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Global physical controls on estuarine habitat distribution during sea level change: Consequences for genetic diversification through time

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ABSTRACT

Determining the extrinsic (physical) factors controlling speciation and diversification of species through time is of key interest in paleontology and evolutionary biology. The role of sea-level change in shaping species richness patterns of marginal marine species has received much attention, but with variable conclusions. Recent work combining genetic data and Geographical Information Systems (GIS)-based habitat modeling yielded a framework for how geomorphology of continental margins mediates genetic connectivity of populations during sea-level change. This approach may ultimately yield insights on how distinct lineages, species, and biodiversity accumulate in coastal settings. Here, we expand this GIS work globally to different geomorphic settings to model estuarine habitat in a larger geographic framework and test how tectonic setting, oceanographic setting, climate, and margin age affect habitat distribution during sea-level change. In addition, independent of estuaries we explore paleobiologic (e.g. Olsson, 1961) and neontologic effects of sea-level change on evolution, and test the relation between overall shelf area and species richness using data of 1721 fish species. We find 82% global reduction of estuarine habitat abundance at lowstand relative to highstand, and find large habitats change in size much more than small habitats. Consistent with prior work, narrow continental margins have significantly less habitat at highstand and lowstand than wide margins, and narrow margins significantly associate with fore-arc settings, effectively linking tectonic setting to habitat abundance. Surprisingly, narrow margins host greater species richness, a finding which violates the canonical species-area relation. This finding can be explained if: 1) the physical isolation imposed by narrow margins facilitates the formation of new species over time; 2) the size-stability of small habitats, which disproportionately occur on narrow margins, accumulate and retain species extirpated in the more variable habitats on wide margins; or 3) the smaller habitats on narrow margins facilitate greater species richness through greater habitat heterogeneity. These results are generally at odds with prior interpretations, but the combination of richness data and population genetic principles offer a different perspective on these long-studied questions. Finally, we emphasize that the nuance of Pleistocene-Holocene sea level oscillations should be more explicitly considered in genetic studies.

1. Introduction

How Earth's climate and surface processes influence genetic and morphological change of species over time is a leading question within evolutionary biology, paleontology, and geobiology. Earth processes that physically isolate populations promote allopatric genetic divergence—the genetic relatedness of the isolated populations drift apart over time in the absence of gene flow (the exchange of genetic

material). In addition, change in the environment can result in biological adaptations as individuals with qualities that maximize survival and reproduction on the new landscape increase in number through disproportionate reproductive success. This can lead to ecologically differentiated populations (Bernier et al., 2010; Crespi and Nosil, 2013; Dettman et al., 2008; Gray and Goddard, 2012; Klosterman et al., 2011; Roesti et al., 2012). If divergence is protracted or selection is strong enough, then isolated or differentially adapted populations may

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become separate species, increasing biodiversity (Coyne and Orr, 2004). Based on genetic evidence, processes known to yield such biological effects include Northern Hemisphere glaciations (Hewitt, 2000, 2004; Jansson and Dynesius, 2002), mountain building (Antonelli et al., 2018; Craw et al., 2015; Hoorn et al., 2010), geographic rainfall asynchrony/variability (Quintero et al., 2014; Thomassen et al., 2013), tectonic rifting (Clark, 2012; Lieberman, 1997), and reorganization of river drainages (Dias et al., 2014; Dolby et al., 2019; Goodier et al., 2011; Hershler and Liu, 2008; Hershler et al., 1999), among others. Recent work also recognized how changes in land configuration during sea level oscillations has affected population connectivity of land-dwelling species (Papadopoulou and Knowles, 2017; Sawyer et al., 2019). These types of studies contribute to our understanding of the cause-effect relation between physical processes and evolutionary responses. Such cause-effect relations are important because they ultimately reveal the ways in which Earth shapes life and how much of biological evolution is extrinsically (versus intrinsically) forced. When knowledge from such relations is detailed and mechanistic, it can be used to make predictions about the biological effects of such processes over deeper timescales and in new geologic settings.

