (Sea Surface Temperature (SST), SST range, salinity, salinity range, primary productivity and shelf area), and one macroecological proxy (median latitudinal range of species) were assessed using a random forest model. The taxonomic structure was used to estimate the degree of niche conservatism of predictor variables and to estimate latitudinal trends in phylogenetic diversity, based on three indices (phylogenetic richness (PD_{SES}), mean pairwise distance (MPD_{SES}), and variation of pairwise

distances (VPD)). The LDG exhibits a hump-shaped trend, with a maximum peak of species richness at ca. 42° S, declining towards northern and southern areas of SEP. The latitudinal pattern was also evident in local samples controlled by sampling effort. The random forest model had a high accuracy (pseudo-r^2 = 0.95) and showed that the LDG could be explained by four variables (median latitudinal range, SST, salinity, and SST range), yet the functional relationship between species richness and these predictors was variable. A significant degree of phylogenetic conservatism was detected for the median latitudinal range and SST. PD_{SES} increased toward the southern region, whereas VPD showed the opposite trend, both statistically significant. MPD_{SES} has the same trend as PD_{SES}, but it is not significant. Our results reinforce the idea that the south Chile fjord area, particularly the Chiloé region, was likely the evolutionary source of new species of marine polychaetes along SEP, creating a hotspot of diversity. Therefore, in the same way as the canonical LDG shows a decline in diversity while moving away from the tropics; on this case the decline occurs while moving away from Chiloé Island. These results, coupled with a strong phylogenetic signal of the main predictor variables suggest that processes operating mainly at evolutionary timescales govern the LDG.

INTRODUCTION

Latitudinal diversity gradients (LDG) have been studied for over two centuries and the search for patterns and their processes remain an active topic in biogeography, macroecology and evolution (*Pianka, 1966*; *Willig, Kaufman & Stevens, 2003*; *Hillebrand, 2004a*; *Mittelbach et al., 2007*; *Tittensor et al., 2010*; *Kinlock et al., 2018*; *Pontarp et al., 2019*). Several meta-analyses have shown the inter-hemispheric consistency of a monotonic increase in species richness from high latitudes to the tropics, producing a unimodal (canonical) pattern on a global scale (*i.e.*, *Willig, Kaufman & Stevens, 2003*; *Hillebrand, 2004a, b*; *Costello & Chaudhary, 2017*; *Worm & Tittensor, 2018*; *Kinlock et al., 2018*; *Menegotto & Rangel, 2018, 2019*; *Rivadeneira & Poore, 2020*). However, there is considerable debate regarding the underlying factors that determine the LDG (*Rohde, 1992*; *Willig, Kaufman & Stevens, 2003*; *Mittelbach et al., 2007*; *Pontarp et al., 2019*).

Synthesis achieved during the last decades recognize that explanations for the canonical LDG (*i.e.*, increasing species richness towards the tropics) can be broadly classified into three major hypotheses categories (*Mittelbach et al., 2007*; *Pontarp et al., 2019*): 'ecological limits', 'diversification dynamics' and 'time for species accumulation'. The category of 'ecological limits' refers to explanations based on present-day environmental conditions *via* higher productivity, carrying capacity, species coexistence, or niche breadth (*Currie, 1991*; *Rosenzweig, 1995*; *Evans, Warren & Gaston, 2005*). The 'diversification dynamics' hypotheses suggest that the LDG are generated by latitudinal variation in diversification rates, with greater speciation and/or lower extinction rates in the tropics (*Evans, Warren &*

Gaston, 2005; *Weir & Schluter, 2007*). The 'time for species accumulation' hypotheses explanations invoke the tropics as sources of evolutionary novelties, where clades originate making the LDG the result of dispersal limitation towards subtropical zones (*Wiens & Donoghue, 2004*; *Wiens & Graham, 2005*; *Jablonski et al., 2013*).

In spite of its apparent generality, the canonical LDG pattern is not matched by many continental and marine taxa (see *Platnick, 1991*; *Kindlmann, Schödelbauerová & Dixon, 2007*; *Tittensor et al. 2010*; *Worm & Tittensor, 2018*, *Kinlock et al., 2018*). A growing body of evidence shows that non-canonical LDG (*i.e.*, inverse or hump-shaped trends) are common among marine organisms at a global scale (*Chaudhary, Saeedi & Costello, 2016*; *Woolley et al., 2016*; *Rivadeneira & Poore, 2020*). This same phenomenon has been reported along the Southeastern Pacific coast (0–56° S, hereafter SEP) and also involve widely different taxa such as macroalgae (*Santelices, 1982*; *Santelices & Marquet, 1998*; *Santelices, Bolton & Meneses, 2009*), sponges (*Desqueyroux & Moyano, 1987*), anthozoans (*Häussermann & Försterra, 2005*), bryozoans (*Moyano, 1991*), polyplacophorans (*Navarrete et al., 2020*), gastropod and bivalves (*Herm, 1969*; *Valdovinos, Navarrete & Marquet, 2003*), polychaetes (*Lancellotti & Vásquez, 2000*; *Hernández, Moreno & Rozbaczylo, 2005*; *Moreno et al., 2006*) and different groups of crustaceans (*Fernández et al., 2009*; *Rivadeneira et al., 2011*). These inverse trends along the SEP have been shown to not be the result of sampling artifacts (see *Valdovinos, Navarrete & Marquet, 2003*; *Rivadeneira et al., 2011*).

In this context, the biogeography of benthic polychaetes from the SEP has historically received little attention and available studies have been mainly descriptive (see *Lancellotti & Vásquez, 1999*, *2000*). Indeed, a significant gap in knowledge in the whole Eastern Pacific and Chile in particular, is recognized on a recent global study of polychaete biogeography (*Pamungkas, Glasby & Costello, 2021*). However, *Hernández, Moreno & Rozbaczylo (2005)* and *Moreno et al. (2006)* evaluated the latitudinal change in species richness of benthic polychaetes along the coast of Chile (between Arica at 18° S and Cape Horn at 56° S), finding a hump-shaped LDG with a maximum peak around Chiloé Island (42° S) in southern Chile. These authors proposed that this pattern might be determined by geometric constraints and historical events such as eustatic movements, cyclic effects of El Niño-Southern Oscillation, shallowing of the oxygen minimum zone and glacial advances and retreats, all of which have mainly occurred since the Neogene (*i.e.*, during the last 23 Mya). Although these studies represented a significant advance in understanding the mechanisms that may generate the hump-shaped LDG, their analyses used a low spatial resolution (3° latitude bands) to register species occurrences and constrained the study area to the geopolitical limits of Chile (an arbitrary decision shared by the majority of studies in other taxa. *i.e.*, *Desqueyroux & Moyano, 1987*; *Moyano, 1991*; *Fernández et al., 2009*; *Rivadeneira et al., 2011*; *Lee & Riveros, 2012*). In these studies (*Hernández, Moreno & Rozbaczylo, 2005*; *Moreno et al., 2006*), therefore, the exclusion of a vast portion of the Warm Temperate Southeastern Pacific biogeographic province (*sensu Spalding et al., 2007*) could generate spurious results derived from truncating the real biogeographic limits of these polychaete species.

Table 1 Summary of the main predictions from classic hypotheses to explain LDG.

Hypothesis categories	Specific hypothesis	SST	Salinity	SST range	Median lat. Range	Salinity range	Shelf area	Primary productivity
Ecological limits	Seasonal coexistence			↓ range, ↑ species		↓ range, ↑ species		
	Species-area effect						↑ area, ↑ species	
	Energy-dependency							↑ PrimProd, ↑ species
Diversification dynamics	Long term climate stability				↓ range, ↑ species			
	Temperature-dependent speciation	↑ SST, ↑ species						
Time for species accumulation	Niche conservatism			= conditions of origination, ↑ species				

Notes:
The arrows (↓ or ↑) denote a relative increase or decrease on the parameter. The change on the first causes the response on the second.
"Time for species accumulation" does not include the variables "Shelf area" and "Primary productivity".

Here, we reappraise the patterns and processes related to the LDG reported for benthic polychaetes in Chile, using a greater spatial extent (3–56° S) and resolution (0.5° latitude) than prior analyses. The northern end is defined by the Guayaquil Gulf (limit between the Panamanian and Peruvian–Chilean Provinces, *Vegas-Velez, 1980*; *Boschi, 2000*; *Robertson & Cramer, 2009*; *Ibanez-Erquiaga et al., 2018*), while the southern limit consist in the end of the South American continent isolated from Antarctica by the Circumpolar Current. Regarding the southern limit, differences in polychaete community composition have been already reported between the Magellan region and Weddell Sea shelves (*Montiel et al., 2005*).

The existence of non-canonical LDG along the SEP could be the result of a complex interaction of several factors, instead of a single dominant one. To give explanation to multi-variate and non-linear phenomena a statistical framework which incorporates and differentially weights each factor is required. Our approach would be to simultaneously evaluate the relative contribution of several proxies (SST, salinity, shelf area, etc.) which have been previously associated with specific hypothesis to explain LDG, using machine learning methods. The explanatory hypotheses considered can be separated into three categories: 'ecological limits', 'diversification dynamics', and 'time for species accumulation' (Table 1). These categories have been adapted from the conceptual framework used to study the canonical LDG (*Mittelbach et al., 2007*; *Pontarp et al., 2019*).

