Marine Bioregions in Australia – Numerical Analysis of Provinces on the East Coast

Matthew R. Kerr
Supervisor: A/Prof John Alroy

A dissertation submitted in fulfilment of the requirements for the Degree of Master of Research in Biological Sciences

This thesis is written in the form of a research paper for the Journal of Biogeography. Author instructions were accessed at onlinelibrary.wiley.com on the 4th October 2017. Page limit, figure size and reference counts have been extended for the purposes of the thesis.

Declaration

I wish to acknowledge the following assistance in the research detailed in this report:

N/A

All other research described in this report is my own original work.

Matthew Roy Kerr, MRes, DIC, BSc

9th October 2017

Acknowledgments

None of this project would have been remotely possible without several people, but the first mention has to be Assoc/Prof John Alroy. Your knowledge of every methodology, how to deal with problems of any size relating to my data and the aid in developing my project from scratch within days of me arriving in an entirely new country have been indispensable. Your passion for both the project outcomes (as well as science generally) have inspired me greatly, and you've increased my competence as a scientist immensely.

Amy Tims acted as both an idea sanding block and a sanity check for the entire year. Having a fellow Brit to have at least a weekly pool-and-bar meet really helped me settle in and kept me going through some of the more stressful parts of the project in the mid-year. Bonnie Teece also deserves a special mention. Our constant dialogue offered me a much-needed escape any time it was needed, and your raw passion for science has helped shape many past (and hopefully future) discussions about almost every topic even tangentially related to our research topics. You've both been incredible to work alongside, and I owe the fact I am finishing this thesis to the both of you very much.

To Zachary Sheehan, for our semi-successful two-man weekly trivia team – your flag and obscure geography knowledge kept my Thursday nights fun and enlightening, and you offered many mental breaks from the project. On a similar note, Jim McClean, who not only offered many fun pool games on a regular basis but also acted as a mathematical whetstone, and sharpened many of my ideas by helping me see past the numbers.

My partner, Laura Aranda Fernández. Despite being the other side of the world, you have provided constant support throughout all stages of the project and have really made the whole thing so much easier. You've offered so much in terms of aid, even if you occasionally struggle to understand my rantings about methods and the struggles of scientific life you always have offered solutions and advice that can only come from an arts student (and all that that implies). I also look forward to reading the Spanish translation of all this, that I will inevitably get you to do…

Finally, to all my friends and family back home in the UK – the constant updates and postcards have helped me keep a level head and just about avoid homesickness over the last year. Even though I still get emotional about being so far away, it's always comforting to hear from you. Thank you all!

Abstract

Bioregions, distinct ecological assemblages of flora and fauna, have long been used to aid conservation decisions. Bioregions containing at-risk taxa have routinely been recommended for assignment as Marine Protected Areas (MPA). However, the number, location and extent of bioregions in Australia has been heavily debated over the previous few decades. The current consensus, based on coastal fishes, does not take into account the diverse benthic taxa present.

A large dataset of Australian east coast molluscs, assembled from museum collection records of the last 100 years, was analysed to identify bioregions. Latitudinal bands were analysed with an array of methods previously utilised to identify bioregions elsewhere in the world. The number and size of provinces from each method were compared to form a consensus.

Faunal turnover was high and consistent across the entire geographic extent, with no distinct separations into bioregions. There was strong support for a distinct Victoria/Tasmania province. Nitrate content, showed the strongest control over southern latitudes and it is likely this province is controlled by nutrient availability.

These results suggest that Australian mollusc distributions are potentially controlled by oceanic currents and nutrient supply from southern waters, with the Bass Strait forming the only distinctive distribution control.

Keywords: Biogeography, Australia, Bioregionalisation, Mollusca, Macroecology

Contents

Introduction

Latitudinal biodiversity gradients

The distinct drop in species diversity from the equator to the poles, termed the latitudinal biodiversity gradient (LBG), is one of the most striking phenomena present in macroecology. As a result, it has been the subject of intense research interest (Willig *et al.*, 2003; Mittelbach *et al.*, 2007). The LBG has been witnessed in almost every part of the tree of life, from mammals (Willig & Lyons, 1998) to marine planktonic bacteria (Fuhrman et al., 2008) and has been shown to have existed since at least the Mesozoic (Cecca, 2002; Fanti & Miyashita, 2009).

The drivers behind the LBG have been explored as early as the 19th Century (Pianka, 1966; Willig, Kaufman, & Stevens, 2003), with several authors conducting large scale reviews into the causes of this distinctive ecological gradient (Rohde, 1992; Blackburn & Gaston, 1996; Roy, Jablonski, & Valentine, 2000; Willig et al., 2003). However, very few drivers are currently agreed upon.

Early explanations focused on the physiology of organisms and how they might not be independent of latitude, notably body size (Blackburn & Gaston, 1996) and geographic range (Stevens, 1989). The controversial "Rapoport's Rule" (Stevens, 1989) holds that the LBG is due to changes in geographic ranges, with organisms living in the tropics having far smaller ones. This theory has widely been put down to a limited pattern as opposed to a rule (Roy, Jablonski, & Valentine, 1994; Gaston, Blackburn, & Spicer, 1998), with no evidence for the effect occurring in latitudes higher than 40°N for North American coastal fishes (Rohde, 1992). Stevens (1989) indeed only accounts for groups of organisms above the tropics, with no data shown for groups above 25°N. The "Rapoport Effect" appears instead to be related to the distribution of oceanic barriers (Roy et al., 1994) and, at least in fishes, to depth range and richness (Smith & Brown, 2002). Body size, too, has widely been related to major oceanic barriers, with

significant relationships between body size and latitude at regional scales and in the tropics, but not on a global scale (Roy & Martien, 2001).

Today, the most widely accepted correlate of latitudinal diversity is energy availability, with sea surface temperature used as a proxy. It exhibits strong correlations with diversity in disparate groups (Roy, Jablonski, Valentine, & Rosenberg, 1998; Roy et al., 2000; Smith & Brown, 2002; Hillebrand, 2004; Jablonski et al., 2013). Evolutionary models show preferential origination of species in the tropics, with a range increase towards the poles (Rohde, 1992; Jablonski, Roy, & Valentine, 2006) and evidenced by steeper gradients in younger taxa (Crame, 2000) and time-area relationships (Fine & Ree, 2006). In the latter case, temperate taxa are shown to be younger and often nested within tropical taxa; diversity in a region correlates with the age of the region (Mittelbach et al., 2007). It has also been shown that fossil taxa preferentially originate in the tropics more so than sampling alone can explain (Jablonski, 1993) and that turnover rates of Recent bivalves were far higher in tropical groups compared to temperate groups (Flessa & Jablonski, 1996).

This correlation is not seen in the southeastern Pacific, where there is a sharp increase in southern latitudes that only corresponds to an increase in shelf area (Valdovinos, Navarrete, & Marquet, 2003) – something that was not found to be significant for the eastern Pacific or western Atlantic (Roy et al., 1998) and may be an effect over a general rule.

Biogeography and biological provinces

The structure of the LBG has also been linked to the presence of biological provinces in North America (Roy et al., 1994), making it imperative to define the number of provinces, the location of their boundaries, and their relationship to diversity patterns. Biological provinces are defined as areas having distinct faunal assemblages contained within dynamic spatial boundaries (Welsh, 1994). Such units have been recognised on several spatial scales, with global scales (Spalding et al., 2007; Oliver & Irwin, 2008) and continental scales (Cook & Auster, 2007;

Last et al., 2010; Narayanaswamy et al., 2010) dominating the macroecological literature.

The exact assignment of biological provinces has been contentious, with many authors assigning provinces based on different criteria: variations in taxonomic group, ordination methodology or spatial scale often result in defining vastly different provinces for the same stretch of land (Briggs, 1995). Traditional assignments have been based on quantifying faunal similarity between latitudinal bands (Valentine, 1966), with binary similarity coefficients being used to recognise tightly clustered groups of similar sites. More recent studies focus on ordination techniques, with it being particularly popular to define province boundaries defined using non-metric multidimensional scaling (Hale, 2010; Williams et al., 2010). In addition to using the broad structure of the LBG, range endpoints – the clustering of range limits for species in a group – have been used to define oceanic boundaries in the North American coastline (Roy et al., 1998; Roy, 2001; MacPherson, 2003) and have shown results similar to Valentine (1966).

Whilst some recent studies have focused on smaller-scale provincial boundaries, either substituting ecological abundance data for genetic connections within a species (e.g. Teske, Sandoval-Castillo, Waters, & Beheregaray, 2017) or focusing on very local abiotic controls on organismal spread (Hale, 2010; Williams et al., 2010), global approaches to biogeography are still commonplace. Global ocean biogeography has been determined by large scale trends in ocean colour, related to plankton abundance and chlorophyll-a concentration (Devred, Sathyendranath, & Platt, 2007a, 2007b; Harvey, Kratzer, & Andersson, 2015) as well as in terms of *dynamic* province boundaries changing due to seasonal effects (Oliver & Irwin, 2008). These approaches, although useful in a global ocean network approach, are often not suitable for looking at small scale processes used in coastal management decisions and discount organism-scale interactions when determining boundaries.

Biological provinces in coastal eastern Australia

Biological provinces have long been used in Australia and beyond for the assignment and assessment of potential marine protected areas (MPAs) (CSIRO, 1996; Kriwoken, 1996; Cook & Auster, 2007; Edgar et al., 2014) and in water zonation for the Exclusive Economic Zone. The separation of waters into regions and reserves placed boundaries between provinces in order to capture features of neighbouring provinces fully (Commonwealth of Australia, 2006; Last et al., 2010); biogeographical splitting remains important in the management of Australian waters.

MPAs currently number well over 250 in Australia and 900 worldwide (McNeill, 1994; Mora et al., 2006; Edgar et al., 2014), with more being added sporadically. The value and usefulness of MPAs as conservation enablers has been controversial (Allison, Lubchenco, & Carr, 1998; Edgar et al., 2014) due to commonality of poor design and lack of proper fishing controls around their borders. However, several reports have also noted the positive effects of MPAs on community structure and resilience (Creighton, Boon, Brookes, & Sheaves, 2015; Mellin, Aaron MacNeil, Cheal, Emslie, & Julian Caley, 2016). Effective MPA design, and the construction of a system of biological provinces to aid this design, is vital to the success of future MPA assignment.

Currently, however, biological provinces in Australia are vastly understudied, with only the occasional extensive analysis having been carried out. An initial study by Bennett and Pope (1952) looked at southern water biogeography in terms of full faunal assemblages. It defined three provinces on the east coast, with tropical provinces taken from Hedley (1904), a broad northern province ("Solanderian"), a south eastern province ("Peronian") and a separate cool-water province for Victoria and Tasmania ("Maugean"). Knox (1960, 1963) divided the coastline similarly based on physical characteristics, with further support for a Tasmania-Victoria province separate from the rest of Australia again determined by Bennett and Pope (1960). This study is easily the most

comprehensive in its taxonomic scope. However, the methods of analysis are dated.

Wilson and Gillett (1974), however, argue for a much simpler structure comprised of a northern ("tropical") and southern ("temperate") province spanning the entire longitudinal extent of Australian waters. Their assessment was based exclusively on gastropod presences. They proposed broad overlap zones stretching from approximately 25.5°S to 37.5°S on the eastern coast, with Tasmania included in the southern geographic zone and not as a separate province. Their conclusions were based purely on observational data, and specifically on shell collection and personal knowledge.

A more extensive study done by CSIRO (1996) has been used as a guide to large-scale Australian provinces (Last et al., 2010). Based on coastal fish distributions, the CSIRO delimited four smaller provinces for demersal fishes on the east coast, with broad overlap zones in between: a Tasmanian province, a Bass Strait Province, a Central Province and a Northern Province. Purely pelagic fishes show a much simpler pattern, with a broad central province, a northern province and Tasmania-Victoria lying as a separate province. Fishes were used as the data for other groups were unreliable. However, their western Australian provinces have been confirmed using megabenthos (Williams et al., 2010).

The east coast of Australia remains unconfirmed both in terms of province boundaries and drivers behind these boundaries. In northwestern Australia, organism dispersal is controlled by trench locations (Last & Séret, 1999) and in the US boundaries are controlled by a variety of factors including temperature (Hale, 2010) and plate tectonics (Gottscho, 2016). These have not yet been related to boundaries on the east coast of Australia.

Project scope

With provinces being so important to conservation efforts and coastal management, a robust system for identifying them is key. This project aims to

elucidate biogeographical provinces on coastal eastern Australia objectively, without making assumptions about previously proposed province boundaries, using a dataset of coastal bivalves and gastropods constructed from museum records across Australia. A large series of data transformations and methodologies will be applied to the dataset.

The newly defined province boundaries are compared to latitudinal trends in biodiversity across the same geographic extent, as well as to abiotic variables that have been shown to control molluscan presence: temperature, salinity, dissolved oxygen content and nutrient availability. Hence, this project not only looks for boundaries, but attempts to identify their consequences and controls.

Taxonomic focus

Molluscs have long been used to study biogeographic patterns (e.g. Coomans, 1962; Valentine, 1966; Wilson & Gillett, 1974; Spalding et al., 2007; Hale, 2010; Itsukushima & Shimatani, 2015) and latitudinal gradients (e.g. Roy et al., 1998; Roy & Martien, 2001; Valdovinos et al., 2003; Jablonski et al., 2006) due not only to their relative ease of collection but also to their lack of motility. Although planktonically dispersed, many adult bivalves and gastropods are benthic and thus remain in one location (Hunt, Maltais, Fugate, & Chant, 2007). Unlike fishes, the usual choice for assigning provinces in Australia, the presence of such organisms in a location is a direct indicator of long-term ecosystem structure.

Molluscan presence has also been linked to ecosystem health (van der Meij, Moolenbeek, & Hoeksema, 2009; Itsukushima & Shimatani, 2015) and may offer insights into anthropogenic effects on ecosystem conditions (Edgar & Barrett, 2000). These properties make them excellent candidates for biogeographic assessment within a conservation framework, especially as they are understudied in terms of extinction risk (Régnier, Fontaine, & Bouchet, 2009).