Processes thought to be important in shaping marginal marine ecosystems include the formation of new, isolated marine embayments or habitats such as the Gulf of California and Red Sea (DiBattista et al., 2016; Dolby et al., 2015; Lau and Jacobs, 2017), currents that facilitate or limit dispersal of individuals such as in the Indo-Pacific Coral Triangle (Barber et al., 2006; Davies et al., 2014; Kool et al., 2011), and formation of physical barriers (Hobbs et al., 2009) such as the Isthmus of Panama that not only bisected and isolated marine populations, but also initiated the large-scale reorganization of marine currents (O'Dea et al., 2016; Schneider and Schmittner, 2006). Often the effects of these processes are mixed because marine species vary greatly in dispersal capacity and their response to external influences (Bernardi, 2013; Kelly and Palumbi, 2010; Marko, 2004).

From the paleontological literature, Dall (1890) and Olsson (1961) proposed that lowered sea level stands (eustatic regressions) reduced the habitat footprint of marginal marine species and led to local or regional extinctions. This idea was based on the greater proportion of shallow shelf area in the Caribbean that hosted lower molluscan diversity relative to the Panamanian region that has less shallow shelf area and higher molluscan diversity even though they originated from the same set of ancestors before the isthmus closed. The argument here is that shallow-shelf Caribbean areas were vulnerable to extirpation via lowered Pleistocene sea levels (Olsson, 1961). Stanley (1986, 1984) contradicted this hypothesis in favor of temperature change as the causal explanation using the rationale that regression-based extinctions should be geographically global while temperature-based extinctions should be regional.

Using a neontological approach, several different studies recently evaluated how late Pleistocene sea-level change affected marginal marine populations (Neiva et al., 2018; Waltari and Hickerson, 2013). Using genetic data and habitat modeling of coastal estuaries, Dolby et al. (2018, 2016) proposed a mechanism that relates shelf morphology to species diversification. The framework proposed that tectonic and sedimentary processes control the geomorphic properties (e.g., slope) and geologic substrate (e.g., unconsolidated sediments, bedrock, etc.) of continental shelves (Algeo and Wilkinson, 1991), and those properties in turn control where many types of coastal habitats can form (e.g., estuaries, mangroves, beaches). When sea-level oscillates against the heterogeneous shelf area it changes the distribution of habitats, which directly controls genetic connectivity (i.e. whether individuals can move between neighboring populations to reproduce). This either results in habitat connectivity and genetic similarity, or in habitat isolation and genetic divergence, depending on the geomorphic setting and the dispersal capacity of the species. Fewer, smaller habitats occur along tectonically active (steep) coastlines than broad coastlines and because dispersal is negatively correlated with geographic distance,

they found more genetically differentiated populations on steep coasts (Dolby et al., 2018). Overall, this framework suggests that large-scale geologic processes exert top-down control on the connectivity and genetic evolution of coastal species and could possibly produce new species when extrapolated over deeper geologic time.

However, the previous work was done over a regional setting (western coast of North America). Here, we test the effects of tectonic setting, oceanographic setting, climate, and margin age on habitat distribution during sea-level change at a global scale. Second, we test Olsson's areal restriction hypothesis by comparing overall shelf area to species richness data and use population genetic and speciation theory to integrate these findings with the prior results (Dolby et al., 2018; Dolby et al., 2016). To do so, we calculate estuarine habitat abundance during Pleistocene sea level oscillations along unglaciated coastlines globally (Fig. 1). We integrate these results with existing datasets and perform a suite of statistical tests to understand the relation of tectonic, sedimentary, and oceanographic properties on habitat abundance and species richness patterns of 1721 fish species.

2. Methods

2.1. Estimating habitat abundance

To estimate putative estuarine habitat we used the SRTM30_PLUS digital elevation model (DEM; Becker et al., 2009) because it integrates topographic and bathymetric data worldwide at relatively high resolution (30 arc-second, about 1-km resolution), making it a good resource for global analysis of marginal marine areas. It also allows for consistency with previous work (Dolby et al., 2018; Dolby et al., 2016). In a geographic information system (GIS) we calculated putative estuarine habitat area for six landmasses (North America, South America, Africa, India, Australia, and Japan) using the regional equal area projection for each continent (Fig. 1, Table S1). Japan is used here as a counterexample to determine what, if any, effect the complex coastline of an archipelago has on habitat distribution (Fig. 2).