Regarding 'ecological limits', we will consider three hypotheses: (1) Seasonal coexistence (*Valentine & Jablonski, 2015*), which predicts that diversity will decline in areas with abiotic seasonal changes (Diversity $1/\propto$ SST range and Salinity range); (2) Species-area effect (*Chown & Gaston, 2000*; *Valdovinos, Navarrete & Marquet, 2003*), which predicts that diversity will be a direct function of the available area (Diversity $\propto$ Shelf area); and (3) Energy-dependency (*Hawkins, Porter & Diniz-Filho, 2003*; *Evans, Warren & Gaston, 2005*), which predicts that diversity will increase with more energy available in the

ecosystem (Diversity $\propto$ Primary Productivity). In the category of 'diversification dynamics', we will consider two hypotheses: (1) Long term climate stability (*Dynesius & Jansson, 2000*), which predicts that more stable areas will accumulate more species (Diversity 1/$\propto$ Median latitudinal range of the species) and (2) Temperature-dependent speciation (*Rohde, 1992*; *Allen et al., 2006*), which predicts a positive association between speciation rates and ambient temperature (Diversity $\propto$ SST). Finally, in the category of 'time for species accumulation', we will assess one hypothesis about Niche conservatism (*Wiens & Donoghue, 2004*), which predicts that species will tend to retain preferences for the ecological conditions where they originally evolved (Diversity $\propto$ constancy in SST, salinity, SST range, Median latitudinal range of the species, and Salinity range). As all these explanatory variables may reflect processes operating at both ecological and evolutionary timescales, we have selected them as candidate variables to build a machine learning model to explain the polychaete LDG in the SEP.

In addition, the study of phylogenetic diversity may shed light into the role of evolutionary processes shaping patterns of species richness (*Davies & Buckley, 2011*; *Fritz & Rahbek, 2012*; *Eme et al., 2020*). For instance, a species-rich area composed by many closely related species (*i.e.*, low phylogenetic diversity) may imply elevated *in situ* speciation rates of some lineages. On the contrary, a species-rich area composed by many distantly related species (*i.e.*, high phylogenetic diversity) may be associated to immigration influenced by filtering effect acting upon a trait phylogenetically over dispersed. There are many α-phylogenetic diversity indices (*Winter, Devictor & Schweiger, 2013*), that can be broadly classified into three categories that measures amount of richness, divergence and regularity (*Tucker et al., 2017*); therefore, the combined used of indices reflecting each one of these three aspects may be more informative of the role of evolutionary processes shaping species richness (*Davies & Buckley, 2011*; *Fritz & Rahbek, 2012*; *Eme et al., 2020*). Despite the fact that these phylogenetic diversity indices are typically based on calibrated molecular phylogenies, the taxonomic structure may be still be used as a coarse proxy of phylogenetic relationships of species in groups lacking robust and complete molecular phylogenies (*Soul & Friedman, 2015*). In fact, multiple studies in marine taxa have analyzed latitudinal trends in phylogenetic diversity using this taxonomic approach (*Woodd-Walker, Ward & Clarke, 2002*; *Ellingsen et al., 2005*; *Tolimieri & Anderson, 2010*; *Rivadeneira et al., 2011*; *Azovsky, Garlitska & Chertoprud, 2016*; *Wu, Chen & Zhang, 2016*). This opens the possibility to explore latitudinal patterns of phylogenetic diversity in benthic polychaetes along SEP and its connection with the LDG phenomenon.

Our study area encompasses a broad latitudinal gradient of oceanographic conditions spanning more than 50 degrees of latitude, from tropics to sub-polar areas, and hence it is ideal to study the role of 'ecological limits' on the LDG (*Astorga et al., 2003*; *Valdovinos, Navarrete & Marquet, 2003*; *Fernández et al., 2009*). At the same time the marine biota at SEP experienced a drastic turnover during the late Cenozoic, driven by tectonic, physiographic, climatic, and oceanographic shifts (*Herm, 1969*; *Rivadeneira & Marquet, 2007*; *Kiel & Nielsen, 2010*; *Villafaña & Rivadeneira, 2014*; *Rivadeneira & Nielsen, 2017*). These alterations induced latitudinal differences in the diversification trends that created
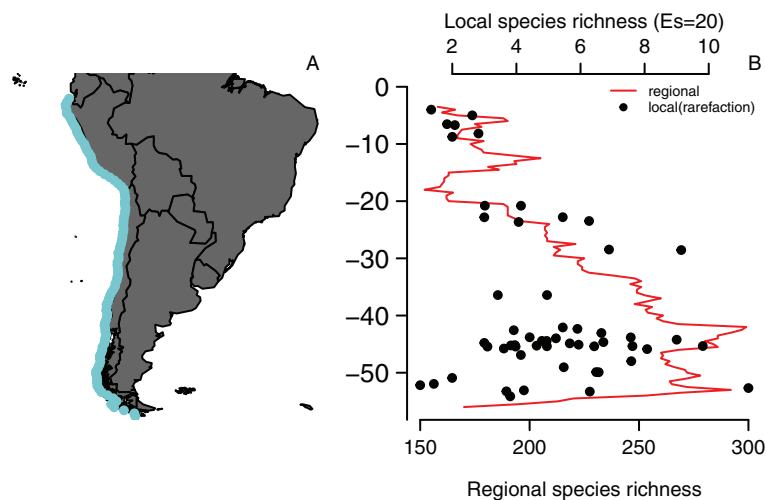
Figure 1 Latitudinal diversity gradient of benthic polychaetes along the SEP. (A) Study area and (B) Regional species richness (using a range-through approach) and local species richness (rarefied species richness, E, using s = 20 individuals per site). Full-size ⬆ DOI: 10.7717/peerj.12010/fig-1

the inverse LDG characterizing present-day bivalves and gastropods along the SEP (*Kiel & Nielsen, 2010*) and may have also driven the LDG of benthic polychaetes (*Moreno et al., 2006*). Thus, SEP is also an ideal region to study the role of evolutionary and historical processes (*i.e.*, 'diversification dynamics', and 'time for species accumulation') shaping the LDG. Therefore, the specific goals of our study are: (1) to re-evaluate the existence of a hump-shaped LDG, including the entire Peruvian and Magellanic biogeographic provinces along the SEP, and (2) to jointly evaluate different hypotheses (by significance assessment of proxies), which could explain the formation of a hump-shaped LDG. Our study confirms the existence of a non-canonical LDG, robust to sampling bias, and suggests that the underlying explanations may be linked to processes occurring at evolutionary timescales.

MATERIALS AND METHODS

Database

This study relies on a database which: (a) includes 643 polychaete species found between 3° S (southern Ecuador) and 56° S (Cape Horn, Chile) inhabiting the continental shelf (*i.e.*, ≤200 m depth) (Fig. 1A), (b) summarizes information compiled from exhaustive reviews of literature (ca. 1,000 bibliographic references), museum collections and field expeditions, integrating more than 160 years of studies over the SEP, (c) was constructed using georeferenced data from geographic information systems (Datum WGS84), (d) was enriched by intensive field samplings conducted over the last decade for updating records and correcting biogeographical biases, particularly in southern Chile where diversity surveys historically had been scarce, specially through the research cruises CIMAR Fiordos 13, 14, 15, 17 and 18 (Comité Oceanográfico Nacional, Chile), and (e) was complemented with existing records from the OBIS database (*OBIS, 2021*). Taxonomy was cross-validated with the World Register of Marine Species (*WoRMS Editorial Board,*

2021). Altogether, such information currently constitutes the most complete database of benthic polychaetes in this region of the world. The reported latitudinal ranges of all species used in this study are provided in the Data S1.

We first determined the maximum and minimum latitude of geographic distribution of each species and assigned species presence into 0.5° latitudinal bands using a range-through approach (*i.e.*, assuming a continuous geographic distribution between their range limits), as commonly done in marine macroecological studies (*Roy et al., 1998*; *Tomašových et al., 2016*). OBIS records were used to estimate the latitudinal limits of species beyond our study area along the eastern Pacific, from Antarctica to Alaska. We also examined whether differences in the sampling intensity may potentially mask the overall pattern, that is to say, whether areas of higher species richness may be the result of higher sampling effort. In order to test this potential confounding factor, we used 57 soft-bottom benthic assemblages sampled in the coastal shelf and collated from a literature survey. Since the sampling effort was not the same (*i.e.*, different sampling devices and number of samples) we used the number of individuals reported for each species and each site to carry out a rarefaction analysis. This method estimates the expected species richness for a similar number of individuals sampled (*Sanders, 1968*; *Gotelli & Colwell, 2001*). In our case, we set $E_s = 20$ (the site with a smaller number of individuals). The information containing the local occurrences and abundances of 152 species in the 57 local assemblages is presented in the Data S2. We estimated the mean rarefied species richness per 0.5° latitudinal bin and correlated it with the species richness estimated with the range-though approach. In the absence of severe spatial bias in sampling intensity, the correlation between rarefied and regional-scale species richness should be positive and significant. However, patterns of species richness may not be necessarily similar across spatial scales (*Gray, 2002*; *Rivadeneira, Fernández & Navarrete, 2002*; *Hillebrand, 2004a*, *2004b*; *Edgar et al., 2017*), and in fact the relationship between local and regional species richness may be non-linear, *i.e.*, at higher regional species richness local assemblages may be saturated (*Ricklefs, 1987*; *Srivastava, 1999*; *Rivadeneira, Fernández & Navarrete, 2002*). The contrary trend, *i.e.*, a linear relationship between local and regional species richness, suggests that local assemblages may be 'open' to the dispersal of species from the regional pool (*Ricklefs, 1987*). We explored this idea by carrying out a second-order polynomial OLS regression, where the significance of the terms can be used to support the saturation (*i.e.*, significant quadratic component) or unsaturation (significant linear component, but non-significant quadratic term) of local assemblages.