Using natural history collections in ecological studies

The use of natural history collections (NHCs) in large scale ecological studies has been heavily discussed in recent literature. They are key sources of organismal occurrence data, collected over several hundred years in many cases (Lane, 1996). The deep temporal extent of NHCs makes them especially useful for tracking invasive species (Zalba, Sonaglioni, Compagnoni, & Belenguer, 2000; Graham, Ferrier, Huettman, Moritz, & Peterson, 2004).

There are major issues with NHCs. For example, the differential collection of rare species often can lead to bias in studies that require quantifying ecological abundance (Magurran et al., 2010; Garcillán & Ezcurra, 2011). Likewise, changes in collection methodologies can also create spurious historical trends in relative abundance (Shaffer, Fisher, & Davidson, 1998; Boakes et al., 2010). Apparent latitudinal shifts may also reflect changes in collection effort (Huisman & Millar, 2013), and purported endemism hotspots may reflect sampling artefacts instead of true diversity peaks (Nelson, Ferreira, da Silva, & Kawasaki, 1990). Conversely, museum collections have actually been shown to offer better long term coverage than published literature or using publicly sourced observations (Boakes et al., 2010), and biases may be eliminated by long-term averaging (Lister & Climate Change Research, 2011).

Data for this project is sourced from the Online Zoological Collections of Australian Museums (OZCAM). OZCAM comprises biodiversity information compiled from several museum and university collections. Data accuracy is key to using NHCs for ecological studies (Boakes et al., 2010; Booth, Williams, & Belbin, 2012). OZCAM offers complete consistency in terms of both taxonomic identification and location information, making it preferable for purposes of this study to sources such as the Atlas of Living Australia which includes information from citizen science projects and observations that are not checked by taxonomic experts.

Project Aims

1.   To construct a database of molluscan occurrences and ranges for the east coast of Australia, and use it to investigate the key drivers of coastal molluscan latitudinal diversity in terms of abiotic variables.

2.   To designate molluscan biogeographical provinces for the east coast of Australia by applying several statistical methods that have been used in the literature to assign provincial boundaries.

3.   To investigate what abiotic variables that define the start and end of each province, and to see if they are instead purely controlled by geographic features.

Methods

Data

All gastropod and bivalve records for the east of Australia were downloaded from OZCAM on 8th March 2017, with a latitudinal extent of 10-45°S and a longitudinal extent of 142-155°E (figure 1). In total, seven institutional collections were used (full list in appendix Table 1).
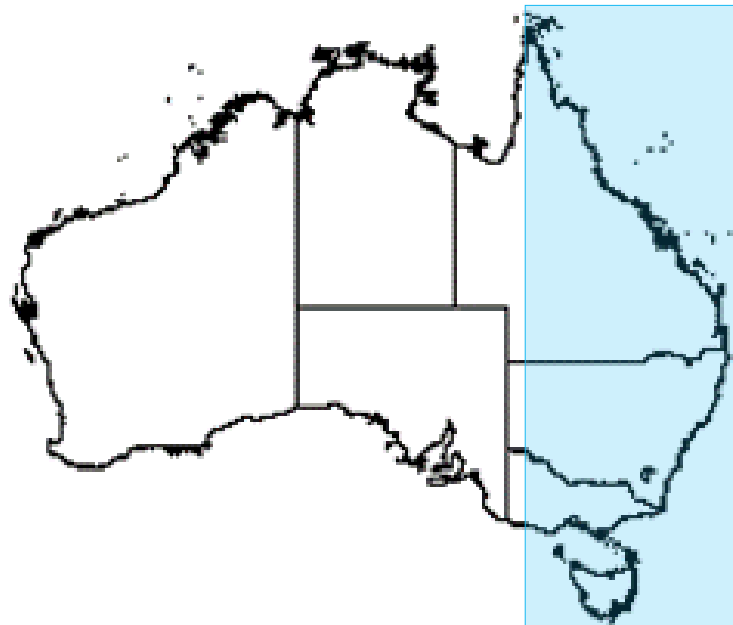

Figure 1: Map showing the geographic extent of records included in the study. Only coastal records from this area were used. Map was drawn using data obtained from Global Administrative Areas spatial database (http://www.gadm.org) and visualised in R.

Records with coordinates having a precision of only 0 to 4 decimal places were excluded to ensure correct placement of the records in latitudinal bands (Ponder, Carter, Flemons, & Chapman, 2001; Graham et al., 2004; Boakes et al., 2010). Family- and genus-level assignments were available for all records. However, their utility is debated with respect to resolving regional differences and serving as units of biodiversity (Roy, Jablonski, & Valentine, 1996;

Humphreys & Barraclough, 2014). Any record without a species name was also excluded from the dataset.

Taxonomic checks were carried out on each record using the World Register of Marine Species (WoRMS) web service (http://www.marinespecies.org/ - Horton et al., 2017) to ensure correct naming of each species, genus and family and to remove junior synonyms. Each taxon was also matched to an environment based on its genus name using the same service. Species that could not be matched, genera matched to an environment other than marine, or genera with unknown affinity were removed from the data. To minimise collecting biases, so were singleton species, i.e., species only occurring at one site, and sites yielding exactly one occurrence.

The final dataset contains 168,601 occurrence records (figure 2) comprising 3796 species, of which gastropods comprise 76% and bivalves 24%. Historically, most of data were collected between 1950 and 2010, with a median year of 1972. Over time, the mean latitudinal position of sampling sites has fluctuated by over 6° of latitude (figure 3). As a result, data were not restricted temporally as to not introduce any latitudinal bias resulting from incomplete sampling in any given period.

Figure 2: Data loss during cleaning process of the dataset used in this study. Initial download consisted of 338,388 molluscan records, and it was then reduced by removing non-marine data, restricting location information to coordinates of 4 decimal places or higher, and removing singleton species and sites. The final dataset numbered 168,601 records.

Figure 3: Mean location of sample sites in the dataset. Mean latitude for unique sampling sites were taken every three years for the period 1900 to 2010, which covers 96% of the data records.

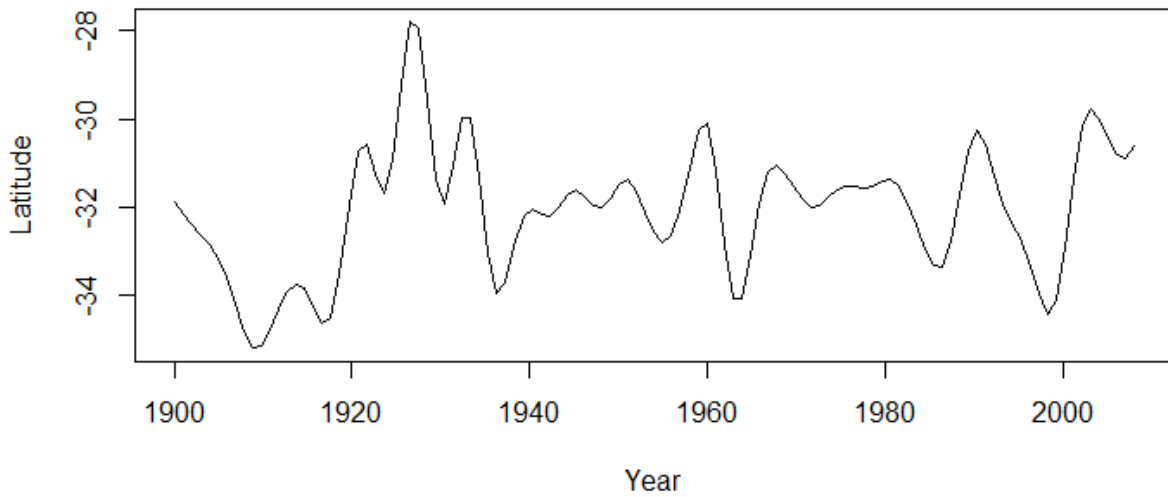Abiotic variables were downloaded from the CSIRO Atlas of Regional Seas (CARS) using the Australian Ocean Data Network portal (https://portal.aodn.org.au/). Data was limited to the same geographic extent as the occurrence data. The variables downloaded were temperature, salinity, dissolved oxygen content, phosphate content and nitrate content of the water.

Temperature, dissolved oxygen content, salinity and nutrient content (nitrate and phosphate levels) data were averaged for the years 2007 through 2012. Temperature has been shown to be a good proxy for energy availability (Roy et al., 1998; Roy et al., 2000), while salinity and dissolved oxygen content put physiological and reproductive stress on organisms (Mellergaard & Nielsen, 1995; Chaparro, Cubillos, Montiel, Paschke, & Pechenik, 2008; Segura et al., 2016). Each of these variables can be linked to the formation of provinces and province boundaries, with temperature being a likely explanation for the formation of the latitudinal diversity gradient in some cases (Jablonski et al., 2013). Ocean colour has also been linked to the location of latitudinal provinces globally (Devred et al., 2007a; Oliver & Irwin, 2008) and at regional scales (Ridgway, Dunn, & Wilkin, 2002; Condie & Dunn, 2006; Devred, Sathyendranath, & Platt, 2009; Harvey et al., 2015). It is a function of the amount of organic matter (plant and planktonic) in a system.

Final datasets, both of abiotic variables and species records, are archived and freely available on the Open Science Foundation website (https://osf.io/twx4m/).

Latitudinal richness

Records were grouped by latitude, rounded either to the nearest degree or to the nearest 2 degrees. Only 14% of the records contained abundance or count information, so instead, the number of records ('presences') of each species was used as a substitute. A 'range-through' matrix was also created, in which a species was considered present if its latitudinal range crossed a given band (Roy et al.,

1994). Species ranges were taken from the dataset: each location was rounded to the nearest degree, and the most northern and southern degree band containing at least two records was taken as the range limit.

The species richness for each band was estimated using Chao 1, Chao 2 and λ_5 extrapolation methods (Chao, 1984; Chao & Chiu, 2006; Alroy, 2017). Three hundred and fifty records were randomly pulled from each latitudinal band 1000 times, with the geometric mean of all trials taken as the richness for that band. This protocol accounts for sample size variation in the data. In addition, species richness was estimated directly using the 'range-through' matrix.

For each band, the mean and median range size of all species it included was also calculated. All statistical analyses were computed in R (R Core Team, 2017). The entire pipeline is available from the author on request.

Biogeographic structure

A partial constrained correspondence analysis (CCA) following the implementation of Legendre and Legendre (2012) was carried out on each version of the dataset using the R-package 'vegan' 2.4-3 (Cajo, 1986; Oksanen et al., 2017) to visualise changes in ecological structure across space. A principal coordinates analysis (PCoA, also called classical multidimensional scaling/Torgerson-Gower scaling (Gower, 1966)) was also carried out to complement the CCA. The reason is that CCA can often yield results that are hard to interpret (Legendre & Gallagher, 2001), such as presenting large outliers. All ordination methods depict differences between sites visually, with sites clustering together when they are similar in terms of faunal composition.

An ordinal, nonmetric MDS was carried out using Bray-Curtis distances by means of the majorization approach (Borg, Groenen, & Mair, 2012) using R package 'smacof' 1.9-6 (De Leeuw & Mair, 2011). MDS has found moderate success in several ecological province delimitation studies (Hale, 2010). However, it has been shown to put dramatic weight on species with high presence

counts. In this dataset, for example, there was a massive offset in two latitudinal bands due to relatively high counts of a handful of species (*e.g. Nassarius nigellus*) present almost exclusively in those two bands (supplementary figure 1). As a result, results based on this method are not presented here, and instead CCA and PCoA are used in conjunction with each other.

These ordination approaches are largely visual – breaks thought to be significant are determined subjectively. To complement them, faunal turnover was calculated using three similarity coefficients for each pair of latitudinal bands. Jaccard's coefficient has been used in several ecological studies looking at provinces and the effects of the environment on communities (Valentine, 1966; Itsukushima & Shimatani, 2015) and is a simple way of assessing the number of species that are common to two samples. It is shown to be downward biased when sampling is incomplete (Alroy, 2015). The Chao index (Chao et al., 2005) was developed as an improvement to Jaccard's that accounts for sample size differences in abundance data. The Forbes index (Forbes, 1907; Alroy, 2015) was shown to be more robust than the Jaccard index when sampling is uneven or incomplete. Pairs with a similarity of greater than 0.85 were considered to reflect very low turnover (almost homogenous) and could be considered part of the same biological province (Valentine, 1966), and regions of relatively high turnover could be considered transition regions or province boundaries (Briggs, 1995; CSIRO, 1996). Visual checks on correspondence analysis breaks were checked against faunal turnover patterns.

Hierarchal clustering was carried out using distances on each transform calculated using the Forbes index. Euclidean distances are not appropriate for ecological data (Legendre & Gallagher, 2001), Bray-Curtis distances will also be used for a comparison. Multiscale bootstrap resampling (10,000 bootstrap replications per distance matrix) was carried out on each cluster produced to calculate *p*-values for each node and identify strongly supported clusters using the R-package pvclust 2.0 (Shimodaira, 2004; Suzuki & Shimodaira, 2015).

Strongly supported clusters can indicate potential provinces that should be visually recognisable in an ordination plot. Endemism was calculated for each cluster identified in this way, and defined as the percentage of species present exclusively in that cluster (Engle & Summers, 2000; Hale, 2010). A standard cluster analysis was carried out using the hclust function in R.

Based on ranges calculated by using the 'range-through' method, the number of range endpoints was calculated for each latitudinal band. The locations of high endpoint clustering were checked against the sets of clusters suggested by each of the other methods, with range endpoints shown as indicators of provincial boundaries (Roy et al., 1994; MacPherson, 2003).

Abiotic variables

The minimum and maximum values over a yearly period for temperature and salinity were elucidated for each latitudinal band in order to identify upper and lower constraints on species distributions (Segura et al., 2016). Summer and winter means were also calculated for each band to account for seasonality (Condie & Dunn, 2006). Dissolved oxygen, nitrate and phosphate content were taken as a yearly average and a yearly maximum. Depth was not considered a factor in this analysis, due to all organisms being found within 0.01°E of the coastline, and so surface values (0-50m water depth) were used for each variable.