Estuaries occur at sea level in the low gradient areas of continental shelves. A slope cutoff of 3.4% was previously useful for predicting coastal estuarine habitat (Dolby et al., 2018). To assess if the previously calculated slope was an appropriate cutoff for this larger setting, we calculated the slope of estuaries over the steep western coast of South America. In brief, we visually inspected the western coastline of South America in Google Earth Pro v7.3 for estuaries and in each estuary we recorded the rise and run at 5 locations to maximize intra-estuarine variability. The maximum slope observed (3.5%) was very similar to previous work (3.4%; Dolby et al., 2018; Seibold and Hinz, 1974) and we used this revised 3.5% value as the upper slope limit for our models.

To calculate area conducive to estuary formation, using the raster_calculator tool we queried the DEM raster for areas of low slope ($\leq 3.5\%$) in 10-m depth bins from present sea level (0 mbsl) to sea level at the maximum glacial lowstand level for Pleistocene glaciations (140 mbsl; Chaytor et al., 2008; Lambeck et al., 2002; Miller et al., 2005; see SI for equation). This process generated 14 depth-based habitat layers that represent where estuarine habitat could have existed at different timepoints as sea level rose from the Last Glacial Maximum (LGM; ~ 20 ka) to present day due to the melting of glaciers. To assess how habitat abundance changed with coastal properties, we manually divided the coastline of the six continental regions into 277 small coastal regions globally. The coastal polygons were drawn just broad enough to include the 0 m and -140 m isobaths (this determines the 'width' of the polygons) and the height of coastal regions were drawn to be as consistent as possible while reflecting the changing properties of the coastline (e.g., orientation, shelf width). For example, polygon edges perpendicular to the coastline were drawn to coincide with transitions in coastal orientation or a change in the shelf width (Fig. S9). We note that the size and shape of the coastal polygons are inherently influenced by coastal heterogeneity (e.g., there are fewer polygons needed to