Hypothesis testing

We evaluated the importance of six oceanographic variables (Sea Surface Temperature (SST), SST range, salinity, salinity range, primary productivity and shelf area), which were used as proxies for three hypothesis categories currently used to explain canonic LDG (*Mittelbach et al., 2007*; *Pontarp et al., 2019*; Table 1). They were obtained from the Bio-Oracle Database v.2.0 (*Assis et al., 2018*) and GMED database (http://gmed.auckland.ac.nz) (information provided in the Data S3). Values were averaged over half-degree latitudinal bins, using only pixels on the coastal shelf (<200 m depth). The entire dataset of

Table 2 Environmental predictors of the LDG of benthic polychaetes along the SEP.

Proxy	VIF	Conditional random forest		Phylogenetic signal	
		Conditional importance	*p*-value	K	*p*-value
Median lat. range	6.26	**831.525**	**0.0001**	**0.307**	**0.003**
SST	9.33	**732.814**	**0.0001**	**0.332**	**0.001**
Salinity	3.71	**541.348**	**0.0001**	0.274	0.725
SST range	3.18	**217.978**	**0.0227**	0.290	0.162
Primary productivity	2.81	149.033	0.0805	**0.301**	**0.007**
Salinity range	1.88	129.715	0.0822	0.286	0.215
Shelf area	1.64	58.671	0.2966	–	–

Note:
These predictors are proxies of different hypotheses grouped into three categories (*sensu Pontarp et al., 2019*). Also shown are their level of collinearity (variance inflation factor, VIF), variable importance according a conditional random forest analysis and their phylogenetic signal (Blomberg's K). Statistically significant results and their respective *p*-values are shown in bold.

environmental predictors is available in the Data S3. In addition, we used the median latitudinal range of all species contained at each latitudinal bin as a coarse proxy of the 'long-term climatic stability hypothesis'. Since many species have latitudinal ranges spanning beyond the study area, we used the actual latitudinal ranges estimated for the entire eastern Pacific coast (from Antarctica to Alaska).

The role of all predictors shaping the LDG was evaluated using a random forest approach. Random forest, a machine learning method, offers multiple advantages over traditional GLM/GLS methods commonly used on previous studies (*Kreft & Jetz, 2007*; *Tittensor et al., 2010*): no error structure is assumed, it deals with classification and regression problems, it can handle a large number of predictors, and is robust to overfitting (*Breiman, 2001*; *Liaw & Wiener, 2002*). We used standard tuning hyperparameters, setting mtry = p/3 (where p is the number of predictors per tree), and node size = 5. Variable importance was estimated using a conditional random forest which accounts for the possible predictor collinearity (*Strobl et al., 2008*), based on the method proposed by *Altmann et al. (2010)*, with *p*-values based on 10,000 permutations, and implemented in the library ranger (*Wright & Ziegler, 2017*) in R. Nevertheless, the degree of predictor multicollinearity, measured as the variance inflation factor (*Dormann et al., 2013*; *Naimi et al., 2014*), was below the threshold of ten commonly used in the literature (Table 2). Partial dependence plots were used to inspect the conditional shape of the predicted species richness *vs.* selected predictors, using the library pdp (*Greenwell, 2017*) in R. A partial dependence plot allows us to visualize the functional relationship between the species richness and the predictor variables isolated from the effect of other predictors. The existence of spatial autocorrelation in the residuals of the model, another potential bias on the identification of variable importance (*Diniz-Filho, Bini & Hawkins, 2003*), was evaluated using a spatial autocorrelogram analysis (*i.e.*, Moran's I *vs.* geographic distance) with 1,000 runs in the library ncf in R (*Bjornstad, 2019*).

Although some of the environmental predictors (*e.g.*, SST) may be considered as a proxy for evolutionary hypotheses, we also evaluated the importance of evolutionary processes

on the LDG using two additional approaches. We used taxonomy as a coarse proxy of the phylogenetic relationships (*Soul & Friedman, 2015*), since we lack a full and well-resolved phylogeny for our species. First, we estimated three indices of α-phylogenetic diversity that summarizes different facets of the evolutionary relatedness of species, namely phylogenetic richness (Faith's PD), divergence (mean pairwise distance, MPD), and regularity (variation of pairwise distances, VPD) (*Tucker et al., 2017*). PD measures the total distance from each tip to the root of the tree, and it is used as a proxy of the total evolutionary history summed by all species in a given region (*Faith, 1992*; *Winter, Devictor & Schweiger, 2013*). The MPD (also known as AvTD, and Δ+, *Clarke & Warwick, 1998*) measures the mean phylogenetic distance (*i.e.*, branch length) among all pairs of species within a given latitudinal bin. We estimated their standardized effect sizes (SES = [observed − mean simulated]/SD simulated) of PD and MPD in order to account for their dependence on species richness, by randomizing the original species matrix 1,000 times. SES values lower than expected by the null model suggest phylogenetic clustering, whereas values higher than expected indicate phylogenetic overdispersion/convergence. We also estimated the VPD (*Warwick & Clarke, 1998*) as a measure of the regularity of the phylogenetic distances among all species in each latitudinal bin. Analyses were carried out using the libraries vegan (*Oksanen et al., 2019*) and picante (*Kembel et al., 2010*) in R.

As a second approach to estimate the importance of evolutionary processes shaping the LDG, we determined the phylogenetic signal of each proxy, using Blomberg's K (*Blomberg, Garland & Ives, 2003*) in order to test the importance of the Niche conservatism hypothesis (within the 'time for species accumulation' category). This was carried out using the median value of each proxy estimated across the entire latitudinal distribution. Larger values of K indicate a strong phylogenetic conservatism of the proxy. Analyses were carried out using the libraries ape (*Paradis, Claude & Strimmer, 2004*), paleotree (*Bapst, 2012*), and picante (*Kembel et al., 2010*) in R. The script used to run all analyses and to create each figure is provided in the Scripts S4.

RESULTS

Our compiled data set shows that the species diversity of benthic polychaetes along the SEP presents a hump-shaped LDG (Fig. 1B). The maximum richness (299 species) occurs at 42° S, which is two-fold higher than in southern Ecuador (3° S) where richness was 152 species. A secondary peak is located ca. 53° S, and then species richness drops abruptly towards 55° S, with species richness levels similar to those observed in Perú and southern Ecuador. The evaluation of potential sampling artifacts showed that rarefied species richness in local assemblages has the same trend observed when using the range-through approach (r = 0.49, *p* = 0.009, *n* = 29 bins, Fig. 1B), and no evidence of saturation was detected, as the linear but not the quadratic term of the local *vs.* regional OLS regression was significant (*p* = 0.008 and 0.179, respectively).

The random forest model showed a high accuracy predicting the LDG (Figs. 2A and 3A), with a pseudo-r^2 = 0.95. The model underestimated the species richness in the most extreme latitudinal bins (Fig. 2B), but overall spatial autocorrelation was not
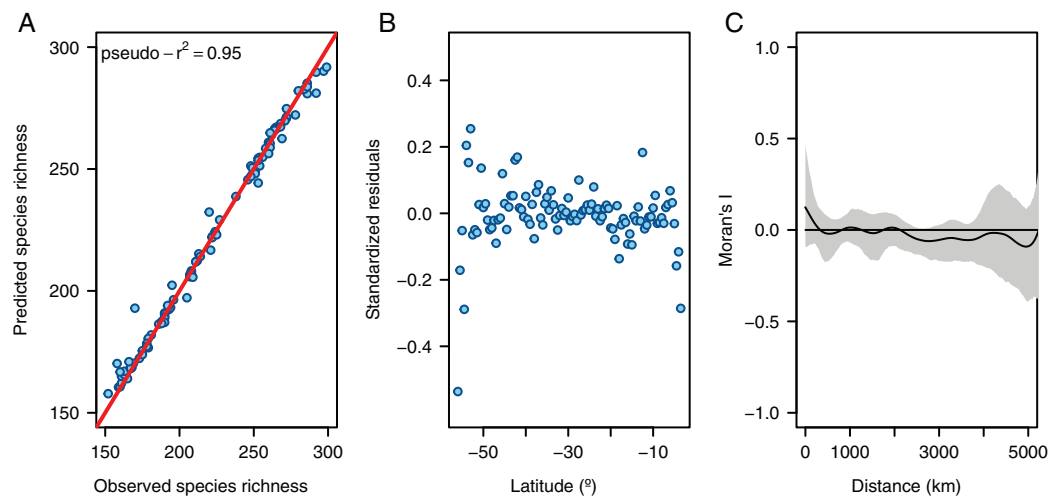
Figure 2 Diagnostic plots for the random forest model. (A) Observed *vs.* predicted species richness, (B) latitudinal distribution of standardized residuals, and (C) spatial autocorrelogram of the residuals (gray area shows the 95% confidence intervals of a null model).