Each latitudinal band was assigned to a temperature category after Bousfield and Thomas (1975) using summer mean temperatures: <12°C, 12-15°C, 15-18°C and >18°C. Temperatures above 18°C were split by using the 75th percentile, 26°C, resulting in a total of five categories. Salinity across the whole extent was considered to be euhaline (30-49%) in the Venice system (Anon, 1958). Thus, the median and 25th and 75th quartiles were used to assign the data into four salinity categories.

To investigate the effect of these variables on the ecology, a distance-based redundancy analysis (dbRDA) was carried out, using both Forbes dissimilarity

and Bray-Curtis distances. Redundancy analyses traditionally show the effects of "short gradients" (Van Den Wollenberg, 1977; Legendre & Gallagher, 2001), although this is not shown in more recent research (Legendre & Legendre, 2012; Oksanen et al., 2017), with dbRDA allowing for use of a multivariate distance measure and partitioning into a complex model (Legendre & Anderson, 1999; McArdle & Anderson, 2001). The analysis was carried out using temperature, salinity, dissolved oxygen, nitrate content and phosphate content in the water. These analyses show the interaction of each variable with the ordination results, and help identify which variables may be resulting in large biogeographical breaks.

The dbRDA was implemented using functions in the R-package 'vegan' 2.4-3 (Cajo, 1986; Oksanen et al., 2017).

Results

Latitudinal gradients

There are strong latitudinal gradients in Australian molluscan diversity in each treatment of the dataset (Figure 4), with a flat profile in tropical waters and a gentle decline towards the south resulting in a richness drop of > 60% across 33 degrees of latitude. Maximum diversity occurs around 23°S (the location of the Tropic of Capricorn).

Figure 4: Latitudinal richness curves for marine bivalves and gastropods on the east coast of Australia. Patterns generated by two methods are shown: subsampling and extrapolating richness using the Chao2 estimator (A) and estimating species in a latitudinal band using range limits (B). Subsamples of 350 randomly pulled records were extrapolated. This process was repeated 1000 times for (A). Range limits were calculated using range extents from the dataset, based on museum collection records. An organism was included in a band if its range crossed that band for (B).

The 'range through' method indicates a much flatter northern gradient, with a drop-off towards the northern tip of Australia. As a result, the trend in richness is not as strong with respect to latitude (Spearman's rank correlation ρ -0.416, *p*-value 0.017) compared to the extrapolation method (Spearman's rank correlation ρ -0.665, *p*-value <0.001 for Chao 2). All three extrapolation methods show a very similar result, with a noisier northern tail lacking the severe dropoff in the far north.

The extrapolated latitudinal gradient positively correlates with temperature and negatively correlates with dissolved oxygen content. However, salinity is not significantly correlated (Table 1). Median range size showed a moderate correlation with extrapolated richness but not with richness based on range sizes. Modal range size showed no correlation with richness.

Table 1: Spearman's rank correlations between variables considered in this study and species richness in different latitudinal belts, calculated in two different ways.

Variable	Extrapolated richness (Chao1)		Species range richness	
	Correlation coefficient	*p*-value	Correlation coefficient	*p*-value
Mean summer sea-surface temperature (°C)	**0.645*** **	**0.000074**	**0.431***	**0.013**
Yearly range in sea-surface temperature (°C)	**0.351***	**0.045**	**0.451** **	**0.0090**
Dissolved oxygen content ($\mu mol\ kg^{-1}$)	**-0.683*** **	**0.000020**	**-0.517** **	**0.0024**
Salinity (‰)	-0.203	0.25	0.177	0.32
Median range size (°)	**0.491** **	**0.0037**	0.284	0.11
Modal range size (°)	0.280	0.115	0.329	0.061

Bolded values are statistically significant. $*p < 0.05$, $**p < 0.01$, $***p < 0.001$

Biogeographic structure

Where there are multiple distance metrics used, only Forbes distances are shown for each analysis due to space restraints. The conclusions drawn from the data are identical for each transform, and the graphs and variances explained in each plot is incredibly similar. On request, the author can provide plots generated from Bray-Curtis or other distance metrics.

In the CCA and PCoA plots, distance between points is relative to dissimilarity in communities between the latitudinal bands: the null hypothesis is a random distribution. In the CCA plot, latitude exerts a very strong control, with an almost perfect ordering of points (Figure 5). In a 'range-through' data transformation (Figure 5b), the points do not separate into obvious clusters, with a continuous curve running through all points. Contrary to this, there is a strong clustering of points -38 through -43 in the 'presence counts' plot (Figure 5a), representing the whole of Tasmania and the Victoria coastline.

PCoA plots are very similar to the CCA plot with respect to the layout of points, with a significant break at 38°S for 'presence counts' (Figure 6a) and many small breaks for the 'range-through' analysis (Figure 6b), with a major break at 38 and 40°S. The variance explained by each axis was much higher for this analysis, with axis 1 explaining over 65%. Both CCA and PCoA retain the major break at 38°S for the 'presence counts' methodology when plotting axes two and three together.

Appendix Table 2 shows the variance explained by the major three axes produced by each ordination method and data treatment.
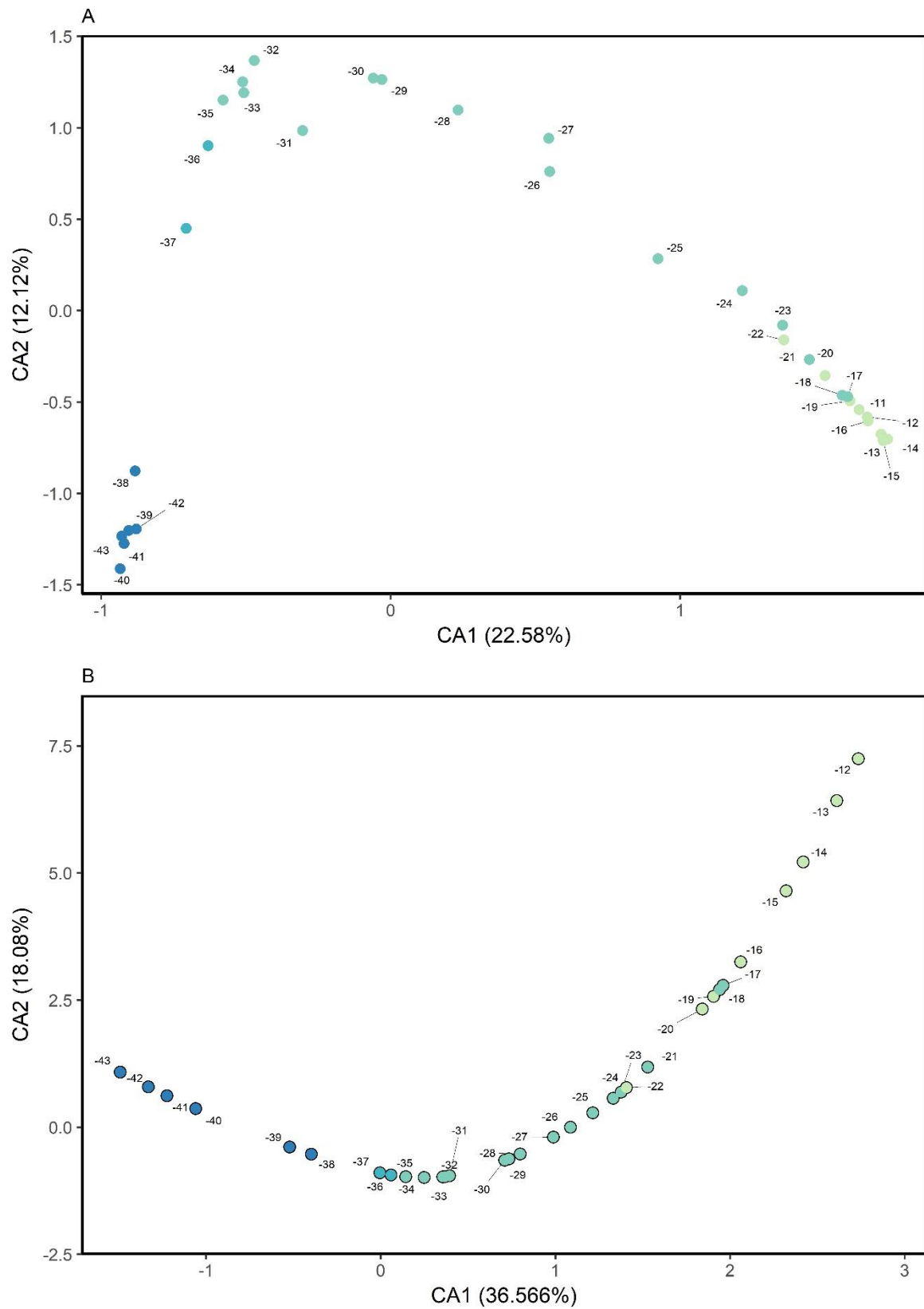
Figure 5: Results for a constrained correspondence analysis of occurrence data for east coast Australian molluscs. Two different transforms are shown, using presence counts (A) and estimating presences based on species ranges (B). Points are coloured according to their temperature category; 12-15°C (dark blue), 15-18°C (blue), 18-26°C (blue-green) and 26+°C (yellow-green).Temperature categories after Bousfield and Thomas (1975), with 75th quartile used as an upper divide. Labels on the points show the latitude of the midpoint of each band (e.g., -40 contains occurrences between -40.5 and -39.5).
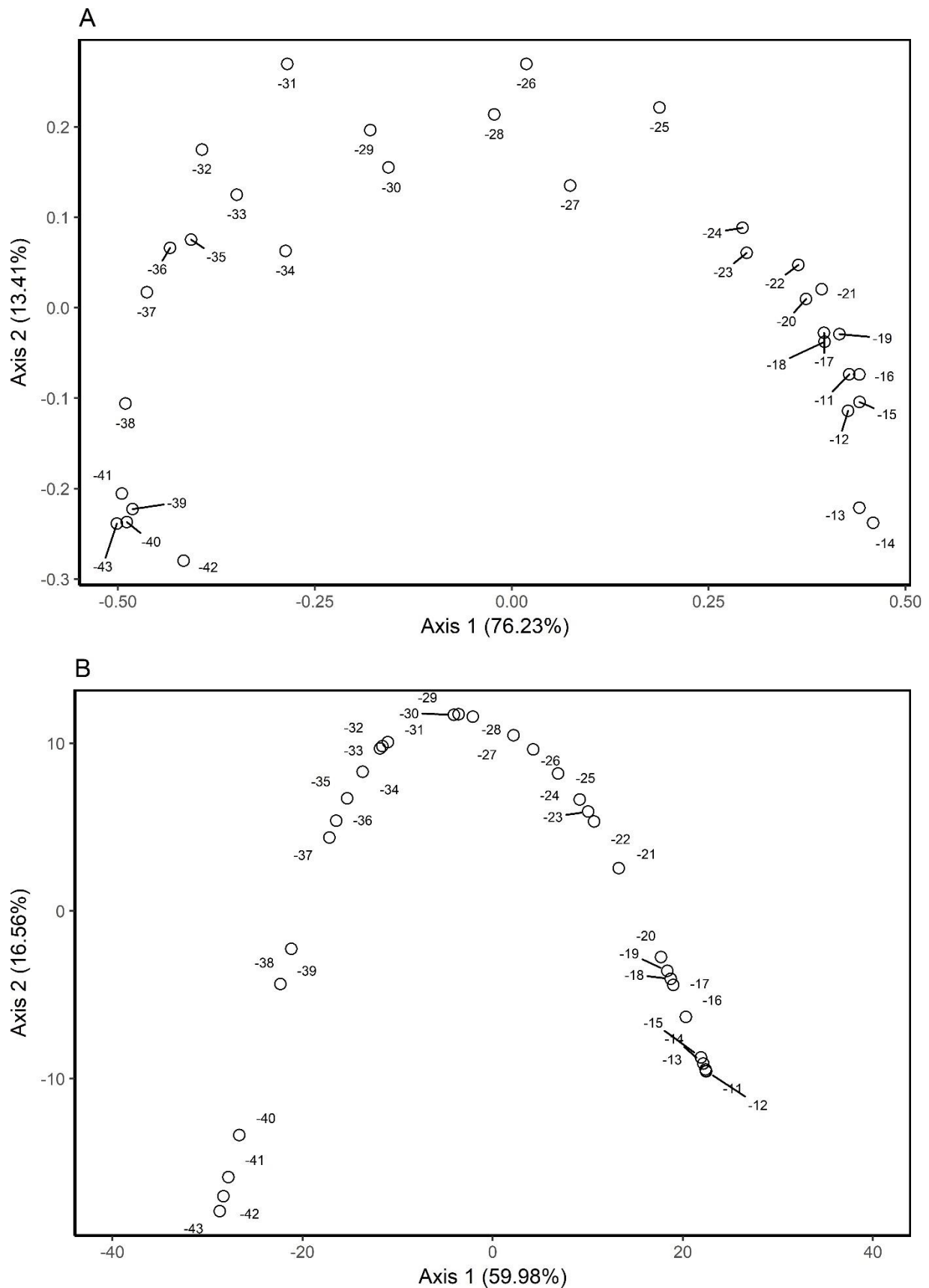
Figure 6: PCoA analyses of occurrence data for east coast Australian molluscs. (A) shows results based on the number of presences of each species, whereas (B) shows presence data extrapolated from known species ranges. Labels on the points show the latitudes of the midpoints of each band (e.g., -40 includes all occurrences between -40.5 and -39.5).

