Field Data Reveal Strong Latitudinal Gradients in Australian Marine Bivalves

Matthew Kerr¹, Nicole Currie¹, Matthew Kosnik¹, and John Alroy¹

¹Macquarie University

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Abstract

Latitudinal diversity gradients are among the most studied macroecological phenomena. However, they tend to be described using large composite datasets that often show taxonomic and geographic sampling bias. Here we describe a latitudinal gradient in marine bivalves along the eastern coastline of Australia, spanning 2,667km of coastline and 20° of latitude. We utilise a large, structured field dataset (5,552 individuals) in conjunction with a routine macroecological dataset downloaded from the Ocean Biogeographic Information System (OBIS - 36,226 specimens). Diversity is estimated using a series of analytical methods to account for undersampling, and biogeographic gradients in taxonomic composition are quantified and compared to existing biogeographical schemes. A strong latitudinal gradient is present in both datasets. However, the strength of the gradient depends on the dataset and analytical method used. The inclusion of observational data in the macroecological dataset obscures any latitudinal pattern. The documented biogeographic gradients are consistent with global and regional reconstructions. However, we find evidence for a strong transition zone between two clusters. Although latitudinal gradients inferred from large macroecological datasets such as OBIS can match those inferred from field data, care should be taken when curating downloaded data as small changes in protocol can generate very different results. By contrast, even modest regional field datasets can readily reconstruct latitudinal patterns.

Field Data Reveal Strong Latitudinal Diversity Gradients in Australian Marine Bivalves

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Matthew R Kerr^{1*}, Nicole Currie¹, Matthew A Kosnik¹, John Alroy¹

¹ Department of Biological Sciences, Macquarie University, NSW 2109, Australia

*Corresponding Author

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Abstract

Latitudinal diversity gradients are among the most studied macroecological phenomena. However, they tend to be described using large composite datasets that often show taxonomic and geographic sampling bias. Here we describe a latitudinal gradient in marine bivalve diversity along the eastern coastline of Australia, spanning 2,667 km of coastline and 20° of latitude. We utilise a large, structured field dataset (5,670 individuals) in conjunction with a routine macroecological dataset downloaded from the Ocean Biogeographic Information System (OBIS: 6,226 specimens). Diversity is estimated using a series of analytical methods to account for undersampling, and biogeographic gradients in taxonomic composition are quantified and compared to existing biogeographical schemes. A strong latitudinal gradient is present in both datasets. However, the strength of the gradient depends on the dataset and analytical method used. The inclusion of observational data in the macroecological dataset obscures any latitudinal pattern. The documented biogeographic gradients are consistent with global and regional reconstructions. However, we find evidence for a strong transition zone between two clusters. Although latitudinal gradients inferred from large macroecological datasets such as OBIS can match those inferred from field data, care should be taken when curating downloaded data as small changes in protocols can generate very different results. By contrast, even modest regional field datasets can readily reconstruct latitudinal patterns.

Introduction

The latitudinal biodiversity gradient peaking in the tropics has been of key interest in macroecology for decades (Hillebrand, 2004, Kinlock*et al.*, 2018) both at regional (Edgar *et al.*, 2017, Saeedi*et al.*, 2019) and global scales (Chaudhary *et al.*, 2016, Gagné *et al.*, 2020, Righetti *et al.*, 2019, Tittensor*et al.*, 2010). In particular, the various possible environmental drivers of latitudinal gradients have been discussed at length (Field*et al.*, 2008, Gagné *et al.*, 2020, Wang *et al.*, 2009). Understanding the impacts of changing environments on such large-scale diversity patterns is of growing importance (Gagné *et al.*, 2020, Pimm *et al.*, 2014).

Because data on large geographic scales are required for these studies, recent research has focused on using composite datasets rather than detailed field collections (for example; Gagné et al., 2020, Menegotto and Rangel, 2018, Miller et al., 2018). However, there are some large-scale fieldwork schemes such as the Reef Life Survey (Barneche et al., 2019, Edgar et al., 2017, Edgar and Stuart-Smith, 2014) and some terrestrial compilation efforts (Cerezer et al., 2020). Historically, species distributions have been based on range data, layering distributions to generate richness estimates (McKinney and Kark, 2017, Roy et al., 1998, Tsianou et al., 2016). Range-through, more often used in temporal studies, tends to artificially increase richness estimates and similarities towards the centre of distributions both spatially and temporally (Boltovskoy, 1988), but has been used to test many latitudinal gradient hypotheses (Hughes et al., 2013, Rovet al., 1994, Rov et al., 1998). Atlases have similar problems and are generally only available for well-studied taxa (Donald and Fuller, 1998, Robertson et al., 2010). Uneven sampling and techniques that vary between countries also have an impact, even in better-surveyed groups like mammals and birds (Robertson et al., 2010, Whittaker et al. , 2005). Both range-through and atlas approaches result in a loss of abundance information and assume even sampling across species ranges, which makes diversity estimates misleading compared to those produced by routine field surveys (Robertson et al., 1995) despite successful modelling studies using atlas data (Sadoti et al., 2013).