Full-size ☑ DOI: 10.7717/peerj.12010/fig-2

detected at any spatial distance (Fig. 2C). Out of the seven predictors, four were significant (median latitudinal range, SST, salinity and SST range; ranked according to its importance, see Table 2). For a reference of the latitudinal variation of the selected variables see Figs. 3B, 3C. Partial dependence shows a hump-shaped response of species richness to SST (Fig. 4A), with maximum values at ca. 12 °C.

A more pronounced hump-shaped response of species richness was observed for SST range (Fig. 4B). Salinity and median latitudinal range showed a monotonic negative relationship with species richness, which reaches maximum values at the lowest salinity levels (Fig. 4C) and bins with lower median latitudinal ranges (Fig. 4D).

The three phylogenetic diversity indices showed different latitudinal trends and their correlation to species richness varied in sign and magnitude (Fig. 5). While PD_{SES} was positively correlated to species richness ($r_{Pearson} = 0.51$, $p < 0.0001$, Fig. 5A), MPD_{SES} did not show a significant relationship ($r_{Pearson} = 0.04$, $p = 0.69$, Fig. 5B), and VPD was negatively correlated with species richness ($r_{Pearson} = -0.49$, $p < 0.0001$, Fig. 5C). PD_{SES} values were not different than expected by the null models for most of the latitudinal gradient (Figs. 5A, 5B), except by areas around northern Chile and Perú (north of 20° S). Observed MDP_{SES} values were significantly lower than expected in two large areas centered around Chiloé (42° S), and northern Chile and Perú (ca. 15° S). For both PD_{SES} and MDP_{SES} these negative values suggested a phylogenetic clustering pattern. Blomberg's K was only significant for the median latitudinal range, SST and primary productivity (Table 2).

DISCUSSION

Our study supports the existence of a hump-shaped LDG for benthic polychaetes along the SEP, increasing the number of exceptions to the canonical pattern of higher species richness towards the tropics, both in the SEP and other regions (*i.e.*, *Moyano, 1991*;
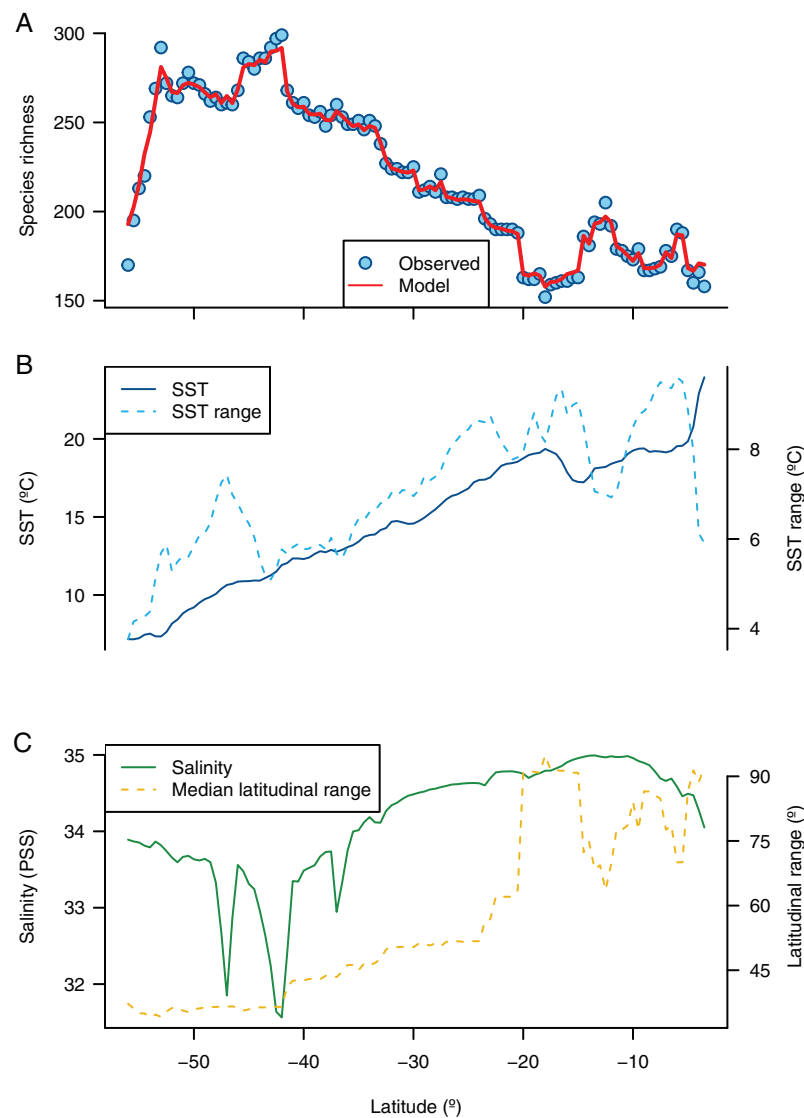
Figure 3 Environmental predictors of the latitudinal diversity gradient of benthic polychaetes along the SEP. (A) Observed and predicted species richness by a random forest model, (B) latitudinal variation of SST and SST range, and (C) latitudinal variation of salinity and median latitudinal range of species.

Full-size 🖼 DOI: 10.7717/peerj.12010/fig-3

Valdovinos, Navarrete & Marquet, 2003; *Willig, Kaufman & Stevens, 2003*; *Hillebrand, 2004a, 2004b*; *Kindlmann, Schödelbauerová & Dixon, 2007*; *Santelices, Bolton & Meneses, 2009*; *Rivadeneira et al., 2011*). Particularly, it is congruent with a recently published global study on latitudinal gradients of polychaetes (*Pamungkas, Glasby & Costello, 2021*). Our research also confirms previous results for benthic polychaetes along SEP (*Hernández, Moreno & Rozbaczylo, 2005*; *Moreno et al., 2006*) based on partial datasets of a more restricted scale and lower spatial resolution (*ca.*, 3° of latitude), and it seems robust to possible sampling artifacts, as the overall shape of the LDG still holds after accounting for differences in sampling in local assemblages. Therefore, the recorded pattern in this study reflects a robust biogeographic pattern for benthic polychaetes in the SEP.
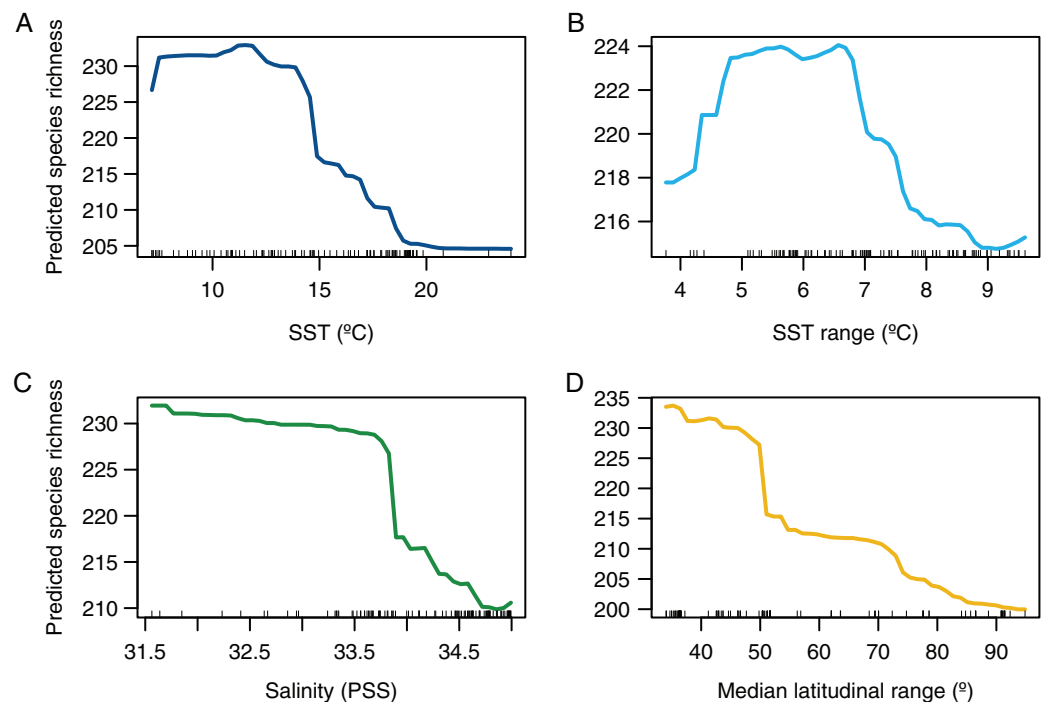
Figure 4 Partial dependence plot showing the relationship between predicted species richness of benthic polychaetes and the selected explanatory variables. (A) SST, (B) SST range, (C) salinity, and (D) median latitudinal range. Full-size ◱ DOI: 10.7717/peerj.12010/fig-4

Our analyses reveal that the LDG of polychaete species is well explained by a reduced subset of predictors that could be attributed to processes operating mainly, but not exclusively, at evolutionary timescales (Table 1). Overall, these significant variables (median latitudinal range, SST, salinity, and SST range) are proxies for the predictions of four (Long term climate stability, Niche conservatism, Temperature-dependent speciation, and Seasonal coexistence) of the six 'specific hypothesis', corresponding to all three hypotheses categories proposed in previous literature (*Mittelbach et al., 2007*; *Pontarp et al., 2019*). It is important to note that all the selected predictors are also linked to 'time for species accumulation' category, and particularly to the hypothesis of 'niche conservatism' (*Wiens & Donoghue, 2004*). This hypothesis is independently supported by the detection of significant phylogenetic signal (Blomberg's K) in the two most important predictors (median latitudinal range and SST). In addition, the LDG is also correlated to spatial patterns of phylogenetic diversity, measured according to two different indices (PD_{SES} and VPD).