Faunal turnover was very stable across the whole extent, with no large variation in similarity between adjacent latitudinal bands (Figure 7). For Jaccard's coefficient only four pairs were above 85% similarity. Forbes and Chao indices show a high similarity south of -31°, but there are no distinct drops anywhere before and after this point, with turnover being very similar the whole way through. Variation in similarity between coefficients was very high, with peaks in similarity varying between measures significantly in places.
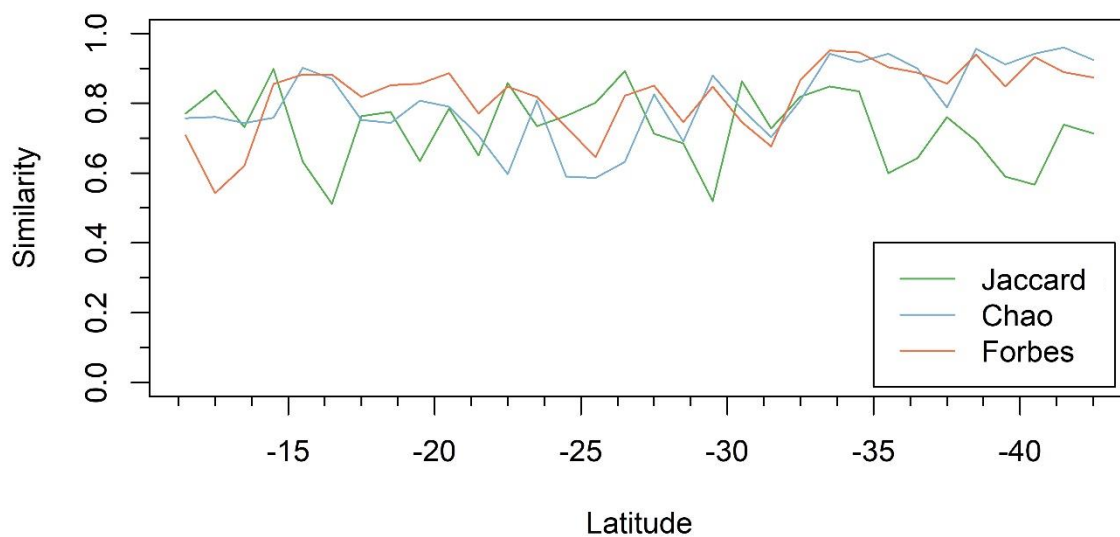

Figure 7: Similarity coefficients for adjacent latitudinal bands, utilising Jaccard coefficient, Chao index (Chao, Chazdon, Colwell, & Shen, 2005) and Forbes index (Alroy, 2015). Similarity is shown at the junctions between bands (e.g., the point at -20.5 represents the similarity between bands -21° and -22°).

Figure 8: Results from hierarchal clustering of three data transformations; untransformed data using presence counts as a proxy for abundance (A) and a 'range-through' data matrix (B). Boxes denote clusters determined from multiscale bootstrap resampling (10000 replications) with a p-value of <0.01. Forbes dissimilarity used for each analysis.

'Range-through' analysis creates a multitude of smaller clusters ranging throughout the geographical extent, with only four bands falling outside any cluster (Figure 8b). Using the function hclust on Bray-Curtis distances shows a similar clustering of points between 38 and 43°S (Figure 9).

Range endpoints (Figure 10) suggest six boundaries. As no formal definition exists concerning what constitutes a boundary using this methodology, any band with an endpoint proportion of 0.2 or higher was used. No boundary was defined by an endpoint proportion of 0.4 or higher.

Figure 9: Results from hierarchal clustering of presence counts for molluscs on the east coast of Australia. Numbers of the tips denote the mid-latitude (degrees south) of the band (-38, for example, would contain all points between 37.5 and 38.5°S). Bray-Curtis distances used.

Figure 10: Latitudinal distribution of range endpoints of bivalve and gastropod species on the east coast of Australia, binned by degree of latitude. Points represent the proportions of species that have range ends in respective bins, meaning the proportion of all species that have ranges falling in particular bins.

Cluster endemism is summarised in Table 2. Southern clusters had high endemism, with >20% endemic species in both treatments of the data, whereas northern clusters included <5%. Cluster size across latitudes was significantly correlated with endemism measures for northern clusters based both treatments

and with all provinces included (Spearmans rank correlation ρ = 0.728, *p*-value = 0.01).

Table 2: Endemism, the number of species found in an area and nowhere else along the coastline, for each cluster, produced by multiscale bootstrap resampling. Only clusters with four or more consecutive latitudinal bands are shown.

Methodology	Cluster Extent	Endemism
Presence counts	38-43°S	20.8%
Range-through	34-43°S	21.0%
	17-23°S	3.15%
	11-14°S	2.84%

Relation of biogeographic structure to abiotic variables

Temperature (Figure 11a) had a strong relationship with CCA axis 1 for both data treatments, suggesting that axis 1 is a latitudinal or temperature control. However, there were no cases in which breaks between temperature categories corresponded with breaks suggested by the presence-count analysis (Figure 4a) or the 'range-through' analysis (Figure 4b). Cluster boundaries found by multiscale bootstrap resampling also did not map with changes in temperature category.

Dissolved oxygen (Figure 11b) tracked the inverse of temperature, with a steady increase south of 23°S totalling 50%. North of this, there is also an increase moving southwards, excepting for a slight decrease from 210 to 190μmolkg^{-1} between 20°S and 23°S. Maximum dissolved oxygen content occurs at 44°S and minimum dissolved oxygen content occurs at 16°S.

Salinity was relatively stable across the entire geographic range, with the entire extent falling into one salinity category - "euhaline" (Anon, 1958). However, fluctuations do occur (Figure 11c). In southern latitudes, salinity varies by less than 0.5%. However, between 28°S and 29°S there is a large drop of approximately 3‰ before a steady increase of 5‰, with the minimum salinity

occurring at 27°S and maximum salinity occurring at 32.5°S. Immediately afterwards, the minimum salinity is a 0.5° thick band at the same level before the drop. After maximum salinity, there is a steady decrease of 2‰ towards the southern extent. Salinity is steady at areas of province boundaries identified.

Nitrate content is almost uniformly low in a yearly average, with a large peak towards very southern latitudes (Figure 12a). Maximum nitrate content is at the southern extent of the dataset, nitrate content north of 40°S is uniformly low. Phosphate content is uniformly very low across the whole dataset (Figure 12b), with a maximum at the southern extent of the dataset. Smaller phosphate peaks are present at the north end and in the mid-latitude bands.

For dbRDA, the projection of a point onto a response variable approximates the points value for that variable. Lines for response variables are shown here in the positive direction only. Nitrate (NTR) content shows a strong effect on very southerly latitudes (figure 13), as expected from the large peaks in southern latitudes. The tight clustering of southern latitudes seen in CCA and PCoA aren't as pronounced in this analysis, with a much looser structure and an apparent break between Victoria and Tasmania present as well as a break at 37/38°S. Dissolved oxygen content (DOX) and temperature (TC) correlated strongly with axis 1 in a single direction, roughly equivalent to latitude. There is no significant change along any explanatory variable for break points in the dataset. ANOVA permutation test results show both temperature and nitrate content as significant (p-value<0.01 for both variables) drivers in the ecological structure, with other variables not significant. Salinity is not shown in the results here due to the incredibly small effect it has on the structure. When included, it has no significant effect on community structure across the dataset (p-value=0.125).

Figure 11: Abiotic variables by latitudinal belt for the east coast of Australia: temperature (A), dissolved oxygen content (B – expressed as µmol kg^{-1}) and salinity (C). Values are taken every 0.5° of latitude as summer means for the period 2007-2012.

Figure 12: Abiotic variables expressing nutrient content on the east coast of Australia; nitrate (A) and phosphate (B). Values are expressed as μmol/kg, and taken every 0.5° of latitude. Values are summer means for the years 2007-2012.

Figure 13: Results for a distance based redundancy analysis on presence data for molluscs on the east coast of Australia. Points mark the location of latitudinal bands, with the annotation representing the mid-point of that band (*e.g.* -38 would represent the band 37.5-38.5°S). Arrows represent the effects of abiotic variables: DOX - dissolved oxygen content, K - temperature, PHOS – phosphate content, NTR – nitrate content. The dbRDA was implemented as in McArdle and Anderson (2001) using the formula; *(species presence table) ~ TC+DOX+NTR+PHOS*.

Discussion

Interpretation of results

Molluscs along the east coast of Australia exhibit a strong latitudinal gradient, and this gradient is strongly correlated with temperature and dissolved oxygen content. With both yearly range in temperature and mean temperature being proxies for energy availability in the system, these results agree with many previous studies linking this key factor to the nature of the latitudinal gradient (Roy et al., 1998). Dissolved oxygen content is the inverse of temperature in this study and therefore shows the opposite pattern. It should be noted that the data here are autocorrelated and therefore these relationships do not offer an explanation for the latitudinal trend. Rather, they show a relationship of interest to the link between biodiversity and ecological structure for the east coast of Australia.

The latitudinal diversity curve, however, did not display any stepwise patterns that would be indicative of provincial boundaries, regardless of the data treatment. Roy et al. (1994) and others (Roy et al., 1998; Roy et al., 2000; Mittelbach et al., 2007) did present stepwise curves for other regions. Instead, the Australian gradient is much smoother. The Jaccard index indicates that there are no clear province boundaries along any part of the coastline, although loose southern clusters are suggested by the Forbes index and Chao index. The Jaccard coefficient, which forms the basis for the provinces in Valentine (1966), identified only four latitudinal pairs with > 85% similarity, and assigns no distinct provinces if his method is emulated. The other two similarity coefficients have not been used for defining province boundaries. However, they depict a southern cluster (south of 31°S) in which pairs have > 85% similarity.

These methodologies are likely to be old-fashioned and inaccurate compared to modern ordination methods. For example, the southern cluster's boundaries do not correspond with the distinct breaks produced by other methods.

CCA analysis presents a visual break between 37/38°S, which corresponds to a Victoria/Tasmania province, and no other visible break in the sequence (Figure 4a). PCoA confirms these results: the same break is present when comparing axes 1 to 2 and axes 2 to 3. In a cluster analysis this band is again supported, with bootstrap resampling demonstrating a very significant cluster encompassing the same geographical area.

The endemism analysis indicates that a southern cluster is highly probable, with candidate province boundaries at both 34 and 38°S having endemism rates of > 20%.

No relationship between the majority of abiotic variables tested and any provincial boundary was found in any analysis. This is unusual because temperature is often cited as a key driver in the formation of provincial boundaries (Valentine, 1966) due to its strong control on survival during juvenile stages (Verween, Vincx, & Degraer, 2007). Low salinity has been related to reproductive success in gastropods (Segura et al., 2016) and to the absorption of amino acids from seawater (Deaton, Derby, Subhedar, & Greenberg, 1989). However, molluscs generally have salinity tolerance ranges that fall within the whole salinity range of the current data (Nell & Gibbs, 1986; Verween et al., 2007).

The only variable that seemed to relate to provincial structure was nitrate content – this variable is incredibly high in southern waters due to the influx of nutrient rich waters from the Antarctic (Cresswell, 2000; Ridgway, 2007; Harvey et al., 2015). When included in the dbRDA, a province boundary was still present at 37/38°S.

It can be inferred, therefore, that the Victoria/Tasmania cluster relates to the structure of the East Australian Current, with reported turbulence greatest at the south-eastern corner of Australia (Huyer *et al.*, 1988) and the current being directly related to nutrient influx in the system (Cresswell, 2000). No fine-scale

current data were tested in this study, and they should be incorporated before any connection is argued for.

Data treatments were shown to have a significant effect on hypothesised province structure, as expected. However, the biggest difference was between using the existing dataset and extrapolating presences based on species ranges ('range-through'). Species ranges have been used to define LBGs and range endpoints in a multitude of related studies (Roy et al., 1994, 1996; Roy et al., 1998; MacPherson, 2003; Valdovinos et al., 2003). However, this methodology appears to oversimplify the system by failing to account for small-scale changes in species distributions and interactions between sets of species. This behaviour is clearly seen here, with 'range-through' analyses giving a much higher weighting to latitude alone as a provincial driver – perfectly ordering points in all ordination methods to match a latitudinal trend (Figure 4b, 6b, 9c). They also elucidate a much higher number of provinces than any other methodology in a cluster analysis (Figure 7c), with all clusters all exactly matching with peaks in endpoint proportions.

This is a circular argument – using published ranges to extrapolate species presences will naturally create clusters around endpoints that may not have any biological meaning. The absence and relative presences of organisms within their ranges are much more telling than the ranges themselves, and so provinces elucidated using some form of abundance data are likely to give more accurate results with respect to geographic similarity. For Australia, range endpoint clustering is a poor methodology for defining boundaries, as suggested by the fact that no range endpoint cluster appears in any ordination as a biogeographical break.

Consequences for Australian biogeography

These results demonstrate that there is a provincial divide present in the south east of Australia, with a province containing Tasmania and Victoria. This location is similar to traditional splits in this region (Bennett & Pope, 1952, 1960), but, unlike more recent analyses (e.g. CSIRO, 1996), does not place Tasmania as a separate region. However, the lack of any clear divide along most of the eastern Australian coastline goes against every published bioregionalization analysis over the past 60 years, with even the simplest binary divides (e.g. Wilson & Gillett, 1974) splitting this coastline. This single provincial divide is supported by every analysis presented here.

The provincial scale shown here is of considerable size when compared to provinces determined both in Australia and worldwide. Coastal USA, for example, has only one province of the size shown on the mainland here (Roy et al., 1994), with many smaller provinces instead being present (Valentine, 1966). Even when range through analyses are taken into account, in a similar way to the methodology employed by Roy et al. (1994), the provinces elucidated are far smaller in scale.

The differences between provinces found in the present study and those found in previous works are likely due to disparity between each study. Taxonomic group never remained constant, and full coastal collections were not available at any time, instead relying on previous published works (Bennett & Pope, 1952, 1960) or on distribution data (Wilson & Gillett, 1974; CSIRO, 1996). The biogeographic split shown here has been supported in the past (Bennett & Pope, 1960; CSIRO, 1996), and the division is supported in global ocean province maps (Spalding et al., 2007; Oliver & Irwin, 2008).