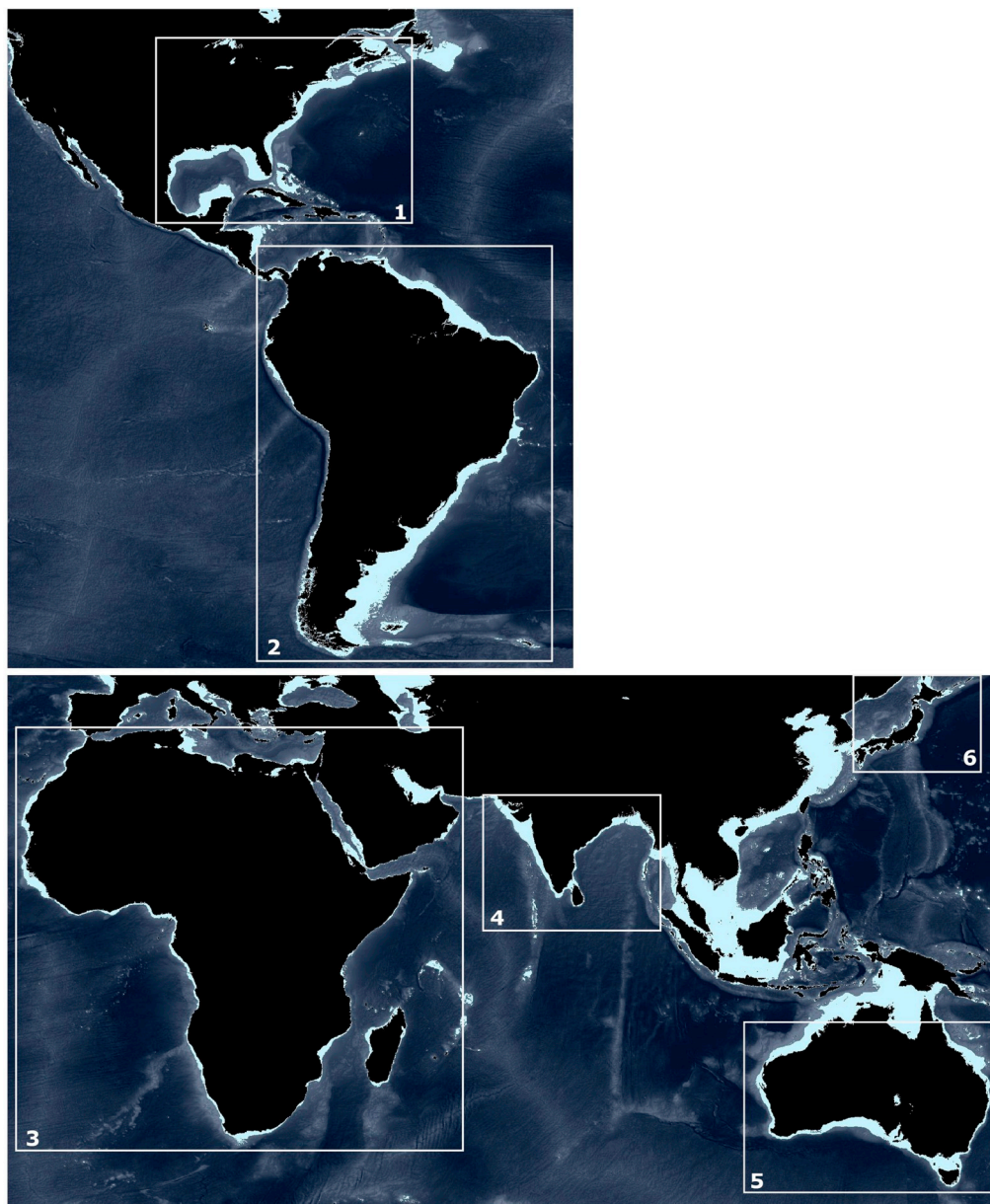


Fig. 1. Map of continents analyzed in this study: 1) eastern coast of North America; 2) South America; 3) Africa (including Madagascar, Red Sea, and Persian Gulf); 4) India including the Maldives; 5) Australia (excluding the northern epicontinental sea region joining Indonesia, but including Tasmania); 6) Japan archipelago (used here as a counterexample because its coastline is highly variable). Land is black, continental shelf (0–140 mbsl) is light blue; deeper than 140 mbsl is dark blue transparently overlying a hillshade DEM that shows major characteristics of the sea floor, such as spreading ridges, sea mounts, and fracture zones (maps use true north).

accurately capture the coastal properties of India than for Japan; Figs. S9, S10). Polygon files are available as Google Earth Keyhole Markup language Zipped (.kmz) files (see Supporting Data).

In each coastal region we divided the amount of low-slope putative estuarine habitat area by the area of that coastal region to standardize for differences in region size and to approximate habitat density so that comparisons could be made across regions. Hereafter, ‘habitat abundance’ refers to this normalized habitat area. We correlated the mid-point of each depth bin (e.g., 25 mbsl for the 20–30 mbsl bin) to time using a reconstructed curve of sea level history (Chaytor et al., 2008; Lambeck et al., 2002); this assigned ages to the habitat abundance calculations for each depth bin. Sea level rose to its present-day height about 6.5 ka, so habitat abundance values are inferred to be the same at 0 ka as they are at 6.5 ka (Fig. S2B). We chose to exclude regions that were glaciated during the Pleistocene because the effects of large-

magnitude isostatic glacial rebound would complicate the depth-time correlations. These regions are also subject to complex effects from glacial erosion and fluvial/sediment processes associated with the outflow of glacial ice and meltwater (see section 2.4 for model limitations and Fig. S9 for excluded regions).