In the context of a non-canonical LDG, as our case, the 'niche conservatism' hypothesis assumes that clades are originated outside of the tropics. Although we lack paleontological or phylogenetic information to fully test this idea, the prevalence of the median latitudinal range as the most important predictor of the species richness, being also the predictor with a high degree of phylogenetic conservatism, strongly supports the idea of an extra-tropical origin for many polychaetes species along the SEP. Areas of high species richness are associated to latitudinal bins with species with narrower latitudinal ranges, as predicted by
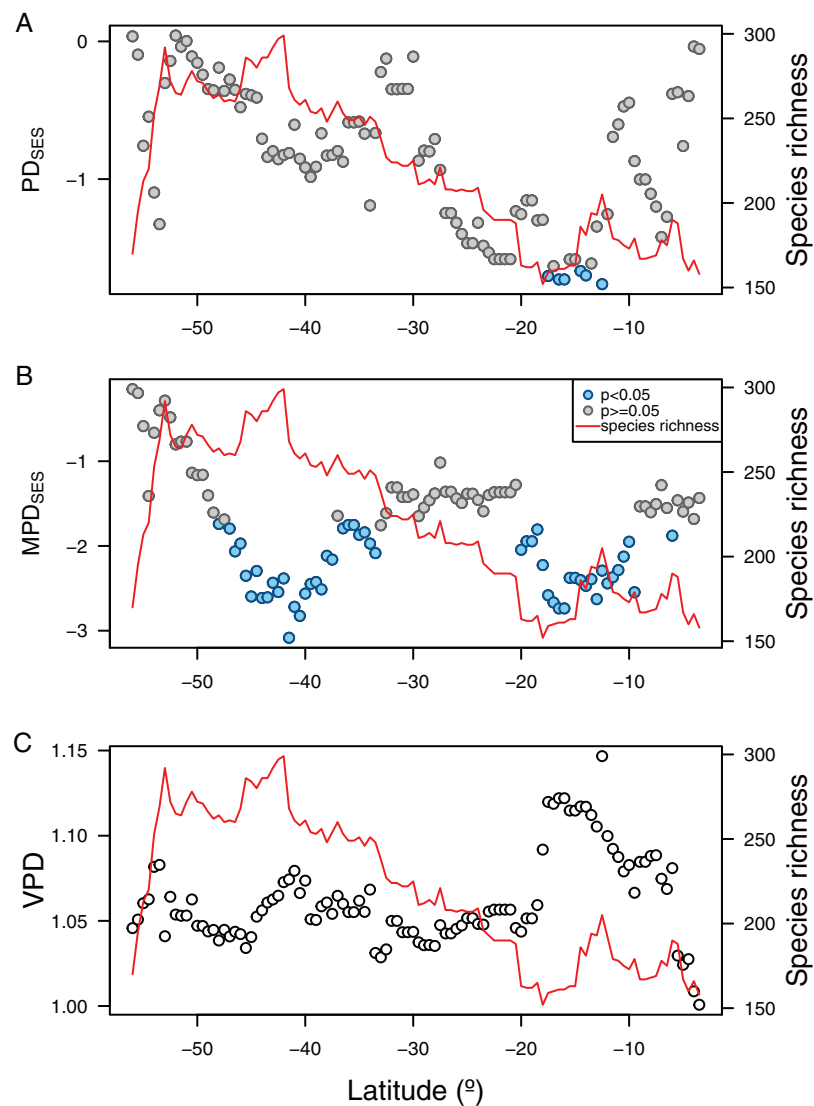
Figure 5 Latitudinal gradient of phylogenetic diversity of benthic polychaetes along SEP. (A) Faith's phylogenetic diversity (PD_{SES}), (B) mean pairwise distance (MDP_{SES}), and (C) variance in pairwise distance (VPD). Full-size 🔳 DOI: 10.7717/peerj.12010/fig-5

the 'Rapoport's rule' (*Stevens, 1989*; *Hernández, Moreno & Rozbaczylo, 2005*). Our results reinforce the idea that the Southern Chile fjord area, particularly the Chiloé region, may act as a source of new species of marine polychaetes along SEP creating a hotspot of diversity (*Moreno et al., 2006*).

A possible historical explanation for the origin of this hotspot is related with the fact that during the Last Glacial Maximum (LGM) the Patagonian Ice Sheet covered a large portion of the fjords probably pushing many species from the canals into the glacial coastal line (*Davies et al., 2020*). Indeed, it has been shown that the populations of the southern bull-kelp (*Durvillaea antarctica*) on the fjord area correspond to recent, probably post glacial, re-colonization (*Fraser et al., 2010*), implying the unavailability of this region during the LGM. Chiloé Island corresponds to the northern most coastal area where the ice

sheet reached sea level, indeed the north-west part of the island has remained ice-free since the last 35,000 years (*Davies et al., 2020*). Therefore, the waters around Chiloé Island, especially in the north-west corner, might have worked as marine coastal refugia preserving species with previous more extended distributions towards the south.

In addition, the relationship between the LDG and phylogenetic diversity indices also suggest the importance of local diversification processes (*i.e.*, origination and extinction, *Davies & Buckley, 2011*; *Fritz & Rahbek, 2012*; *Eme et al., 2020*). Thus, the significant phylogenetic clustering found in the fjords area (*i.e.*, many species are phylogenetically closely related) suggests that this area may have not only acted as a potential glacial refugia, but also a hotspot of *in situ* diversification, as seen in the fossil record of marine mollusks of the region (*Kiel & Nielsen, 2010*).

Oceanographically, bidirectional dispersion from this area could be facilitated because precisely at this latitude the West Wind Drift diverges into the Humboldt and Cape Horn currents; running north and south, respectively (*Strub et al., 2019*). Biologically, the extent of the dispersion might be limited due to the strong niche conservatism detected on latitudinal range and median SST experienced for the species. Additionally, the West Wind Drift might work as a colonization pathway of the SEP from the western Pacific. Altogether, in the same way as the canonical LDG shows a decline in diversity while moving away from the tropics; on this case the decline occurs while moving away from Chiloé Island.

On another hand, the existence of phylogenetic clustering in areas of low species richness such as northern Chile and Perú is more consistent with a negative net diversification trend, produced by high extinction rates coupled to species sorting (*via* selective survival). Paleontological studies have shown the existence of high extinction rates of marine forms during the late Neogene–Pleistocene along the Peruvian and northern Chile coast (*Herm, 1969*; *Kiel & Nielsen, 2010*), which are linked to the Neogene onset of the modern Humboldt Current (*Dekens, Ravelo & McCarthy, 2007*). In particular, extinction rates of bivalves and marine vertebrates at that time were phylogenetically clustered (*Rivadeneira & Marquet, 2007*; *Villafaña & Rivadeneira, 2014*), likely associated to a strong environmental filtering (*e.g.*, thermal tolerance). If similar processes affected polychaetes at SEP, a high extinction rate with higher survivorship of particular clades *via* environmental filtering process, may lead to an impoverished species richness highly phylogenetically clustered, as it characterizes the northern Chile and Perú regions.

Despite the prevalence of evolutionary-based explanations for the LDG of polychaetes, the lack of phylogenetic signal of the SST range and salinity suggest that processes operating at ecological timescales (*i.e.*, 'ecological limitations') may be also important. In fact SST range is much higher in vast areas of Perú and northern Chile, likely related to the effect of 'El Niño' events, which governs the inter-annual variability of the sea water temperature (*Shaffer et al., 1999*). Associated with this and congruent with the selection of SST as a predictor of our model, a recent study also refers to SST as an important factor to globally shape the polychaetes LDG (*Pamungkas, Glasby & Costello, 2021*).

CONCLUSIONS

The SEP provides a natural laboratory for marine biogeography studies given the high diversity of shapes of the LDG in marine taxa. In addition to the existence of canonical LDG (*Ojeda, Labra & Muñoz, 2000*; *Astorga et al., 2003*) and inverse LDG (*Santelices & Marquet, 1998*; *Fernández et al., 2009*; *Rivadeneira et al., 2011*), our results validate the existence of a hump-shaped LDG in marine benthic polychaetes centered ca. Chiloé Island (42° S). More importantly, the same conceptual framework used to study the canonical LDG phenomenon could also be used to investigate non-canonical LDGs. The latitudinal patterns of distribution of benthic polychaetes needs to be evaluated in other geographical areas, *e.g.*, central and northeastern Pacific coast, in order to fully understand the generality of the non-canonical LDG, and whether the underlying processes are the same in other regions. In the absence of suitable fossil record for polychaetes, molecular phylogenies of selected clades may shed more direct evidence of the importance of evolutionary processes shaping the LDG in this group. Future studies may be also evaluating the role of dispersal of taxa from other areas of the southern ocean (*e.g.*, *Glasby & Alvarez, 1999*; *Glasby, 2005*) shaping the 'Chiloé hotspot'. An integration of functional traits of species, and phylogenetic and phylogeographic analysis may help to test and validate the importance of ecological and evolutionary determinants of the diversity of benthic polychaetes.