There are, however, no clear relations between the boundary and any abiotic variable, including temperature, salinity and dissolved oxygen content. Instead, the boundary appears to correlate with recorded extents of the East Australian Current (Huyer, Smith, Stabeno, Church, & White, 1988) and with the

coastline's physical extent. The stretch of the coastline at the boundary is far greater than that of any other latitudinal band due to Victoria having an east-west coastline instead of a north-south coastline. In addition, as an island, Tasmania has two north-south orientated coastlines influenced by different oceanic processes.

Tasmania as a system

All large-scale studies have shown no break between the eastern and western halves of the island (Bennett & Pope, 1960; CSIRO, 1996) and instead show potential differences between the water masses to the north and south (CSIRO, 1996). It is becoming more and more recognised that there may indeed be differences between all aspects of the island in terms of ecology. Recent phylogeographical studies show at least four distinct ecological zones on the island (York, Blacket, & Appleton, 2008; Teske et al., 2017), with the largest changes between east and west, and within the Bass Strait (Teske et al., 2017).

The most likely explanation for these changes are the differing current regimes in eastern and western Tasmania. On the east coast, the East Australian Current brings warm, nutrient poor water from the north down to Tasmania (Ridgway, 2007). The west coast is affected by the Zeehan Current from the west, which during winter wraps around and penetrates towards the north against the East Australian Current (Cresswell, 2000; Ridgway, 2007), during summer the East Australian Current reaches the southern tip of Tasmania. These current systems provide vastly different water types and nutrient levels to both halves of the island, with strong seasonal variation (Harris, Nilsson, Clementson, & Thomas, 1987). It is very likely this results in very different ecological structure and in differing relationships with the Victoria coastline.

These relationships may also have changed temporally. The intensity of the East Australian Current, and its seasonal variation, has been noted to have increased significantly with ocean warming and acidification (Johnson et al.,

2011; Rodolfo-Metalpa et al., 2011). These changes may also be affecting the ecological make up of eastern Tasmania more so than western Tasmania, with molluscan communities being affected by not only the changing currents but also directly by the water changes (Nell & Gibbs, 1986; Rodolfo-Metalpa et al., 2011).

In preliminary analyses done by the author, western Tasmania shows a much higher similarity with Victoria than eastern Tasmania when divided simply into east and west coasts. A full analysis of this type is beyond the scope of this study - there is a distinct lack of data for the western coastline in this dataset. Full ecological sampling would be needed to elucidate any real biological differences between these areas. Of particular interest would be small scale changes in southern Tasmania ecosystems due to changes in nutrient availability on a yearly basis.

Conclusions

Based on the aims proposed earlier, the following was achieved during this project:

> 1. To construct a database of molluscan occurrences and ranges for the east coast of Australia, and use it to investigate the key drivers of coastal molluscan latitudinal diversity in terms of abiotic variables.

The final dataset numbered 168,601 occurrences for the entire stretch of eastern Australia, containing 3796 species and 260 families. Molluscs along eastern Australia exhibit a strong latitudinal diversity gradient that is strikingly different in structure from that of both North American coastlines, with a much smoother profile and no stepwise pattern matching with existing biological provinces. Species range sizes show no correlation with this gradient, but temperature (a proxy for energy availability) and dissolved oxygen content were strongly correlated with it. No other abiotic variable was found to be correlated with latitudinal richness.

2. To designate molluscan biogeographical provinces for the east coast of Australia by applying several statistical methods that have been used in the literature to assign provincial boundaries.

Assigning provinces to Australia is extremely difficult, as each method depicted slightly different biogeographical structure. There was strong support for a across a few methods for a province including southern Victoria and Tasmania. However, the rest of mainland Australia remained difficult to split into distinct regions. Faunal turnover was relatively stable and high across the whole area, suggesting that distinct province boundaries may not exist for the mainland.

The 'range-through' method proved ineffective when looking for province boundaries, and no relation could be found between the suggested provinces and the nature of the latitudinal gradient. Modern ecological sampling would provide much better resolution when considering ecological change across the area.

3. To investigate what abiotic variables that define the start and end of each province, and to see if they are instead purely controlled by geographic features.

All suggested province boundaries were unrelated with previously defined temperature boundaries, salinity or dissolved oxygen content. Large-scale studies looking purely at these variables to define province boundaries may be inaccurate for this region. When nutrient content was included in the analysis, a strong southern effect was shown for nitrate content in the water. It is likely, therefore, that the boundary is nutrient driven, with conflicting current regimes separating nutrient-poor northern waters from nutrient-rich southern waters.

Recommendations for further study

The main outcome in this study was the lack of a consistent dataset for the full extent of the coastline in Australia, especially in terms of temporal coverage and availability of bona fide ecological abundance data. A future study would be

primarily based on ecological sampling, ideally covering all the coastline and collected within a season. A comparison between this collection and robust data collections from 1960-1980 in the existing dataset could then be used to investigate how province boundaries have changed over time, as well as more accurately define them.

In addition, higher resolution sampling for eastern and western coastlines of Tasmania is needed to fully differentiate these coastlines, if indeed there is a major ecological difference, and settle debate over the uniformity of Tasmanian molluscan ecology. For the next stage of this study, the data should be split into degree squares, and not just by latitude, for the southern regions.

References

Allison, G. W., Lubchenco, J., & Carr, M. H. (1998). Marine reserves are necessary but not sufficient for marine conservation. *Ecological Applications, 8*(1), S79-S92.

Alroy, J. (2015). A new twist on a very old binary similarity coefficient. *Ecology, 96*(2), 575-586.

Alroy, J. (2017). Effects of habitat disturbance on tropical forest biodiversity. *Proceedings of the National Academy of Sciences, 114*(23), 6056-6061.

Anon. (1958). The venice system for the classification of marine waters according to salinity. *Limnology and Oceanography, 3*(3), 346-347.

Bennett, I., & Pope, E. C. (1952). Intertidal zonation of the exposed rocky shores of victoria, together with a rearrangement of the biogeographical provinces of temperate australian shores. *Australian Journal of Marine and Freshwater Research, 4*, 105-159.

Bennett, I., & Pope, E. C. (1960). Intertidal zonation of the exposed rocky shores of tasmania and its relationship with the rest of australia. *Marine and Freshwater Research, 11*(2), 182-221.

Blackburn, T. M., & Gaston, K. J. (1996). A sideways look at patterns in species richness, or why there are so few species outside the tropics. *Biodiversity Letters, 3*(2), 44-53.

Boakes, E. H., McGowan, P. J., Fuller, R. A., Chang-qing, D., Clark, N. E., O'Connor, K., & Mace, G. M. (2010). Distorted views of biodiversity: Spatial and temporal bias in species occurrence data. *PLoS Biology, 8*(6), e1000385.

Booth, T. H., Williams, K. J., & Belbin, L. (2012). Developing biodiverse plantings suitable for changing climatic conditions 2: Using the atlas of living australia. *Ecological Management & Restoration, 13*(3), 274-281.

Borg, I., Groenen, P. J., & Mair, P. (2012). *Applied multidimensional scaling*: Springer Science & Business Media.

Bousfield, E. L., & Thomas, M. L. H. (1975). Post-glacial changes in distribution of littoral marine invertebrates in the canadian atlantic region. *Proceedings of Nova Scotia Institute of Science, 27*(Supp 3), 47-60.

Briggs, J. C. (1995). *Global biogeography* (Vol. 14): Elsevier.

Cajo, J. F. T. B. (1986). Canonical correspondence analysis: A new eigenvector technique for multivariate direct gradient analysis. *Ecology, 67*(5), 1167-1179.

Cecca, F. (2002). *Palaeobiogeography of marine fossil invertebrates: Concepts and methods*: CRC Press.

Chao, A. (1984). Nonparametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics, 11*(4), 265-269.

Chao, A., Chazdon, R. L., Colwell, R. K., & Shen, T.-J. (2005). A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology Letters, 8*(2), 148-159.

Chao, A., & Chiu, C. H. (2006). Species richness: Estimation and comparison. In *Encyclopedia of statistical sciences*.

Chaparro, O. R., Cubillos, V. M., Montiel, Y. A., Paschke, K. A., & Pechenik, J. A. (2008). Embryonic encapsulation and maternal incubation: Requirements for survival of the early stages of the estuarine gastropod crepipatella dilatata. *Journal of Experimental Marine Biology and Ecology, 365*(1), 38-45.

Commonwealth of Australia. (2006). *A guide to the integrated marine and coastal regionalisation of australia version 4.0.* . Retrieved from National Oceans Office, Canberra: http://www.environment.gov.au/coasts/mbp/publications/imcra/pubs/imcra4.pdf

Condie, S. A., & Dunn, J. R. (2006). Seasonal characteristics of the surface mixed layer in the australasian region: Implications for primary production regimes and biogeography. *Marine and Freshwater Research, 57*, 1-22.

Cook, R. R., & Auster, P. J. (2007). A bioregional classification of the continental shelf of northeastern north america for conservation analysis and planning based on representation. *Marine Sanctuaries Conservation Series, NMSP-07-03*, 1-14.

Coomans, H. E. (1962). The marine mollusk fauna of the virginian area as a basis for defining zoogeographical provinces. *Beaufortia, 9*(98), 83-104.

Crame, J. A. (2000). Evolution of taxonomic diversity gradients in the marine realm: Evidence from the composition of recent bivalve faunas. *Paleobiology, 26*(2), 188-214.

Creighton, C., Boon, P. I., Brookes, J. D., & Sheaves, M. (2015). Repairing australia's estuaries for improved fisheries production – what benefits, at what cost? *Marine and Freshwater Research, 66*(6).

Cresswell, G. (2000). Currents of the continental shelf and upper slope of tasmania. *Papers and Proceedings of the Royal Society of Tasmania, 133*(3), 21-30.

CSIRO. (1996). Interim marine bioregionalisation for australia: Towards a national system of marine protected areas. Retrieved from http://www.cmar.csiro.au/datacentre/ext_marlin_docs/bioregion/contents.html

De Leeuw, J., & Mair, P. (2011). Multidimensional scaling using majorization: Smacof in r. Department of Statistics, UCLA.

Deaton, L. E., Derby, J. G. S., Subhedar, N., & Greenberg, M. J. (1989). Osmoregulation and salinity tolerance in two species of bivalve mollusc: Limnoperna fortunei and mytilopsis leucophaeta. *Journal of Experimental Marine Biology and Ecology, 133*(1), 67-79.

Devred, E., Sathyendranath, S., & Platt, T. (2007a). Delineation of ecological provinces using ocean colour radiometry. *Marine Ecology Progress Series, 346*, 1-13.

Devred, E., Sathyendranath, S., & Platt, T. (2007b). Relationship between the q factor and inherent optical properties: Relevance to ocean-colour inversion algorithms. *Geophysical Research Letters, 34*(18), n/a-n/a.

Devred, E., Sathyendranath, S., & Platt, T. (2009). Decadal changes in ecological provinces of the northwest atlantic ocean revealed by satellite observations. *Geophysical Research Letters, 36*(19), L19607.

Edgar, G. J., & Barrett, N. S. (2000). Effects of catchment activities on macrofaunal assemblages in tasmanian estuaries. *Estuarine, Coastal and Shelf Science, 50*(5), 639-654.

Edgar, G. J., Stuart-Smith, R. D., Willis, T. J., Kininmonth, S., Baker, S. C., Banks, S., . . . Thomson, R. J. (2014). Global conservation outcomes depend on marine protected areas with five key features. *Nature, 506*(7487), 216-220.

Engle, V. D., & Summers, J. K. (2000). Biogeography of benthic macroinvertebrates in estuaries along the gulf of mexico and western atlantic coasts. *Hydrobiologia, 436*(1-3), 17-33.

Fanti, F., & Miyashita, T. (2009). A high latitude vertebrate fossil assemblage from the late cretaceous of west-central alberta, canada: Evidence for dinosaur nesting and vertebrate latitudinal gradient. *Palaeogeography, Palaeoclimatology, Palaeoecology, 275*(1), 37-53.

Fine, P., & Ree, R. H. (2006). Evidence for a time-integrated species-area effect on the latitudinal gradient in tree diversity. *The American Naturalist, 168*(6), 796-804.

Flessa, K. W., & Jablonski, D. (1996). The geography of evolutionary turnover: A global analysis of extant bivalves. *Evolutionary paleobiology*, 376-397.

Forbes, S. A. (1907). *On the local distribution of certain illinois fishes: An essay in statistical ecology* (Vol. 7): Illinois State Laboratory of Natural History.

Fuhrman, J. A., Steele, J. A., Hewson, I., Schwalbach, M. S., Brown, M. V., Green, J. L., & Brown, J. H. (2008). A latitudinal diversity gradient in planktonic marine bacteria. *Proceedings of the National Academy of Sciences, 105*(22), 7774-7778.

Garcillán, P. P., & Ezcurra, E. (2011). Sampling procedures and species estimation: Testing the effectiveness of herbarium data against vegetation sampling in an oceanic island. *Journal of Vegetation Science, 22*(2), 273-280.

Gaston, K. J., Blackburn, T. M., & Spicer, J. I. (1998). Rapoport's rule: Time for an epitaph? *Trends in ecology & evolution, 13*(2), 70-74.

Gottscho, A. D. (2016). Zoogeography of the san andreas fault system: Great pacific fracture zones correspond with spatially concordant phylogeographic boundaries in western north america. *Biological Reviews, 91*(1), 235-254.

Gower, J. C. (1966). Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika, 53*(3-4), 325-338.

Graham, C. H., Ferrier, S., Huettman, F., Moritz, C., & Peterson, A. T. (2004). New developments in museum-based informatics and applications in biodiversity analysis. *Trends in ecology & evolution, 19*(9), 497-503.

Hale, S. S. (2010). Biogeographical patterns of marine benthic macroinvertebrates along the atlantic coast of the northeastern USA. *Estuaries and Coasts, 33*(5), 1039-1053.

Harris, G., Nilsson, C., Clementson, L., & Thomas, D. (1987). The water masses of the east coast of tasmania: Seasonal and interannual variability and the influence on phytoplankton biomass and productivity. *Marine and Freshwater Research, 38*(5), 569-590.