In modern studies, large composite databases are often used to generate diversity estimates and taxonomic ranges. Although many such databases exist, the largest and most heavily cited are the Global Biodiversity Information Facility (GBIF) for terrestrial and marine studies and the Ocean Biogeographic Information System (OBIS) for marine studies. Despite the obvious benefits of these datasets, their properties can create significant issues in global-scale studies. Data included are haphazard, idiosyncratic and, like atlases, unevenly distributed across countries (Beck *et al.*, 2014, Boakes *et al.*, 2010) and globally (Menegotto and Rangel, 2018). Despite large numbers of records, they also do not give as much range information as many manual compilation methods (Beck *et al.*, 2013), and without true abundance information, they are of limited usefulness in estimating true diversity. In addition, sampling effort varies temporally (Boakes *et al.*, 2010),

in intensity (Ballesteros-Mejia *et al.*, 2013), and between countries (Mora *et al.*, 2008), resulting in a lack of understanding of local-scale processes.

In this study we investigate a latitudinal diversity gradient in marine bivalves using a field dataset spanning 2,667 km of Australia's eastern coastline. Although marine bivalves are underrepresented in large datasets (Troudet *et al.*, 2017), they are well-studied in other continents (Jablonski *et al.*, 2013, Roy, 2001, Roy *et al.*, 1994) and easy to collect in large abundance in the field. Bivalves are not included in major field surveys of Australian waters, such as the Reef Life Survey. Thus, diversity estimates have been limited to small numbers of specimens and observations in OBIS. We will describe variation in bivalve diversity with respect to varying environmental conditions along the coastline, as well as across a previously identified major biogeographic transition. Finally, the strength, variation, and environmental response of this gradient will be compared to the latitudinal gradient found in analyses of a macroecological dataset generated using bivalve occurrence data from OBIS.

Data and Methods

Field Collection

Bivalve shell assemblages were collected from 16 beaches across the eastern coastline of Australia (Fig. 1) in August of 2018 and 2019. Beaches were selected to be evenly distributed along the eastern coastline, eastwards facing and completely open to the ocean. Ten samples were taken from each beach using 0.25 m2 quadrats: five samples were taken north of the beach midpoint and five were taken to the south. Sampling was only carried out during clear days not following a storm to avoid artefacts of depositional changes. Quadrats were randomly placed along the beach between the high and low tide marks, ensuring they were [?] 10 m apart.

Sediment taken down to a 5 cm depth within each sample was processed through 16-, 8-, and 4-mm sieves, with all shell material retained. Valves that were 70% complete and identifiable to species level were identified and counted. A full list of species and taxonomic authorities used for identification is available as Supplementary Material (Data S1).

Regional and Environmental Data

For comparison to the field dataset, a regional dataset was created using identifications from OBIS. All bivalve records for Australia were downloaded on 4th May 2020 using the R package robis (Provoost and Bosch, 2020). Data were spatially restricted to only include coastal cells within the latitudinal range of the field sites (16.7 - 37.2 degS). Species names were checked against the World Register of Marine Species using the package worms in R (Holstein, 2018, WoRMS Editorial Board, 2018) in order to remove erroneous species names and synonyms and to check family assignments. Only records with georeferenced collection locality data recorded to 2 decimal places, valid species names, and collection dates after 1980 were included. This resulted in a regional dataset including 7,480 records of 600 species.

For bivalves in our study area, 612 records are recorded on OBIS as "Human Observation". To avoid potentially erroneous identifications, only records tagged as "Preserved Specimen" were retained for our main analysis. We ran an additional analysis with the observational data included to make comparisons.

Records were pooled into 0.1deg cells to approximate the spatial scale of the field data. Cells with fewer than 10 records were omitted to allow for more accurate diversity estimation. To account for the difference in the number of cells between datasets, a subset of the OBIS data was created that only included cells centred on field sites.