ACKNOWLEDGEMENTS

ADDITIONAL INFORMATION AND DECLARATIONS

Funding

was supported with his personal funds. The research of Marcelo M Rivadeneira was funded by ANID/FONDECYT 1200843 and by the "Concurso de Fortalecimiento al Desarrollo Científico de Centros Regionales 2020-R20F0008-CEAZA". There was no additional external funding received for this study. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests

Nicolás Rozbaczylo is employed by FAUNAMAR Ltda.

Author Contributions

- Rodrigo A. Moreno conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Fabio A. Labra conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Darko D. Cotoras analyzed the data, authored or reviewed drafts of the paper, and approved the final draft.
- Patricio A. Camus conceived and designed the experiments, analyzed the data, authored or reviewed drafts of the paper, and approved the final draft.
- Dimitri Gutiérrez conceived and designed the experiments, performed the experiments, authored or reviewed drafts of the paper, and approved the final draft.

- Luis Aguirre conceived and designed the experiments, performed the experiments, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Nicolás Rozbaczylo conceived and designed the experiments, performed the experiments, authored or reviewed drafts of the paper, and approved the final draft.
- Elie Poulin conceived and designed the experiments, performed the experiments, authored or reviewed drafts of the paper, and approved the final draft.
- Nelson A. Lagos analyzed the data, authored or reviewed drafts of the paper, and approved the final draft.
- Daniel Zamorano analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Marcelo M. Rivadeneira conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.

Field Study Permissions

The following information was supplied relating to field study approvals (*i.e.*, approving body and any reference numbers):

Field collection was supported by research cruises CIMAR Fiordos 13, 14, 15, 17 and 18 (Comité Oceanográfico Nacional, Chile). There was no field study approval number. The research survey was directly supported by the Comité Oceanográfico Nacional, Chile, by allowing researchers to stay on board the research cruises CIMAR.

Data Availability

The following information was supplied regarding data availability:

Raw data and and R script are available in the Supplemental Files.

Supplemental Information

Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.12010#supplemental-information.

REFERENCES

Allen PA, Gillooly JF, Savage VM, Brown JH. 2006. Kinetic effects of temperature on rates of genetic divergence and speciation. *Proceedings of the National Academy of Sciences of the United States of America* **103(24)**:9130–9135 DOI 10.1073/pnas.0603587103.

Altmann A, Toloşi L, Sander O, Lengauer T. 2010. Permutation importance: a corrected feature importance measure. *Bioinformatics* **26(10)**:1340–1347 DOI 10.1093/bioinformatics/btq134.

Assis J, Tyberghein L, Bosch S, Verbruggen H, Serrão EA, De Clerck O. 2018. Bio-ORACLE v2. 0: extending marine data layers for bioclimatic modelling. *Global Ecology and Biogeography* **27(3)**:277–284 DOI 10.1111/geb.12693.

Astorga A, Fernández M, Boschi EE, Lagos N. 2003. Two oceans, two taxa and one mode of development: latitudinal diversity patterns of South American crabs and test for possible causal processes. *Ecology Letters* **6(5)**:420–427 DOI 10.1046/j.1461-0248.2003.00445.x.

Azovsky A, Garlitska L, Chertoprud E. 2016. Multi-scale taxonomic diversity of marine harpacticoids: does it differ at high and low latitudes? *Marine Biology* **163(5)**:94 DOI 10.1007/s00227-016-2876-0.

Bapst DW. 2012. Paleotree: an R package for paleontological and phylogenetic analyses of evolution. *Methods in Ecology and Evolution* **3(5)**:803–807 DOI 10.1111/j.2041-210X.2012.00223.x.

Bjornstad ON. 2019. NCF: spatial covariance functions. R package version 1.2-8. *Available at* *https://CRAN.R-project.org/package=ncf*.

Blomberg SP, Garland T, Ives AR. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57(4)**:717–745 DOI 10.1111/j.0014-3820.2003.tb00285.x.

Boschi EE. 2000. Biodiversity of marine decapod brachyurans of the Americas. *Journal of Crustacean Biology* **20(5)**:337–342 DOI 10.1163/1937240X-90000036.

Breiman L. 2001. Random forests. *Machine Learning* **45(1)**:5–32 DOI 10.1023/A:1010933404324.

Chaudhary C, Saeedi H, Costello MJ. 2016. Bimodality of latitudinal gradients in marine species richness. *Trends in Ecology & Evolution* **31(9)**:670–676 DOI 10.1016/j.tree.2016.06.001.

Chown SL, Gaston KJ. 2000. Areas, cradles and museums: the latitudinal gradient in species richness. *Trends in Ecology & Evolution* **15(8)**:311–315 DOI 10.1016/S0169-5347(00)01910-8.

Clarke KR, Warwick RM. 1998. A taxonomic distinctness index and its statistical properties. *Journal of Applied Ecology* **35(4)**:523–531 DOI 10.1046/j.1365-2664.1998.3540523.x.

Costello MJ, Chaudhary C. 2017. Marine biodiversity, biogeography, deep-sea gradients, and conservation. *Current Biology* **27(11)**:511–527 DOI 10.1016/j.cub.2017.04.060.

Currie DJ. 1991. Energy and large-scale patterns of animal-and plant-species richness. *The American Naturalist* **137(1)**:27–49 DOI 10.1086/285144.

Davies TJ, Buckley LB. 2011. Phylogenetic diversity as a window into the evolutionary and biogeographic histories of present-day richness gradients for mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences* **366(1576)**:2414–2425 DOI 10.1098/rstb.2011.0058.

Davies JN, Darvill CM, Lovell H, Bendle JM, Dowdeswell JA, Fabel D, García J, Geiger A, Glasser NF, Gheorghiu DM, Harrison S, Hein AS, Kaplan MR, Martin JRV, Mendelova M, Palmer A, Pelto A, Rodés Á, Sagredo EA, Smedley RK, Smellie JL, Thorndycraft VR. 2020. The evolution of the Patagonian Ice Sheet from 35 ka to the present day (PATICE). *Earth-Science Reviews* **204(3)**:103152 DOI 10.1016/j.earscirev.2020.103152.

Dekens PS, Ravelo AC, McCarthy MD. 2007. Warm upwelling regions in the Pliocene warm period. *Paleoceanography* **22(3)**:PA3211–PA3n/a DOI 10.1029/2006PA001394.

Desqueyroux R, Moyano G. 1987. Zoogeografía de demospongias chilenas. *Boletín de la Sociedad de Biología de Concepción, Chile* **58**:39–66.

Diniz-Filho JAF, Bini LM, Hawkins BA. 2003. Spatial autocorrelation and red herrings in geographical ecology. *Global Ecology and Biogeography* **12(1)**:53–64 DOI 10.1046/j.1466-822X.2003.00322.x.

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **36(1)**:27–46 DOI 10.1111/j.1600-0587.2012.07348.x.

Dynesius M, Jansson R. 2000. Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. *Proceedings of the National Academy of Sciences of the United States of America* **97(16)**:9115–9120 DOI 10.1073/pnas.97.16.9115.

Edgar GJ, Alexander TJ, Lefcheck JS, Bates AE, Kininmonth SJ, Thomson RJ, Duffy JE, Costello MJ, Stuart-Smith RD. 2017. Abundance and local-scale processes contribute to multi-phyla gradients in global marine diversity. *Science Advances* **3(10)**:e1700419 DOI 10.1126/sciadv.1700419.

Ellingsen KE, Clarke KR, Somerfield PJ, Warwick RM. 2005. Taxonomic distinctness as a measure of diversity applied over a large scale: the benthos of the Norwegian continental shelf. *Journal of Animal Ecology* **74(6)**:1069–1079 DOI 10.1111/j.1365-2656.2005.01004.x.

Eme D, Anderson MJ, Myers EM, Roberts CD, Liggins L. 2020. Phylogenetic measures reveal eco-evolutionary drivers of biodiversity along a depth gradient. *Ecography* **43(5)**:689–702 DOI 10.1111/ecog.04836.

Evans KL, Warren PH, Gaston KJ. 2005. Species-energy relationships at the macroecological scale: a review of the mechanisms. *Biological Reviews* **80(1)**:1–25 DOI 10.1017/S1464793104006517.

Faith DP. 1992. Conservation evaluation and phylogenetic diversity. *Biological Conservation* **61(1)**:1–10 DOI 10.1016/0006-3207(92)91201-3.

Fernández M, Astorga A, Navarrete SA, Valdovinos C, Marquet PA. 2009. Deconstructing latitudinal species richness patterns in the ocean: does larval development hold the clue? *Ecology Letters* **12(7)**:601–611 DOI 10.1111/j.1461-0248.2009.01315.x.