Harvey, E. T., Kratzer, S., & Andersson, A. (2015). Relationships between colored dissolved organic matter and dissolved organic carbon in different coastal gradients of the baltic sea. *Ambio, 44*(Suppl 3), 392-401.

Hedley, C. (1904). *The effect of the bassian isthmus upon the existing marine fauna: A study in ancient geography*.

Hillebrand, H. (2004). On the generality of the latitudinal diversity gradient. *The American Naturalist, 163*(2), 192-211.

Horton, T., Kroh, A., Bailly, N., Boury-Esnault, N., Brandão, S. N., Costello, M. J., . . . Zeidler, W. (2017). World register of marine species (worms). Retrieved 2017-08-22, from WoRMS Editorial Board http://www.marinespecies.org

Huisman, J. M., & Millar, A. J. (2013). Australian seaweed collections: Use and misuse. *Phycologia, 52*(1), 2-5.

Humphreys, A. M., & Barraclough, T. G. (2014). The evolutionary reality of higher taxa in mammals. *Proceedings of the Royal Society B: Biological Sciences, 281*(1783).

Hunt, H. L., Maltais, M.-J., Fugate, D. C., & Chant, R. J. (2007). Spatial and temporal variability in juvenile bivalve dispersal: Effects of sediment transport and flow regime. *Marine Ecology Progress Series, 352*, 145-159.

Huyer, A., Smith, R. L., Stabeno, P. J., Church, J. A., & White, N. J. (1988). Currents off south-eastern australia: Results from the australian coastal experiment. *Australian Journal of Marine and Freshwater Research, 39*, 245-288.

Itsukushima, R., & Shimatani, Y. (2015). Relationship between estuarine shellfish fauna and physical environmental characteristics for estuary conservation in kyushu, japan. *Current World Environment, 10*(3), 715-728.

Jablonski, D. (1993). The tropics as a source of evolutionary novelty through geological time. *Nature, 364*(6433), 142-144.

Jablonski, D., Belanger, C. L., Berke, S. K., Huang, S., Krug, A. Z., Roy, K., . . . Valentine, J. W. (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, 110*(26), 10487-10494.

Jablonski, D., Roy, K., & Valentine, J. W. (2006). Out of the tropics: Evolutionary dynamics of the latitudinal diversity gradient. *Science, 314*(5796), 102-106.

Johnson, C. R., Banks, S. C., Barrett, N. S., Cazassus, F., Dunstan, P. K., Edgar, G. J., . . . Taw, N. (2011). Climate change cascades: Shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern tasmania. *Journal of Experimental Marine Biology and Ecology, 400*(1), 17-32.

Knox, G. A. (1960). Littoral ecology and biogeography of the southern oceans. *Proceedings of the Royal Society of London. Series B, Biological Sciences, 152*(949), 577-624.

Knox, G. A. (1963). The biogeography and intertidal ecology of the australasian coasts. *Oceanography and Marine Biology, Annual Review, 1*.

Kriwoken, L. K. (1996). Australian biodiversity and marine protected areas. *Ocean and Coastal Management, 33*(1-3), 113-132.

Lane, M. A. (1996). Roles of natural history collections. *Annals of the Missouri Botanical Garden, 83*(4), 536-545.

Last, P., & Séret, B. (1999). Comparative biogeography of the chondrichthyan faunas of the tropical south-east indian and south-west pacific oceans.

Last, P. R., Lyne, V. D., Williams, A., Davies, C. R., Butler, A. J., & Yearsley, G. K. (2010). A hierarchical framework for classifying seabed biodiversity with application to planning and managing australia's marine biological resources. *Biological Conservation, 143*(7), 1675-1686.

Legendre, P., & Anderson, M. J. (1999). Distance-based redundancy analysis: Testing multispecies responses in multifactorial ecological experiments. *Ecological monographs, 69*(1), 1-24.

Legendre, P., & Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia, 129*(2), 271-280.

Legendre, P., & Legendre, L. F. (2012). *Numerical ecology* (Vol. 24): Elsevier.

Lister, A. M., & Climate Change Research, G. (2011). Natural history collections as sources of long-term datasets. *Trends in ecology & evolution, 26*(4), 153-154.

MacPherson, E. (2003). Species range size distributions for some marine taxa in the atlantic ocean. Effect of latitude and depth. *Biological Journal of the Linnean Society, 80*(3), 437.

Magurran, A. E., Baillie, S. R., Buckland, S. T., Dick, J. M., Elston, D. A., Scott, E. M., . . . Watt, A. D. (2010). Long-term datasets in biodiversity research and monitoring: Assessing change in ecological communities through time. *Trends in ecology & evolution, 25*(10), 574-582.

McArdle, B. H., & Anderson, M. J. (2001). Fitting multivariate models to community data: A comment on distance-based redundancy analysis. *Ecology, 82*(1), 290-297.

McNeill, S. E. (1994). The selection and design of marine protected areas: Australia as a case study. *Biodiversity and Conservation, 3*, 586-605.

Mellergaard, S., & Nielsen, E. (1995). Impact of oxygen deficiency on the disease status of common dab limanda limanda. *Diseases of Aquatic Organisms, 22*(2), 101-114.

Mellin, C., Aaron MacNeil, M., Cheal, A. J., Emslie, M. J., & Julian Caley, M. (2016). Marine protected areas increase resilience among coral reef communities. *Ecology Letters, 19*(6), 629-637.

Mittelbach, G. G., Schemske, D. W., Cornell, H. V., Allen, A. P., Brown, J. M., Bush, M. B., . . . Turelli, M. (2007). Evolution and the latitudinal diversity gradient: Speciation, extinction and biogeography. *Ecology Letters, 10*(4), 315-331.

Mora, C., Andréfouët, S., Costello, M. J., Kranenburg, C., Rollo, A., Veron, J., . . . Myers, R. A. (2006). Coral reefs and the global network of marine protected areas. *Science, 2006*, 1750.

Narayanaswamy, B. E., Renaud, P. E., Duineveld, G. C., Berge, J., Lavaleye, M. S., Reiss, H., & Brattegard, T. (2010). Biodiversity trends along the western european margin. *PLoS One, 5*(12), e14295.

Nell, J., & Gibbs, P. (1986). Salinity tolerance and absorption of l-methionine by some australian bivalve molluscs. *Marine and Freshwater Research, 37*(6), 721-727.

Nelson, B. W., Ferreira, C. A., da Silva, M. F., & Kawasaki, M. L. (1990). Endemism centres, refugia and botanical collection density in brazilian amazonia. *Nature, 345*(6277), 714-716.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., . . . Wagner, J. (2017). Vegan: Community ecology package. Retrieved from https://CRAN.R-project.org/package=vegan

Oliver, M. J., & Irwin, A. J. (2008). Objective global ocean biogeographic provinces. *Geophysical Research Letters, 35*(15).

Pianka, E. R. (1966). Latitudinal gradients in species diversity: A review of concepts. *The American Naturalist, 100*(910), 33-46.

Ponder, W. F., Carter, G. A., Flemons, P., & Chapman, R. R. (2001). Evaluation of museum collection data for use in biodiversity assessment. *Conservation Biology, 15*(3), 648-657.

R Core Team. (2017). R: A language and environment for statistical computing. Vienna, Austria. Retrieved from https://www.R-project.org/

Régnier, C., Fontaine, B., & Bouchet, P. (2009). Not knowing, not recording, not listing: Numerous unnoticed mollusk extinctions. *Conservation Biology, 23*(5), 1214-1221.

Ridgway, K. R. (2007). Long-term trend and decadal variability of the southward penetration of the east australian current. *Geophysical Research Letters, 34*(13).

Ridgway, K. R., Dunn, J. R., & Wilkin, J. L. (2002). Ocean interpolation by four-dimensional least squares - application to the waters around australia. *Journal of Atmospheric and Oceanic Technology, 19*(9), 1357-1375.

Rodolfo-Metalpa, R., Houlbrèque, F., Tambutté, É., Boisson, F., Baggini, C., Patti, F. P., . . . Gattuso, J. (2011). Coral and mollusc resistance to ocean acidification adversely affected by warming. *Nature Climate Change, 1*(6), 308.

Rohde, K. (1992). Latitudinal gradients in species diversity: The search for the primary cause. *Oikos, 65*(3), 514-527.

Roy, K. (2001). Analyzing temporal trends in regional diversity: A biogeographic perspective. *Paleobiology, 27*(4), 631-645.

Roy, K., Jablonski, D., & Valentine, J. W. (1994). Eastern pacific molluscan provinces and latitudinal diversity gradient: No evidence for "rapoport's rule". *Proceedings of the National Academy of Sciences, 91*, 8871-8874.

Roy, K., Jablonski, D., & Valentine, J. W. (1996). Higher taxa in biodiversity studies: Patterns from eastern pacific marine molluscs. *Philosophical Transactions: Biological Sciences, 351*(1347), 1605-1613.

Roy, K., Jablonski, D., & Valentine, J. W. (2000). Dissecting latitudinal diversity gradients: Functional groups and clades of marine bivalves. *Proceedings of the Royal Society B: Biological Sciences, 267*, 293-299.

Roy, K., Jablonski, D., Valentine, J. W., & Rosenberg, G. (1998). Marine latitudinal gradients: Tests of casual hypotheses. *Proceedings of the National Academy of Sciences, 95*, 3699-3702.

Roy, K., & Martien, K. K. (2001). Latitudinal distribution of body size in north-eastern pacific marine bivalves. *Journal of Biogeography, 28*(4), 485-493.

Segura, C. J., Pechenik, J. A., Montory, J. A., Navarro, J. M., Paschke, K. A., Cubillos, V. M., & Chaparro, O. R. (2016). The cost of brooding in an estuary: Implications of declining salinity for gastropod females and their brooded embryos. *Marine Ecology Progress Series, 543*, 187-199.

Shaffer, H. B., Fisher, R. N., & Davidson, C. (1998). The role of natural history collections in documenting species declines. *Trends Ecol Evol, 13*(1), 27-30.

Shimodaira, H. (2004). Approximately unbiased tests of regions using multistep-multiscale bootstrap resampling. *The Annals of Statistics, 32*(6), 2616-2641.

Smith, K. F., & Brown, J. M. (2002). Patterns of diversity, depth range and body size among pelagic fishes along a gradient of depth. *Global Ecology and Biogeography, 11*, 313-322.

Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdaña, Z. A., Finlayson, M., . . . Robertson, J. (2007). Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. *BioScience, 57*(7), 573-583.

Stevens, G. C. (1989). The latitudinal gradient in geographical range: How so many species coexist in the tropics. *The American Naturalist, 133*(2), 240-256.

Suzuki, R., & Shimodaira, H. (2015). Pvclust: Hierarchical clustering with p-values via multiscale bootstrap resampling. Retrieved from https://CRAN.R-project.org/package=pvclust

Teske, P. R., Sandoval-Castillo, J., Waters, J., & Beheregaray, L. B. (2017). An overview of australia's temperate marine phylogeography, with new evidence from high-dispersal gastropods. *Journal of Biogeography, 44*(1), 217-229.

Valdovinos, C., Navarrete, S. A., & Marquet, P. A. (2003). Mollusk species diversity in the southeastern pacific: Why are there more species towards the pole? *Ecography, 26*, 139-144.

Valentine, J. W. (1966). Numerical analysis of marine molluscan ranges on the extratropical northeastern pacific shelf. *Limnology and Oceanography, 11*(2), 198-211.

Van Den Wollenberg, A. L. (1977). Redundancy analysis an alternative for canonical correlation analysis. *Psychometrika, 42*(2), 207-219.

van der Meij, S. E., Moolenbeek, R. G., & Hoeksema, B. W. (2009). Decline of the jakarta bay molluscan fauna linked to human impact. *Marine Pollution Bulletin, 59*(4-7), 101-107.

Verween, A., Vincx, M., & Degraer, S. (2007). The effect of temperature and salinity on the survival of mytilopsis leucophaeata larvae (mollusca, bivalvia): The search for environmental limits. *Journal of Experimental Marine Biology and Ecology, 348*(1), 111-120.

Welsh, H. J. (1994). Bioregions: An ecological and evolutionary perspective and a proposal for california. *California Fish and Game, 80*(3), 97-124.

Williams, A., Althaus, F., Dunstan, P. K., Poore, G. C. B., Bax, N. J., Kloser, R. J., & McEnnulty, F. R. (2010). Scales of habitat heterogeneity and megabenthos biodiversity on an extensive australian continental margin (100-1100 m depths). *Marine Ecology, 31*(1), 222-236.

Willig, M. R., Kaufman, D. M., & Stevens, R. D. (2003). Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics, 34*(1), 273-309.

Willig, M. R., & Lyons, S. K. (1998). An analytical model of latitudinal gradients of species richness with an empirical test for marsupials and bats in the new world. *Oikos, 81*(1), 93-98.

Wilson, B. R., & Gillett, K. (1974). *Australian shells*. Sydney: Reed Press.

York, K. L., Blacket, M. J., & Appleton, B. R. (2008). The bassian isthmus and the major ocean currents of southeast australia influence the phylogeography and population structure of a southern australian intertidal barnacle catomerus polymerus (darwin). *Molecular Ecology, 17*(8), 1948-1961.

Zalba, S. M., Sonaglioni, M. I., Compagnoni, C. A., & Belenguer, C. J. (2000). Using a habitat model to assess the risk of invasion by an exotic plant. *Biological Conservation, 93*(2), 203-208.

Appendices

Table 1: List of contributing institutions, with numbers of records contributed. Data were taken from OZCAM and filtered (see text); only the final dataset is shown here.

Institution	Records Contributed
Australian Museum	97826
Museum and Art Gallery of the Northern Territory	628
National Museum of Victoria	24343
Queensland Museum	602
Queen Victoria Museum and Art Gallery	1482
Tasmanian Museum and Art Gallery	19127
Western Australian Museum	73

Table 2: Variance explained (%) by major axes in the Constrained Correspondence Analysis (CCA) and Principal Coordinates Analysis (PCoA) for each data treatment.