Environmental data for the eastern coastline were downloaded from the CSIRO Atlas of Living Seas (Ridgway *et al.*, 2002), which provides ocean water properties on a 0.5deg grid, on 10th May 2020. Variables downloaded were the most recently available ones for mean annual sea surface temperature, mean annual salinity, mean annual dissolved oxygen content, and mean annual nitrate, silicate, and phosphate content.

Diversity Estimation

To account for potential sampling issues in both datasets, diversity was estimated using three methods. Richness was estimated using the S^2/m equation of Alroy (2020). This gives similar results (Fig. S1) to that of Chao 1 (Chao, 1984) in our analyses but is more aggressive and a consistent lower bound (Alroy, 2020), so we emphasise it in the main text.

To supplement this, we used the analytical version (Chao and Jost, 2012) of shareholder quorum subsampling (SQS - Alroy [2010a, 2010b, 2010c]). We note that SQS is routinely referred to as coverage-based rarefaction (CBR) in the ecological literature and that the distinction between SQS and CBR is not conceptual but operational, as with the distinction between the original formulation of rarefaction (Sanders, 1968) and the analytical formulation (Hurlbert, 1971) that is now widely used.

As these methods are influenced by sample size in our data (Fig. S2), we use Simpson's D (Simpson, 1949) as a diversity metric. When computed using the modern formula (Hurlbert, 1971), Simpson's D is almost independent of sample size, and it has long been used in the analysis of ecological field data (Magurran, 2013, Morris *et al.*, 2014). Additionally, we use Fisher's alpha, which is often used in the study of high diversity systems (Hubbell, 2015).

All analyses were done in R (version 4.0.2; R Core Team [2020]), and the functions for generating diversity and richness estimates have been included in the Supplementary Information.

Taxonomic Composition

We investigated taxonomic composition at the species and family level. In order to show how taxonomic composition changes with latitude, presence-absence data were transformed into a dissimilarity matrix using a revised version of the Forbes index (Alroy, 2015, Forbes, 1907). We then used Principal Coordinates Analysis (PCoA: Gower [1966]) to visualise the differences. We implemented PCoA using the cmdscale function in the base R package. Based on accepted biogeographical schemes for molluscs in the study area (Ebach *et al.*, 2013, Wilson and Allen, 1971), two major provinces and a long transition zone were expected to be seen.

Analysis

Spatial autoregression was used to investigate the relationship between bivalve diversity and environmental variables (R package spatial reg: Bivand *et al.*, 2013). For each model, logged diversity was compared with the eight environmental variables as predictors. This was repeated for each dataset and diversity metric. Finally, to identify the best predictor variables for each diversity metric and dataset, an optimal submodel was chosen using the function RegBest in the R package FactoMineR (Le *et al.*, 2008). This analysis was repeated using the taxonomic composition data to test for the underlying causes of any biogeographic gradient.

Results

Data

Field collections included 5,670 individuals of 179 species. Two sites ("Shelly Central" and "Bermagui") did not contain enough shell material (<30 individuals) to accurately predict richness, so they were excluded from the analyses. Northern quadrats made up 3,218 individuals and southern quadrats made up 2,334 individuals.

The full OBIS dataset numbered 600 species and 7,480 records. After low sample size cells were removed, the dataset numbered 579 species and 6,226 records. One hundred forty-six cells were used in the final analysis. Observational data contributed an additional 775 records.

Latitudinal Gradients

Strong latitudinal gradients can be seen in both the field data and the OBIS data (Fig. 2). For the field S^2/m data, the relationship with latitude was stronger ($\rho = 0.765$, p < 0.001) than it was in the OBIS S^2/m data ($\rho = 0.682$, p < 0.001). When using SQS, no significant pattern was found in the field data; Simpson's D

returned a stronger gradient in the OBIS data (Table 1). When only cells centred on field sites were included, a much weaker pattern was observed using S²/m ($\rho = 0.556$, p < 0.05), a stronger pattern was observed using SQS, and no pattern was returned using Simpson's D. Including observational data in the OBIS dataset consistently reduced the latitudinal signal, as measured by ρ , across all combinations of analytical methods and diversity metrics (Fig. 2, Table 1). Fisher's alpha returned a significant signal in all datasets, but was much weaker in the field data (Table 1).

The spatial autoregressions show that field diversity is strongly predicted by a set of abiotic variables ($R^2 = 86.5\%$ for S^2/m : Table 2). Diversity is not as well predicted by abiotic variables when using OBIS datasets. Submodels for each dataset and metric show that temperature is the best consistent overall predictor of richness in each case (Table 2, Table S1-2), with nitrate and phosphate content also important for subsets of OBIS data.