Fraser CI, Thiel M, Spencer HG, Waters JM. 2010. Contemporary habitat discontinuity and historic glacial ice drive genetic divergence in Chilean kelp. *BMC Evolutionary Biology* **10(1)**:203 DOI 10.1186/1471-2148-10-203.

Fritz SA, Rahbek C. 2012. Global patterns of amphibian phylogenetic diversity. *Journal of Biogeography* **39(8)**:1373–1382 DOI 10.1111/j.1365-2699.2012.02757.x.

Glasby CJ, Alvarez B. 1999. Distribution patterns and biogeographic analysis of Austral Polychaeta (Annelida). *Journal of Biogeography* **26(3)**:507–533 DOI 10.1046/j.1365-2699.1999.00297.x.

Glasby CJ. 2005. Polychaete distribution patterns revisited: an historical explanation. *Marine Ecology* **26(3–4)**:235–245 DOI 10.1111/j.1439-0485.2005.00059.x.

Gotelli NJ, Colwell RK. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* **4(4)**:379–391 DOI 10.1046/j.1461-0248.2001.00230.x.

Gray JS. 2002. Species richness of marine soft sediments. *Marine Ecology Progress Series* **244**:285–297 DOI 10.3354/meps244285.

Greenwell BM. 2017. PDP: an R Package for constructing partial dependence plots. *The R journal* **9(1)**:421–436 DOI 10.32614/RJ-2017-016.

Häussermann V, Försterra G. 2005. Distribution patterns of Chilean shallow-water sea anemones (Cnidaria: Anthozoa: Actiniaria, Corallimorpharia); with a discussion of the taxonomic and zoogeographic relationships between the actinofauna of the South East Pacific, the South West Atlantic and the Antarctic. *Scientia Marina* **69**:91–102 DOI 10.3989/SCIMAR.2005.69S291.

Hawkins BA, Porter EE, Diniz-Filho JAF. 2003. Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. *Ecology* **84**:1608–1623 DOI 10.1890/0012-9658(2003)084[1608:PAHAPO]2.0.CO;2.

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 CE, Moreno RA, Rozbaczylo N. 2005. Biogeographical patterns and Rapoport's rule in southeastern Pacific benthic polychaetes of the Chilean coast. *Ecography* **28**:363–373 DOI 10.1111/j.0906-7590.2005.04013.x.

Hillebrand H. 2004a. On the generality of the latitudinal diversity gradient. *The American Naturalist* **163**:192–211 DOI 10.1086/381004.

Hillebrand H. 2004b. Strength, slope and variability of marine latitudinal gradients. *Marine Ecology Progress Series* **273**:251–268 DOI 10.3354/meps273251.

Ibanez-Erquiaga B, Pacheco AS, Rivadeneira MM, Tejada CL. 2018. Biogeographical zonation of rocky intertidal communities along the coast of Peru (3.5–13.5° S Southeast Pacific). *PLOS ONE* **13**:e0208244 DOI 10.1371/journal.pone.0208244.

Jablonski D, Belanger CL, Berke SK, Huang S, Krug AZ, Roy K, Tomašových A, Valentine JW. 2013. Out of the tropics, but how? Fossils, bridge species, and thermal ranges in the dynamics of the marine latitudinal diversity gradient. *Proceedings of the National Academy of Sciences of the United States of America* **110**:10487–10494 DOI 10.1073/pnas.1308997110.

Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, Blomberg SP, Webb CO. 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* **26**:1463–1464 DOI 10.1093/bioinformatics/btq166.

Kiel S, Nielsen SN. 2010. Quaternary origin of the inverse latitudinal diversity gradient among southern Chilean mollusks. *Geology* **38**:955–958 DOI 10.1130/G31282.1.

Kindlmann P, Schödelbauerová I, Dixon AFG. 2007. Inverse latitudinal gradients in species diversity. In: Storch D, Marquet P, Brown JH, eds. *Scaling Biodiversity*. Cambridge: Cambridge University Press, 246–257.

Kinlock NL, Prowant L, Herstoff EM, Foley CM, Akin-Fajiye M, Bender N, Umarani M, Ryu HY, Şen B, Gurevitch J. 2018. Explaining global variation in the latitudinal diversity gradient: meta-analysis confirms known patterns and uncovers new ones. *Global Ecology and Biogeography* **27(1)**:125–141 DOI 10.1111/geb.12665.

Kreft H, Jetz W. 2007. Global patterns and determinants of vascular plant diversity. *Proceedings of the National Academy of Sciences of the United States of America* **104(14)**:5925–5930 DOI 10.1073/pnas.0608361104.

Lancellotti DA, Vásquez JA. 2000. Zoogeografía de macroinvertebrados bentónicos de la costa de Chile: contribución para la conservación marina. *Revista Chilena de Historia Natural* **73(1)**:99–129 DOI 10.4067/S0716-078X2000000100011.

Lancellotti DA, Vásquez JA. 1999. Biogeographical patterns of benthic macroinvertebrates in the Southeastern Pacific litoral. *Journal of Biogeography* **28**:1001–1006 DOI 10.1046/j.1365-2699.1999.00344.x.

Lee MR, Riveros M. 2012. Latitudinal trends in the species richness of free-living marine nematode assemblages from exposed sandy beaches along the coast of Chile (18–42° S). *Marine Ecology* **33(3)**:317–325 DOI 10.1111/j.1439-0485.2011.00497.x.

Liaw A, Wiener M. 2002. Classification and regression by randomForest. *Rnews* **2**:18–22.

Menegotto A, Rangel TF. 2018. Mapping knowledge gaps in marine diversity reveals a latitudinal gradient of missing species richness. *Nature Communications* **9(1)**:4713 DOI 10.1038/s41467-018-07217-7.

Menegotto A, Kurtz MN, Lana PDC. 2019. Benthic habitats do show a significant latitudinal diversity gradient: a comment on Kinlock et al. *2018 Global Ecology and Biogeography* **28(11)**:1712–1717 DOI 10.1111/geb.12970.

Mittelbach GG, Schemske DW, Cornell HV, Allen AP, Brown JM, Bush MB, Harrison SP, Hurlbert AH, Knowlton N, Lessios HA, McCain CM, McCune AR, McDade LA,

McPeek MA, Near TJ, Price TD, Ricklefs RE, Roy K, Sax DF, Schluter D, Sobel JM, Turelli M. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters* **10(4)**:315–331 DOI 10.1111/j.1461-0248.2007.01020.x.

Montiel A, Gerdes D, Hilbig B, Arntz WE. 2005. Polychaete assemblages on the Magellan and Weddell Sea shelves: comparative ecological evaluation. *Marine Ecology Progress Series* **297**:189–202 DOI 10.3354/meps297189.

Moreno RA, Hernández CE, Rivadeneira MM, Vidal MA, Rozbaczylo N. 2006. Patterns of endemism in south-eastern Pacific benthic polychaetes of the Chilean coast. *Journal of Biogeography* **33(4)**:750–759 DOI 10.1111/j.1365-2699.2005.01394.x.

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

Naimi B, Hamm NA, Groen TA, Skidmore AK, Toxopeus AG. 2014. Where is positional uncertainty a problem for species distribution modelling? *Ecography* **37(2)**:191–203 DOI 10.1111/j.1600-0587.2013.00205.x.

Navarrete AH, Sellanes J, Pardo-Gandarillas MC, Sirenko B, Eernisse DJ, Camus PA, Ojeda FP, Ibáñez CM. 2020. Latitudinal distribution of polyplacophorans along the South-eastern Pacific coast: unravelling biases in geographical diversity patterns. *Marine Biodiversity* **50(4)**:1–12 DOI 10.1007/s12526-020-01060-0.

OBIS. 2021. Ocean biodiversity information system. Intergovernmental Oceanographic Commission of UNESCO. *Available at* www.obis.org (accessed 17 May 2021).

Ojeda FP, Labra FA, Muñoz AA. 2000. Biogeographic patterns of Chilean littoral fishes. *Revista Chilena de Historia Natural* **73(4)**:625–641 DOI 10.4067/S0716-078X2000000400007.

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H. 2019. Vegan: community ecology package. R package version 2.5–5. *Available at* http://CRAN.R-project.org/package=vegan.

Pamungkas J, Glasby CJ, Costello MJ. 2021. Biogeography of polychaete worms (Annelida) of the world. *Marine Ecology Progress Series* **657**:147–159 DOI 10.3354/meps13531.

Paradis E, Claude J, Strimmer K. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20(2)**:289–290 DOI 10.1093/bioinformatics/btg412.

Pianka ER. 1966. Latitudinal gradients in species diversity: a review of concepts. *The American Naturalist* **100(910)**:33–46 DOI 10.1086/282398.

Platnick NI. 1991. Patterns of biodiversity: tropical *vs.* temperate. *Journal of Natural History* **25(5)**:1083–1088 DOI 10.1080/00222939100770701.

Pontarp M, Bunnefeld L, Cabral JS, Etienne RS, Fritz SA, Gillespie R, Graham CH, Hagen O, Hartig F, Huang S, Jansson R, Maliet O, Münkemüller T, Pellissier L, Rangel TF, Storch D, Wiegand T, Hurlbert AH. 2019. The latitudinal diversity gradient: novel understanding through mechanistic eco-evolutionary models. *Trends in Ecology & Evolution* **34(3)**:211–223 DOI 10.1016/j.tree.2018.11.009.