Transform	Variance explained by axis		
	1	2	3
Presence counts (CCA)	22.5	12.1	6.69
Range-through (CCA)	36.6	18.1	9.95
Presence counts (PCoA)	76.2	13.4	6.52
Range-through (PCoA)	60.0	16.6	7.98

Figure 1: Results for ordinal, nonmetric multidimensional scaling of occurrence data for east coast Australian molluscs using two dimensions. The results here are based on a matrix of presence counts, with each point shown as the midpoint of each latitudinal band (-39 would be all points between -38.5 and -39.5, for example). -34 and -38 have very high counts of a small number of species, relative to the whole dataset, and thus sit far out from the main cluster of points.

Author Guidelines for *Journal of Biogeography*

Accessed 4th October 2017

1. SUBMISSION

Authors should kindly note that submission implies that the content has not been published or submitted for publication elsewhere except as a brief abstract in the proceedings of a scientific meeting or symposium. All submissions must be concisely and clearly written in grammatically correct English.

Once the submission materials have been prepared in accordance with the Author Guidelines, manuscripts should be submitted online at https://mc.manuscriptcentral.com/jbi

The submission system will prompt authors to use an ORCID iD (a unique author identifier) to help distinguish their work from that of other researchers. Click here to find out more.

Click here for more details on how to use ScholarOne

For help with submissions, please contact Iris and Tom from the Editorial Office at jbioffice@wiley.com.

2. AIMS AND SCOPE

Papers dealing with all aspects of spatial, ecological and historical biogeography are considered for publication in the *Journal of Biogeography*. The mission of the Journal is to contribute to the growth and societal relevance of the discipline of biogeography through its role in the dissemination of biogeographical research. To that end, the editorial policy is that the Journal seeks to be representative of the discipline of biogeography, to be global in scope, and to be inclusive of major traditions and viewpoints in the discipline. Authors are particularly encouraged to submit concise, clearly written papers focused on precisely framed questions or hypotheses of broad interest to the wide international readership of the Journal, in addition we also publish synthesis, methods, data and opinion papers. The challenge in biogeography is to extract general relationships from complex natural data. This often requires carefully designed studies of multiple species, which incorporate contextual information on, for example, the past or present biology of the taxa and/or the environments in which they occur. Papers that are primarily descriptive and are focussed only on the taxon being studied should be submitted to a more specialized journal.

3. MANUSCRIPT CATEGORIES AND REQUIREMENTS

The Journal publishes articles under the following main headers: 1) **Research Paper**, 2) **Methods and Tools**, 3) **Data**, 4) **Synthesis**, 5) **Perspective**, 6) **Commentary** and 7) **Correspondence**. All submissions are subject to peer review.

1) Research Paper. Research papers present new biogeographic research resulting from the analysis of a question in biogeography. Authors should prepare their manuscript so that, when published, the article will comprise not more than 10 to 12 published pages. A single page of the journal can carry one of the following: (1) the article title, author list, abstract, and keywords; (2) about 1000 words of text (including subheadings); (3) about 30 references. For a typical Research paper, in which illustrative material (Tables and Figures) occupies about 3 pages of the journal when printed at final journal sizing, the text, inclusive of abstract and reference list, should not exceed 7000 words. Manuscripts should include a biosketch (see below); tables with their legends above; list of figure legends; and embedded figures, and the main headers in the main text of Research Papers should normally be Introduction, Materials and Methods, Results, Discussion, Acknowledgements, References. Methods need to be described in a manner that allows a competent practitioner in the field

to repeat the study. Authors must allow repeatability by either providing a thorough description of the methods or by providing relevant computer code.

Structured abstracts. Abstracts should be of no more than 300 words, presented as a series of factual statements under the following headings: Aim, Location, Taxon, Methods, Results and Main conclusions. The Aim should give a clear statement of the principal research question(s) or hypotheses, the Taxon indicate the main group (eg angiosperms), the Methods should give details of materials/sampling/methods of analysis, and the Main conclusions should give the main take-home message.

Biosketch/Biosketches. A short Biosketch/Biosketches entry (30-100 words for one author/150 words total for the first three authors, respectively) describing the research interests of the author(s) should be provided. For papers with four or more authors, biosketch details should be supplied for the first author only and/or a general statement of the focus of the research team (which may include a link to a group web page) plus, in all cases, a statement of author contributions, e.g. Author contributions: A.S. and K.J. conceived the ideas; K.J. and R.L.M. collected the data; R.L.M. and P.A.K. analysed the data; and A.S. and K.J. led the writing.

For an example click here.

2) Methods and Tools. These are structured as in Research papers, but the main focus is to present or investigate a new method, rather than to explore a biogeographical problem. Papers in this section are expected to apply new methods to the analysis of biogeographic data and discuss the potential of those methods for advancing the study of the field. For an example click here.

3) Data. Datasets that are likely to be of interest to the broader biogeography community are published under this category. Data papers allow scientists to publish and receive credit for work in which the nature of the collected, mobilized, or integrated data more than a specific analysis may be most impactful. The structure of a Data paper should be similar to that of a Research paper. Data papers must include a characterization of overall scope (e.g. organismal, spatial), a description of how the data were collected (protocols), a detailed characterization of all data fields and metadata, information on data records (e.g. SI or in a suitable repository), a section on technical validation, and usage notes addressing potential caveats for analysis and interpretation. Additional analyses that exemplify potential uses of the data are encouraged but not essential. Note that the Data papers category is intended for novel datasets - data used in a published or submitted research paper should be fully addressed and made available there.

4) Synthesis. Papers that have the character of a theoretical synthesis or review, even if incorporating an element of original analysis within them, should use the article type Synthesis. Guidelines are as for Research papers but submissions to the Synthesis section may be of up to 10,000 words, or exceptionally more, if the additional length is fully justified. Authors of synthesis papers are encouraged to discuss their planned paper with one of the Chief Editors, especially if the length will exceed 10,000 words. For an example click here.

5) Perspective. Perspectives papers are should be stimulating and reflective essays providing personal perspectives on key research fields and issues within biogeography. When published, Perspectives should be of no more than eight printed pages (main text maximum 5000 words; word count including abstract, main text and references 7000 words maximum but note that shorter articles are encouraged), and they should include a short, single-paragraph abstract. A biosketch (see below) may be included after the references providing the overall paper length limit is not exceeded. For an example click here.

6) Commentary. Commentary submissions should provide readily intelligible comment on the latest original research in biogeography. The prose style should be light, and the article should be written

with the minimum of technical language and jargon, so as to be understandable to a general audience or an undergraduate taking an introductory course in biogeography. Contributions will be subject to rapid peer review. Commentaries should occupy a maximum of two pages of the journal, and should have a maximum of 10 references: thus the overall word count should not exceed 1600. No biosketch is included for commentaries. Should you wish to include a small figure or other illustration, this can be accommodated by a reduction in the number of words on a pro rata basis. For an example click here.

7) Correspondence. The Journal welcomes short items of correspondence prompted by papers previously published in this or occasionally in other journals. The text should not normally exceed 2500 words, inclusive of a short one-paragraph abstract (up to 150 words), and a list of 6–10 keywords. No biosketch is necessary for Correspondence papers. For an example click here.

4. PREPARING THE SUBMISSION

Cover Letters

A cover letter to the editor, indicating in less than 100 words why this paper is of interest to the readers of the Journal, must be uploaded separately

Parts of the Manuscript

The manuscript should be submitted in separate files: main text file with embedded figures; supporting information.

LaTeX users do not have to translate their manuscripts into MSWord, but may upload them as PDF files. Any explanatory notes, companion papers etc. for the attention of reviewers should be uploaded under 'Comments to reviewers'

Main Text File

The text file should be presented in the following order:

i. Title
ii. A short running title of less than 40 characters
iii. The full names of the authors
iv. The author's institutional affiliations where the work was carried out, with a footnote for the author's present address if different from where the work was carried out
v. Acknowledgements
vi. Abstract and keywords
vii. Main text
viii. References
ix. Biosketch
x. Tables (each table complete with title and footnotes)
xi. Figure legends and embedded figures
xii. Appendices (if relevant)
xiii. Supporting information should be supplied as separate files.

Title. The title should be short and informative, containing major keywords related to the content. The title should not contain abbreviations (see Wiley's best practice SEO tips).

Authorship. For details on eligibility for author listing, please refer to the journal's Authorship policy outlined in the Editorial Policies and Ethical Considerations section.

Acknowledgements. Contributions from individuals who do not meet the criteria for authorship should be listed, with permission from the contributor, in an Acknowledgements section. Financial and material support should also be mentioned. Thanks to anonymous reviewers are not appropriate.

Conflict of Interest Statement. Authors will be asked to provide a conflict of interest statement during the submission process. See 'Conflict of Interest' section in Editorial Policies and Ethical Considerations for details on what to include in this section. Authors should ensure they liaise with all co-authors to confirm agreement with the final statement.

Abstract and Keywords

Abstracts and keywords are required for some manuscript types. For details on manuscript types that require abstracts and/or keywords, as well as how to prepare them, please refer to the 'Manuscript Categories and Requirements' section. Please provide 6-10 keywords, arranged alphabetically, separated by commas. Note that optimally the most important keywords are repeated in the title and the keywords.

Main Text

The journal uses British spelling; however, authors may submit using either option, as spelling of accepted papers is converted during the production process

References
References are styled according to the sixth edition of the Publication Manual of the American Psychological Association. List all sources in the reference alphabetically by name.

In text citations should follow the author-date method. This means that the author's last name and the year of publication for the source should appear in the text, for example, (Jones, 1998), and a complete reference should appear in the reference list at the end of the paper.

When a work has two authors, cite both names every time the reference occurs in text. When a work has three, four, or five authors, cite all authors the first time the reference occurs; subsequent citations include only the surname of the first author followed by et al., (not Italicized and with a period after "al.") and the year if it is the first citation of the reference within a paragraph.

If there are two or more citations that shorten to the same lead author and date, give as many additional names as needed to identify them, e.g., (Smith, Jones, et al., 1991) and (Smith, Burke, et al., 1991).

Unpublished data, works in preparation and papers submitted but not yet accepted may be cited in the text as personal communication, giving the author's initials and surname, but should not be included in the reference list. It is the author's responsibility to obtain permission from colleagues to include their work as a personal communication. Please add the person's initials, surname and if applicable institute for personal communications.

The basic reference form for a journal paper is: Author (date).Paper title. Journal, Volume, page; and for a book citation: Author (date). Book title. Place of publication, publisher.

Please note that for journal articles, issue numbers are not included unless each issue in the volume begins with page one. Journals names are written out in full.

Please ensure that in the paper titles only proper names are capitalized, and that all scientific binomials are in italics.

Please include up to seven authors in the list (use "&" before last author name). For eight or more authors please list the first six and then use ellipses followed by last author (do not use "&" before last author name)

Journal article:
Light, M. A., & Light, I. H. (2008). The geographic expansion of Mexican immigration in the United States and its implications for local law enforcement. *Law Enforcement Executive Forum Journal*, 8(1), 73–82.

Book:
Goldstein, H. (1990). *Problem-oriented policing*. New York, NY: McGraw-Hill. Miles, M. B., & Huberman, A. M. (1994). *Qualitative data analysis* (2nd ed.). Thousand Oaks, CA: Sage.

Edited Book:
Gilbert, D. G., McClernon, J. F., Rabinovich, N. E., Sugai, C., Plath, L. C., Asgaard, G., ... Botros, N. (1983). Situational crime prevention: Its theoretical basis and practical scope. In M. Tonry & N. Morris (Eds.), *Crime and justice: An annual review of research* (Vol. 4, pp. 225–256). Chicago, IL: University of Chicago Press.

Citations to data sources
Some studies (e.g., meta-analyses) use data drawn from multiple published sources. If these sources are not otherwise cited in the main text, they should be listed in one or more appendices with titles similar to the following: "Appendix 1 – Data sources". These data appendices will be printed in the main paper (so that citation indexing services will capture them), but in a reduced font. These appendices should be cited in the main text (e.g. "A list of the data sources is found in Appendix 1.").

Tables
Tables should be self-contained and complement, not duplicate, information contained in the text. They should be supplied as editable files, not pasted as images. Legends should be concise but comprehensive – the table, legend, and footnotes must be understandable without reference to the text, giving the study organism and study location and 'n' values where applicable. Column headings should be brief, with units of measurement in parentheses. All abbreviations must be defined in footnotes

Figure Legends
Legends should be concise but comprehensive – the figure and its legend must be understandable without reference to the text, to this end both the geographical region and the taxon should be mentioned in each caption. Include definitions of any symbols used and define/explain all abbreviations and units of measurement.

Figures
For review purposes, figures should be embedded at the end of the text file. All illustrations (including photographs and maps) are classified as figures and they should be numbered consecutively as first cited in the text. Panels should be labelled (a), (b), (c), etc. rather than (A), (B), (C) etc. and referred to in the text as, for example, Fig. 1a. Figure legends should be listed at the end of the paper before the embedded figures. Legends should be explicit and informative and should 'stand alone' from the main text, giving the study organism and study location where applicable. All abbreviations should be defined.

Click here for the basic figure requirements for figures submitted with manuscripts for initial peer review, as well as the more detailed post-acceptance figure requirements.

If and when your paper is accepted for publication, the editorial office will request you to upload your figures as separate files in the format(s) specified below. When supplying these files, use the

following naming convention: manuscript number, figure number and then the appropriate file extension e.g. 'JBI-08-0500_Fig1.tif'.

Photographic figures should be saved in .tif format at 300 d.p.i. (or failing that in .jpg format with low compression). Line figures should be saved as vector graphics (i.e. composed of lines, curves, points and fonts) in .eps or .pdf format, as this enhances their display when published online. Combination figures (those composed of vector and pixel/raster elements) should also be saved in .eps or .pdf format where possible. If line figures and combination figures cannot be saved in vector graphics format, they should be saved in .tif format at high resolution (i.e. 600–800 d.p.i.) (do not save them in .jpg format). If you are unsure about the resolution of your .tif files, please zoom in and check that fonts, curves and diagonal lines are smooth-edged and do not appear blocky. Note that .tif files are downsampled for online publication and so authors should preferentially opt for vector graphic formats for line and combination figures (full resolution .tif files are used for print publication). Colour figures should be saved in CYMK rather than RGB.