Taxonomic Composition

The PCoA shows that the majority of taxonomic variation can be explained by one axis (68.8% for field data, 52.0% for the full OBIS dataset: Fig. 3). Latitudinally, this axis represents a broad northern and southern cluster with a transition in between (Fig. 3). This biogeographic pattern is present regardless of data subsetting, but clustering is more apparent in the field data than in any OBIS dataset. This is consistent with results based on family level data (Fig. S3). When comparing family-level changes in the field data, northern sites have higher proportions of Cardiidae, Psammobiidae, Tellinidae, and Veneridae (Fig. 4). Southern sites are represented by higher proportions of Cardiidae and of smaller families (Fig. 4).

When biogeographic variables were compared to environmental variables in a series of spatial autoregressions, temperature was consistently a significant predictor of biogeographic structure across all datasets (Table S3).

Discussion

A strong latitudinal diversity pattern can be seen for marine bivalves along the eastern coastline of Australia. This pattern is consistent regardless of which diversity estimators are used and whether field sites are subdivided along a midpoint.

Strong latitudinal gradients were found regardless of the diversity metric used. Depending on the method used, however, the intensity of the latitudinal gradient changed significantly. Estimated richness values (S^2/m) were the most compelling in the field data, which showed weaker gradients using other metrics. OBIS data showed a consistent gradient using all methods but failed to show consistency when the dataset was reduced to measure richness at a local scale, presumably due to insufficient sample sizes.

Including observational data in the OBIS datasets resulted in the largest shift in gradient strength. Observational records made up less than 20% of the data, but their inclusion massively reduced the latitudinal diversity signal across all the analytical treatments (Fig. 2, Table 1). Previous studies have shown large discrepancies in sampling effort across space (Brown *et al.*, 2000, Pressey, 2004), with a higher degree of observations often resulting in apparent undersampling (Geldmann *et al.*, 2016). Observational values are typically included in global studies, where they are often subject to screening based on species ecology (Gagné *et al.*, 2020), but as shown here, they may present issues at the regional scale. Compiling citizen science information presents a similar challenge to that of using composite datasets: the sampling method often highly varies (Pocock *et al.*, 2017) and very few schemes operate at scales large enough to measure latitudinal patterns – especially for invertebrate groups.

Despite inconsistencies in sampling effort and methods present in large datasets such as OBIS, they do suggest latitudinal diversity patterns in marine bivalves that are broadly consistent with those demonstrated by field collections arrayed at a regional scale. This fact indicates that OBIS data, previously used in many global studies for marine diversity and biogeographic patterns (Chaudhary *et al.*, 2016, Costello*et al.*, 2017, Miller *et al.*, 2018, Menegotto and Rangel, 2018, Gagné *et al.*, 2020), are at least minimally suitable for studying diversity dynamics at regional scales – even in underrepresented groups such as bivalved molluscs. Additionally, temperature was found to be the main predictor of taxonomic diversity in the field data, with

spatial autoregression explaining 67% of the variation, consistent with previous studies (Barneche *et al.*, 2019, Saeedi *et al.*, 2019, Gagné *et al.*, 2020). Abiotic variables could not predict diversity patterns to the same extent in the OBIS data: the variation explained in models based on those data was half as great. This is likely due to the smaller individual sample sizes in cells for the OBIS dataset. Our field dataset may be a better reflection of true latitudinal diversity patterns because our sampling effort was uniform and intense.

Neither the OBIS data nor the field data are consistent with latitudinal patterns for bivalves seen in other continents (Roy *et al.*, 1994) or in global reconstructions (Chaudhary *et al.*, 2016), with a much smoother gradient and no stepwise change that matches a provincial boundary. On the other hand, the biogeographic gradient seen in the field and OBIS data is broadly consistent with published regional biogeographic schemes (Ebach *et al.*, 2013, Wilson and Allen, 1971), including two provinces, and is similar to Australian provincial patterns shown in global schemes (Costello *et al.*, 2017). The biogeographic interpretation in our data is that bivalves do not form clear clusters along the Australian coastline, but a long transition that spans a biogeographic boundary.

The biogeographic transition is robust at both species and family level (Fig. 3, Fig. S3), with northern and southern provinces having distinct proportional composition (Fig. 4) despite most families being present at every field site. Ebach *et al.* (2013) list the upper limit of the Peronian (a province containing NSW and Victoria) as -32.7° , which falls at the start of the transition zone seen here in both datasets. However, little attention has been drawn to the presence of the transitional gradient itself, and both global and local assessments tend to agree on a two-cluster scheme (Ebach *et al.* 2013, Costello *et al.*2017).