Finally, to revisit Olsson’s hypothesis (Olsson, 1961) we calculated total shelf area within each coastal region to compare to species richness data (Section 2.2). To do this we calculated *all area* (not just low-slope area) between 0 and 140 mbsl in each coastal region using the raster calculator tool and recorded these values as the total shelf area.

2.2. Statistics with physical setting, habitat, and diversity

To determine what factors correlate with and/or control estuarine habitat abundance we performed a suite of statistical tests between the

Table 1
Characteristics used for classification of coastal regions.

Tectonic setting	Passive Fore-arc
Continental shelf width	Narrow: ≤ 25 km Mid: $25 < x \leq 75$ Wide: > 75 km Miscellaneous ^a
Oceanographic setting	Tide dominated Wave dominated
Climate	Arid Equatorial Polar Snow Warm temperate
Seafloor age	Raster in Myr
Average species richness	Ranges of 1721 fish species

^a Miscellaneous regions are primarily epicontinental seas.

habitat abundances calculated in Section 2.1 and published coastal data from three sources. First, we used the published global GIS analysis from Nyberg and Howell (2016) which uses the results of a ternary classification approach from wave, tide, and fluvial data as well as published literature to identify sediment, tectonic, climatic, and oceanographic properties of coastlines globally at 5-km resolution (<https://github.com/BjornNyberg/Datasets>). Second, we incorporated seafloor age data from Müller et al. (2016; <https://www.earthbyte.org>) as a proxy for margin age. We converted this 2-arc-minute seafloor age raster to points using raster_to_point tool after projecting the WGS84-datum layer to the World_Equidistant_Cylindrical projection of Nyberg and Howell (2016). Third, we used published marine biodiversity data from Jenkins and Van Houtan (2016a, 2016b), using only the species richness data for fishes because they are globally distributed and found in a wide range of habitats, unlike other groups in the database (e.g., cone snails, corals) that are confined to certain climates. For all datasets we used overlapping spatial join to link each of the 277 coastal regions with the attributes from these published datasets (variables listed in Table 1). For the seafloor age data, we used the data point nearest to each coastal polygon because the seafloor age dataset often did not extend onto the continental shelf far enough to overlap with the coastal polygons.

Because the fish species richness dataset is not exclusive to estuarine fishes, we compared these data to the *total shelf area* calculated in each coastal region polygon (end of section 2.1). In addition, because coral reef regions are speciose and could bias our analyses, we created a filtered dataset that removed geographic regions that could contain reefs according to the PacIOOS Voyager online interactive data viewer (PacIOOS, 2019). We then calculated the downstream statistics both with and without these reef-associated regions to see if there was an effect.

To search for meaningful patterns among variables we performed a suite of statistical tests comparing habitat abundance at present day (0–6.5 ka) and habitat abundance at lowstand (19.5 ka) to coastal attributes (Tables 1, 2). First, we used statistical software (JMP v14) to analyze habitat abundance data and found its distribution was best explained by an exponential function according to the corrected Akaike Information Criterion (AICc) and the data were significantly non-normal via Shapiro Wilk test. We therefore used nonparametric Mann Whitney U (MWU) tests. We tested whether habitat abundance at highstand (6.5 ka) and lowstand (19.5 ka) varied with the following variables: passive versus fore-arc margin, wide versus narrow shelf width, and tide versus wave dominated coastlines. We chose these comparisons because they are endmembers of a continuum and/or had

the greatest sample sizes. Some categories, including fluvial (oceanographic setting) and strike-slip, intracratonic (tectonic setting) are less extensive on Earth and were excluded due to low sample size. To test if highstand and lowstand habitat abundances correlate with seafloor age on passive margins we ran a generalized linear model (GLM) using an exponential distribution and reciprocal link function (default) corrected for overdispersion. To test if passive margins significantly associate with wider shelves more than fore-arc settings, we used contingency analysis to analyze the association of the two categorical variables. Finally, to determine the relative importance of variables found to significantly predict habitat abundance, we generated a multivariate GLM using tectonic setting, shelf width, seafloor age as well as interactions (*shelf width * seafloor age*; *shelf width * tectonic setting*) to predict highstand and lowstand habitat combined. This analysis used maximum likelihood and was fitted with an exponential distribution, log link function, was corrected for overdispersion, and used a false discovery rate.