Prepare figures such that, after reduction to print size, all lettering and symbols will be clear and easily read, and such that each figure makes effective use of space. Font size in figures should be 8 pt. To check this, fix the image size in Illustrator to the required column width, and check the font size. Possible figure sizes: single column = 79mm, 2/3rd column = 110mm, double column = 168mm, maximum height of figure = 230mm.

Bar scales for maps and photographs are preferred to numerical scales and must be given on all such items. Maps that display area data and organism distribution at a continental, hemispheric, or world scale must always use an equal-area map projection (e.g. Mollweide or Aitoff's). Note especially that Mercator's projection is not acceptable for such data. Please indicate the precise projection employed in the caption. On these maps, the equatorial scale should be indicated, while scale information should be provided, preferably as a scale bar within the figure, for all maps of whatever size and area; use 'km' or 'kilometres', not 'kilometers'. Maps should include adequate geo-referencing information (preferably the latitude and longitude).

Additional Files

Supporting Information
Supporting information is information that is not essential to the article, but provides greater depth and background. It is hosted online and appears without editing or typesetting. It may include tables, figures, videos, datasets, etc. Click here for Wiley's FAQs on supporting information.

Note: if data, scripts, or other artefacts used to generate the analyses presented in the paper are available via a publicly available data repository, authors should include a reference to the location of the material within their paper.

Such supporting information should be referred to in the text as, for example, 'see Appendix S1 in Supporting Information'; subsequent mention should be in the form 'see Appendix S2'. Figures and tables in the Supporting Information must be numbered consecutively by Appendix number and figure number: e.g. the first figure in Appendix 1 as Fig. S1.1, the first in Appendix 2 as Fig. S2.2 (if there is only one figure in Appendix 1). All appendices, figures and tables must be cited in the text.

Supporting Information files are hosted by the Publisher in the format supplied by the author and are not copy-edited by the Publisher. **It is the responsibility of the author to supply Supporting Information in an appropriate file format and to ensure that it is accurate and correct.** Authors should therefore prepare Supporting Information with the same rigour as their main paper, including adherence to journal style (e.g. formatting of references, figure captions, headings). Sources cited only

in the Supporting Information should be listed in a reference section within the supplementary files and not with the main paper. Supporting Information can be provided as separate editable files or, preferably, as one combined file. Authors are discouraged from supplying very large files or files in non-standard file formats, both of which may reduce their use to the readership. At the point a paper is accepted, these files should be prepared without line numbers or wide line spacing, and with all track-change edits accepted.

General Style Points

The following points provide general advice on formatting and style.

- **Abbreviations:** In general, terms should not be abbreviated unless they are used repeatedly and the abbreviation is helpful to the reader. Initially, use the word in full, followed by the abbreviation in parentheses. Thereafter use the abbreviation only. A list of preferred abbreviations can be found here.

- **Units of measurement:** Measurements should be given in SI or SI-derived units. Visit the Bureau International des Poids et Mesures (BIPM) website at www.bipm.fr for more information about SI units.

- **Numbers:** numbers under 10 are spelt out, except for: measurements with a unit (8mmol/l); age (6 weeks old), or lists with other numbers (11 dogs, 9 cats, 4 gerbils).

- **Computer programs:** All software programs should be written in small caps, followed at first mention by the version number (e.g. MRBAYES 3.1.0, Geneious, MEGA, FaBox, PopArt, MrBayes, Tracer, SPaGeDi) and reference. Packages in R should be in roman and quotations (e.g. `vegan´) and the relevant reference provided.

Wiley Author Resources

Manuscript Preparation Tips: Wiley has a range of resources for authors preparing manuscripts for submission available here. In particular, authors may benefit from referring to Wiley's best practice tips on Writing for Search Engine Optimization.

Editing, Translation, and Formatting Support: Wiley Editing Services can greatly improve the chances of a manuscript being accepted. Offering expert help in English language editing, translation, manuscript formatting, and figure preparation, Wiley Editing Services ensures that the manuscript is ready for submission.

Guidelines for Cover Image Submissions: If you would like to send suggestions for artwork related to your manuscript to be considered to appear on the cover of the journal, please follow these general guidelines.

5. EDITORIAL POLICIES AND ETHICAL CONSIDERATIONS

Editorial Review and Acceptance

The acceptance criteria for all papers are the quality and originality of the research and its significance to journal readership. Papers will only be sent to review if the Editor-in-Chief determines that the paper meets the appropriate quality and relevance requirements.

Wiley's policy on confidentiality of the review process is available here.

Referrals to the Open Access Journal "Ecology and Evolution" and "Geo: Geography and Environment"

This Journal works together with Wiley's Open Access journals, Ecology and Evolution and Geo: Geography and Environment, to enable rapid publication of good quality research that we are unable to accept for publication. Authors may be offered the option of having their paper, along with any related reviews, automatically transferred for consideration by the Editors of *Ecology and Evolution* or *Geo: Geography and Environment*. Authors will not need to reformat or rewrite their manuscript at this stage, and publication decisions will be made a short time after the transfer takes place. The Editors of *Ecology and Evolution* and *Geo: Geography and Environment* will accept submissions that report well-conducted research and which reach the standard acceptable for publication. Accepted papers can be published rapidly, typically within 15 days of acceptance. *Ecology and Evolution* and *Geo: Geography and Environment* are Wiley Open Access journals and article publication fees apply. More information can be found here. Occasionally we refer papers to our sister journals DDI or GEB.

Data Storage and Documentation

Data are important products of the scientific enterprise, and they should be preserved and available for the scientific community. The *Journal of Biogeography* requires that data supporting the results in published papers will presented in Supporting Information, or be archived in an appropriate public archive, such as Dryad, TreeBASE, NERC data centre, GenBank, figshare or another archive of the author's choice that provides comparable access and guarantee of preservation. Authors may elect to have the data made publicly available at time of publication or, if the technology of the archive allows, may opt to embargo access to the data for a period of up to a year after publication. Exceptions, including longer embargoes or an exemption from the requirement, may be granted at the discretion of the editor, especially for sensitive information such as confidential social data or the location of endangered species. Authors should provide a consolidated statement of how readers can access the data used in their paper in a statement before the Biosketch entry. A typical entry might read as follows:

DATA ACCESSIBILITY
All topographic and environmental GIS layers, the habitat suitability model and BTM results generated for this study are available as raster grids from the Pangaea database: http://doi.pangaea.de/10.1594/PANGAEA.808540.

Sequence Data

Sequence data have to be submitted in electronic form to any one of the three major collaborative databases: DDBJ, EMBL, or GenBank. The suggested wording for referring to accession-number information is: 'These sequence data have been submitted to the DDBJ/EMBL/GenBank databases under accession number U12345'. Addresses are as follows:

- DNA Data Bank of Japan (DDBJ) www.ddbj.nig.ac.jp

- EMBL Nucleotide Archive: ebi.ac.uk/ena

- GenBank www.ncbi.nlm.nih.gov/genbank

Collecting permission and the Nagoya Protocol

Authors must ensure that any data utilised in the submitted manuscript have been lawfully acquired in accordance with The Nagoya Protocol on Access to Genetic Resources and the Fair and Equitable Sharing of Benefits Arising from Their Utilization to the Convention on Biological Diversity. It is recommended that it is explicitly stated that the relevant fieldwork permission was obtained, and to list the permit numbers, in Materials and Methods or the Acknowledgements.

Species Names

Upon its first use in the title, abstract, and text, the common name of a species should be followed by the scientific name (genus, species) in parentheses. For well-known species, however, scientific names may be omitted from article titles. If no common name exists in English, only the scientific name should be used. For the focal species in the study, the authority(ies) should be provided at the first mention in the main text, in the format specified by the relevant code.

Conflict of Interest

The journal requires that all authors disclose any potential sources of conflict of interest. Any interest or relationship, financial or otherwise that might be perceived as influencing an author's objectivity is considered a potential source of conflict of interest. These must be disclosed when directly relevant or directly related to the work that the authors describe in their manuscript. Potential sources of conflict of interest include, but are not limited to: patent or stock ownership, membership of a company board of directors, membership of an advisory board or committee for a company, and consultancy for or receipt of speaker's fees from a company. The existence of a conflict of interest does not preclude publication. If the authors have no conflict of interest to declare, they must also state this at submission. It is the responsibility of the corresponding author to review this policy with all authors and collectively to disclose with the submission ALL pertinent commercial and other relationships.

Funding

Authors should list all funding sources in the Acknowledgements section. Authors are responsible for the accuracy of their funder designation. If in doubt, please check the Open Funder Registry for the correct nomenclature: https://www.crossref.org/services/funder-registry/

Authorship

The list of authors should accurately illustrate who contributed to the work and how. All those listed as authors should qualify for authorship according to all of the following criteria:

1. Have made substantial contributions to conception and design, or acquisition of data, or analysis and interpretation of data;

2. Been involved in drafting the manuscript or revising it critically for important intellectual content;

3. Given final approval of the version to be published. Each author should have participated sufficiently in the work to take public responsibility for appropriate portions of the content; and

4. Agreed to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

Contributions from anyone who does not meet the criteria for authorship should be listed, with permission from the contributor, in an Acknowledgements section (for example, to recognize

contributions from people who provided technical help, collation of data, writing assistance, acquisition of funding, or a department chairperson who provided general support). Prior to submitting the article all authors should agree on the order in which their names will be listed in the manuscript.

Additional Authorship Options: Joint first or senior authorship: In the case of joint first authorship, a footnote should be added to the author listing, e.g. 'X and Y should be considered joint first author' or 'X and Y should be considered joint senior author.'

ORCID

As part of the journal's commitment to supporting authors at every step of the publishing process, the journal requires the submitting author (only) to provide an ORCID iD when submitting a manuscript. This takes around 2 minutes to complete. Find more information here.

Publication Ethics

This journal is a member of the Committee on Publication Ethics (COPE). Note this journal uses iThenticate's CrossCheck software to detect instances of overlapping and similar text in submitted manuscripts. Read the Top 10 Publishing Ethics Tips for Authors here. Wiley's Publication Ethics Guidelines can be found at authorservices.wiley.com/ethics-guidelines/index.html.

6. AUTHOR LICENSING

If a paper is accepted for publication, the author identified as the formal corresponding author will receive an email prompting them to log in to Author Services, where via the Wiley Author Licensing Service (WALS) they will be required to complete a copyright license agreement on behalf of all authors of the paper.

Authors may choose to publish under the terms of the journal's standard copyright agreement, or OnlineOpen under the terms of a Creative Commons License.

General information regarding licensing and copyright is available here. To review the Creative Commons License options offered under OnlineOpen, please click here. (Note that certain funders mandate a particular type of CC license be used; to check this please click here.)

Self-Archiving Definitions and Policies: Note that the journal's standard copyright agreement allows for self-archiving of different versions of the article under specific conditions. Please click here for more detailed information about self-archiving definitions and policies.

Open Access fees: Authors who choose to publish using OnlineOpen will be charged a fee. A list of Article Publication Charges for Wiley journals is available here.

Funder Open Access: Please click here for more information on Wiley's compliance with specific Funder Open Access Policies

7. PUBLICATION PROCESS AFTER ACCEPTANCE

Accepted Article Received in Production

When an accepted article is received by Wiley's production team, the corresponding author will receive an email asking them to login or register with Wiley Author Services. The author will be asked to sign a publication license at this point.

Proofs

Once the paper is typeset, the author will receive an email notification with the URL to download a PDF typeset page proof, as well as associated forms and full instructions on how to correct and return the file.

Please note that the author is responsible for all statements made in their work, including changes made during the editorial process – authors should check proofs carefully. Note that proofs should be returned within 48 hours from receipt of first proof.

At proof correction stage authors will be given access to their Supporting Information (via the web) and should check it for accuracy and updates. If changes are required, corrected versions of the files that were received with the proof must be emailed to the Production Editor, with a brief description of the changes made. Supporting Information **must be checked alongside the main proof** and corrections for both returned to the Production Editor at the same time.

Publication Charges

Colour figures. Colour figures may be published online free of charge; however, the journal charges for publishing figures in colour in print. If the author supplies colour figures, they will be sent a Colour Work Agreement once the accepted paper moves to the production process. If the Colour Work Agreement is not returned by the specified date, figures will be converted to black and white for print publication.

Please note that the vast majority of readers access the digital versions of the journal; printed copies are increasingly rare. For the convenience of readers, we ask that you design your colour artwork so that it can be understood as best as possible in greyscale. Note that the same figure file must be used for both the print and online versions (we do not accept differing colour and black-and-white versions of the same figure).

Early View

The journal offers rapid publication via Wiley's Early View service. Early View (Online Version of Record) articles are published on Wiley Online Library before inclusion in an issue. Note there may be a delay after corrections are received before the article appears online, as Editors also need to review proofs. Once the article is published on Early View, no further changes to the article are possible. The Early View article is fully citable and carries an online publication date and DOI for citations.

8. POST PUBLICATION

Access and Sharing
When the article is published online:

- The author receives an email alert (if requested).

- The link to the published article can be shared through social media.

- The author will have free access to the paper (after accepting the Terms & Conditions of use, they can view the article).

- The corresponding author and co-authors can nominate up to ten colleagues to receive a publication alert and free online access to the article.

Print copies of the article can now be ordered (instructions are sent at proofing stage or use the below contact details). Email offprint@cosprinters.com

To find out how to best promote an article, click here*.*

Measuring the Impact of an Article

Wiley also helps authors measure the impact of their research through specialist partnerships with Kudos and Altmetric.

9. EDITORIAL OFFICE CONTACT DETAILS

Iris and Tom

jbioffice@wiley.com

Author Guidelines updated April 2017