Historically, transitions have either been recognised as overlapping biotic zones or as mixing zones (Hermogenes De Mendonça and Ebach, 2020). Here, a gradient between two tight clusters can be seen across datasets, with temperature being able to explain it in most cases (Table S3). A change in beach geomorphology along the transition zone (Short*et al.*, 2000, Short *et al.*, 2007) may be a contributing factor, but further research is needed to fully determine the histories of the zones in order to assess the relationship.

Here we show that latitudinal gradients seen in data downloaded from OBIS match those shown in field data – confirming their comparability in diversity studies. OBIS data are less useful, however, for recreating local patterns, where the presence and strength of the gradient are largely dependent on the choice of diversity measure. Adding observational data weakens or removes any clear latitudinal signal, which is likely to be of concern when data sets are largely made up of such information. At the same time, latitudinal and biogeographic patterns were uncovered here using a relatively small number of field sites. Thus, we suggest that regional diversity patterns can be quantified easily using well-spaced, high-intensity sampling to supplement existing databases.

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Dataset	S^2/m	D	\mathbf{SQS}	Fisher's alpha
Field	0.765**	0.544**	0.494	0.746**
OBIS	0.682^{**}	0.694^{**}	0.618^{**}	0.601^{**}
OBIS (including observations)	0.313^{**}	0.282^{**}	0.156	0.393^{**}
OBIS (field matched)	0.556^{*}	0.064	0.741^{*}	0.710^{**}

Table 1 Spearman's rank correlation (ρ) coefficients for marine bivalve diversity contrasted with latitude.

Data are for the eastern coastline of Australia, based either on field collections ("field") or on subsets of OBIS (the full dataset containing records after 1980, OBIS inclusive of observational data, and a subset of OBIS that contains cells centered on field data). Diversity metrics shown are the S²/m equation of Alroy (2020), Simpson's D (D), Shareholder Quorum Subsampling (SQS) and Fisher's alpha. Asterisks show significant values (*p < 0.05, **p < 0.01).

	Field	OBIS	OBIS (including observations)	OBIS (field matched)
MAT	0.287*	1.463**	1.079**	0.608*
Salinity	-0.021	0.091	-0.021	0.070
Nitrate	0.243^{*}	0.339	0.233	-0.184
Silica	0.219^{*}	-0.246	-0.209	-0.352*
Phosphate	-0.441**	0.589^{**}	0.634	0.449^{*}
Adjusted- R^2	0.865	0.358	0.200	0.611
Optimal submodel	MAT^{**} (0.673)	MAT^{**} (0.145)	MAT/Phosphate (0.146)	Nitrate* (0.339)

Table 2 Results of spatial autoregressions of marine bivalve diversity on environmental variables. Diversity values shown are for the S²/m equation of Alroy (2020); other diversity metrics are detailed in the supplementary material (Table S1-2). Values are beta coefficients generated by each model (significance values *p < 0.05, **p < 0.01). R² values are for the whole model. "Optimal submodel" details the best subset of environmental predictors for each dataset (see main text); the values in parentheses are the R²s for those submodels. MAT = Mean Annual Temperature.



Figure 1 Location of sites sampled during field collection (\mathbf{a}) and the 100 0.1° cells in the OBIS dataset (\mathbf{b}).



Figure 2 Variation in the species richness of marine bivalves across a latitudinal gradient on the eastern coastline of Australia, estimated using the corrected jackknife equation of Alroy (2020). Panels show different subsets of an OBIS dataset – the full dataset (\mathbf{a}), inclusive of observational data (\mathbf{b}), and with cells matched to field data (\mathbf{c}). Blue points in each panel show estimates based on field data for comparison. All y-axes are logged for clarity.



Figure 3 Variation in species-level taxonomic composition of marine bivalves across a latitudinal gradient along the eastern coastline of Australia. The y-axis in each panel shows the position of the point along the first axis of a Principal Coordinates Analysis (PCoA). Sites that cluster together vertically are inferred to have a similar taxonomic composition. (\mathbf{a}) Results from field collection. The other panels show different subsets of an OBIS dataset – the full dataset (\mathbf{b}), inclusive of observational data (\mathbf{c}) and matched to field sites (\mathbf{d}).



Figure 4 Variation in the family-level taxonomic composition of marine bivalves across a latitudinal gradient along the eastern coastline of Australia. Data shown are based on field surveys of 16 sites. Proportions are of individuals at each site. Only the most common 10 families are shown for clarity.

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