Ricklefs RE. 1987. Community diversity: relative roles of local and regional processes. *Science* **235**:167–171 DOI 10.1126/science.235.4785.167.

Rivadeneira MM, Marquet PA. 2007. Selective extinction of late Neogene bivalves on the temperate Pacific coast of South America. *Paleobiology* **33**:455–468 DOI 10.1666/06042.1.

Rivadeneira MM, Nielsen SN. 2017. Diversification dynamics, species sorting, and changes in the functional diversity of marine benthic gastropods during the Pliocene-Quaternary at temperate western South America. *PLOS ONE* **12**:e0187140 DOI 10.1371/journal.pone.0187140.

Rivadeneira MM, Fernández M, Navarrete SA. 2002. Latitudinal trends of species diversity in rocky intertidal herbivore assemblages: spatial scale and the relationship between local and regional species richness. *Marine Ecology Progress Series* **245**:123–131 DOI 10.3354/meps245123.

Rivadeneira MM, Thiel M, González ER, Haye PA. 2011. An inverse latitudinal gradient of diversity of peracarid crustaceans along the Pacific Coast of South America: out of the deep south. *Global Ecology and Biogeography* **20**:437–448 DOI 10.1111/j.1466-8238.2010.00610.x.

Rivadeneira MM, Poore GCB. 2020. Latitudinal gradient of diversity of marine crustaceans: towards a synthesis. In: Poore GCB, Thiel M, eds. *The Natural History of the Crustacea.* Vol. 8. New York: Oxford University Press, 389–413.

Rohde K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* **65(3)**:514–527 DOI 10.2307/3545569.

Rosenzweig ML. 1995. *Species diversity in space and time.* Cambridge: Cambridge University Press, 436.

Robertson DR, Cramer KL. 2009. Shore fishes and biogeographic subdivisions of the Tropical Eastern Pacific. *Marine Ecology Progress Series* **380**:1–17 DOI 10.3354/meps07925.

Roy K, Jablonski D, Valentine JW, Rosenberg G. 1998. Marine latitudinal diversity gradients: tests of causal hypotheses. *Proceedings of the National Academy of Sciences of the United States of America* **95(7)**:3699–3702 DOI 10.1073/pnas.95.7.3699.

Sanders HL. 1968. Marine benthic diversity: a comparative study. *The American Naturalist* **102(925)**:243–282 DOI 10.1086/282541.

Santelices B, Marquet PA. 1998. Seaweeds, latitudinal diversity patterns, and Rapoport's rule. *Diversity and Distributions* **4(2)**:71–75 DOI 10.1046/j.1472-4642.1998.00005.x.

Santelices B, Bolton JJ, Meneses I. 2009. Marine algal communities. In: Whitman JD, Roy K, eds. *Marine macroecology.* Chicago: University of Chicago Press, 153–192.

Santelices B. 1982. Caracterización fitogeográfica de la costa temperada del Pacífico de Sudamérica. Verificación de hipótesis y consecuencias ecológicas. *Archivos de Biología y Medicina Experimentales* **15**:513–524.

Shaffer G, Hormazabal S, Pizarro O, Salinas S. 1999. Seasonal and interannual variability of currents and temperature off central Chile. *Journal of Geophysical Research: Oceans* **104(C12)**:29951–29961 DOI 10.1029/1999JC900253.

Soul LC, Friedman M. 2015. Taxonomy and phylogeny can yield comparable results in comparative paleontological analyses. *Systematic Biology* **64(4)**:608–620 DOI 10.1093/sysbio/syv015.

Spalding MD, Fox HE, Allen GR, Davidson N, Ferdaña ZA, Finlayson M, Halpern BS, Jorge MA, Lombana A, Lourie SA, Martin KD, McManus E, Molnar J, Recchia CA, Robertson J. 2007. Marine ecoregions of the world: a bioregionalization of Coastal and Shelf Areas. *BioScience* **57(7)**:573–583 DOI 10.1641/B570707.

Srivastava DS. 1999. Using local-regional richness plots to test for species saturation: pitfalls and potentials. *Journal of Animal Ecology* **68(1)**:1–6 DOI 10.1046/j.1365-2656.1999.00266.x.

Strobl C, Boulesteix AL, Kneib T, Augustin T, Zeileis A. 2008. Conditional variable importance for random forests. *BMC Bioinformatics* **9**:307 DOI 10.1186/1471-2105-9-307.

Stevens GC. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. *The American Naturalist* **133**:240–256.

Strub PT, James C, Montecino V, Rutllant JA, Blanco JL. 2019. Ocean circulation along the southern Chile transition region (38°-46°S): Mean, seasonal and interannual variability, with a focus on 2014-2016. *Progress in Oceanography* **172**:159–198 DOI 10.1016/j.pocean.2019.01.004.

Tittensor DP, Mora C, Jetz W, Lotze HK, Ricard D, Vanden-Berghe E, Worm B. 2010. Global patterns and predictors of marine biodiversity across taxa. *Nature* **466**:1098–1101 DOI 10.1038/nature09329.

Tolimieri N, Anderson MJ. 2010. Taxonomic distinctness of demersal fishes of the California current: moving beyond simple measures of diversity for marine ecosystem-based management. *PLOS ONE* **5**:e10653 DOI 10.1371/journal.pone.0010653.

Tomašových A, Kennedy JD, Betzner TJ, Kuehnle NB, Edie S, Kim S, Supriya K, White AE, Rahbek C, Huang S. 2016. Unifying latitudinal gradients in range size and richness across marine and terrestrial systems. *Proceedings of the Royal Society B: Biological Sciences* **283(1830)**:20153027 DOI 10.1098/rspb.2015.3027.

Tucker CM, Cadotte MW, Carvalho SB, Davies TJ, Ferrier S, Fritz SA, Grenyer R, Helmus MR, Jin LS, Mooers AO, Pavoine S. 2017. A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biological Reviews* **92(2)**:698–715 DOI 10.1111/brv.12252.

Valdovinos C, Navarrete SA, Marquet PA. 2003. Mollusk species diversity in the Southeastern Pacific: why are there more species towards the pole? *Ecography* **26(2)**:139–144 DOI 10.1034/j.1600-0587.2003.03349.x.

Valentine JW, Jablonski D. 2015. A twofold role for global energy gradients in marine biodiversity trends. *Journal of Biogeography* **42(6)**:997–1005 DOI 10.1111/jbi.12515.

Vegas-Velez M. 1980. Algunas consideraciones biogeográficas sobre el Pacífico sudoriental. *Boletim do Instituto Oceanográfico* **29(2)**:371–373 DOI 10.1590/S0373-55241980000200074.

Villafaña JA, Rivadeneira MM. 2014. Rise and fall in diversity of Neogene marine vertebrates on the temperate Pacific coast of South America. *Paleobiology* **40(4)**:659–674 DOI 10.1666/13069.

Warwick RM, Clarke KR. 1998. Taxonomic distinctness and environmental assessment. *Journal of Applied Ecology* **35(4)**:532–543 DOI 10.1046/j.1365-2664.1998.3540532.x.

Weir JT, Schluter D. 2007. The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science* **315(5818)**:1574–1576 DOI 10.1126/science.1135590.

Wiens JJ, Donoghue MJ. 2004. Historical biogeography, ecology and species richness. *Trends in Ecology & Evolution* **19(12)**:639–644 DOI 10.1016/j.tree.2004.09.011.

Wiens JJ, Graham CH. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution and Systematics* **36(1)**:519–539 DOI 10.1146/annurev.ecolsys.36.102803.095431.

Willig MR, Kaufman DM, Stevens RD. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution and Systematics* **34(1)**:273–309 DOI 10.1146/annurev.ecolsys.34.012103.144032.

Winter M, Devictor V, Schweiger O. 2013. Phylogenetic diversity and nature conservation: where are we? *Trends in Ecology & Evolution* **28(4)**:199–204 DOI 10.1016/j.tree.2012.10.015.

Woodd-Walker RS, Ward P, Clarke A. 2002. Large-scale patterns in diversity and community structure of surface water copepods from the Atlantic Ocean. *Marine Ecology Progress Series* **236**:189–203 DOI 10.3354/meps236189.

Woolley SNC, Tittensor DP, Dunstan PK, Guillera-Arroita G, Lahoz-Monfort JJ, Wintle BA, Worm B, O'Hara TD. 2016. Deep-sea diversity patterns are shaped by energy availability. *Nature* **533(7603)**:393–396 DOI 10.1038/nature17937.

Worm B, Tittensor DP. 2018. *A theory of global biodiversity. monographs in population biology 60.* Princeton, NJ: Princeton University Press, 214.

WoRMS Editorial Board. 2021. World register of marine species. *Available at* https://www. marinespecies.org at VLIZ (accessed 24 August 2020).

Wright MN, Ziegler A. 2017. Ranger: a fast implementation of random forests for high dimensional data in C++ and R. *Journal of Statistical Software* **77(1)**:1–17 DOI 10.18637/jss.v077.i01.

Wu J, Chen H, Zhang Y. 2016. Latitudinal variation in nematode diversity and ecological roles along the Chinese coast. *Ecology and Evolution* **6(22)**:8018–8027 DOI 10.1002/ece3.2538.