We expect the coastal regions in this study to be spatially auto-correlated within continents. To test for spatial autocorrelation relative to tectonic setting (which was a categorical variable), we generated two spatial weight matrices in GeoDa v1.12 (Anselin et al., 2006) using alternative approaches: 1) contiguity weight (Queen setting), and 2) Euclidian distance weight using K-nearest neighbors set to two because the linearity of the coastline means generally each polygon has two neighbors. With statistical software (R v3.5.1) we used SPDEP v1.0 (Bivand et al., 2013; Bivand and Wong, 2018) and RGDAL v1.4 (Bivand et al., 2017) packages to perform a Monte-Carlo permutation test with joincount.mc() with 100 simulations and join count test with joincount.test() setting zero.policy = TRUE for both analyses because there were true islands in the data (see Appendix 1).

2.3. Model limitations

Each data source in this study has some associated error, and there are limitations to the analyses employed here that should be noted. There were not sufficient population genetic data available on this global scale to pair with the estuary habitat reconstructions as was done previously (Dolby et al., 2018; Dolby et al., 2016). So, we used the species richness data which provide a different biological perspective as these data record the number of species in a location rather than the genetic diversity or relatedness within those species. We therefore rely on the previous population genetic inferences as well as basic speciation theory (Coyne and Orr, 2004) for the genetic perspective.

The modeling of estuarine habitat abundance also has limitations. First, we use modern bathymetry as a proxy for the paleo-bathymetric surface because of the challenges of correcting for deformation and sediment processes on large scales. Coastal processes (longshore transport, wave-based erosion, submarine canyon development), mass wasting (slumps, slides, flows), turbidites, fault movements (Johnson and Beeson, 2019; Maloney et al., 2015), and crustal flexure (Moucha and Ruetenik, 2017) can all affect the shelf morphology over millennial timescales and are not accounted for in our models.

Second, some regions considered in this study have non-trivial tectonic uplift rates, which biases the time-depth correlations. Previous work showed that using 10-m depth bins makes the habitat calculations insensitive to uplift rates of ≤ 0.25 mm/yr, but for regions with very high uplift rates (≥ 2 mm/yr), our depth-time correlations are biased toward young ages (see supplemental information in Dolby et al., 2016). The main regions affected by this are the western coast of South America where the coast has experienced moderate-low Quaternary uplift rates along Ecuadorian and Peruvian coastlines of 0.10–0.50 mm/yr (Pedoja et al., 2006) and along the Colombian and central Andes coastline of 0.2–0.3 mm/yr (Gregory-Wodzicki, 2000) and 0.13 ± 0.04 mm/yr (Melnick, 2016). In contrast, the southern Andes has high uplift rates of up to 10 mm/yr (Hervé and Ota, 2010; Melnick et al., 2009) due to convergent tectonics and glacial isostatic rebound,

Table 2

Summary of relations tested in this study, the type of test used, and the statistical result. Abbreviations are HS-highstand, LS-lowstand, hab.-habitat, ES-effect size, γ -gamma measure of association. Significant values are bolded; [†]p value excluding the 65 coastal regions that have reef habitat.

Variable 1	Variable 2	Statistical test	Result	Interpretation
Seafloor age (passive margins)	HS hab.	GLM	$p = .054$ (ES = 1.26)	There is more estuarine habitat on older passive margins.
	LS hab.	GLM	$P = .782$ (ES = 0.12)	
Tectonic setting	HS hab.	MWU	$p < .0001$	There is more estuarine habitat on passive than fore-arc margins.
	LS hab.	MWU	$p = .0028$	
	Shelf width	Contingency analysis	Pearson $p < .0001$; $\gamma = 0.83 \pm 0.17$	
Shelf width	HS hab.	MWU	$p < .0001$	There is more estuarine habitat on wide shelves than narrow shelves.
	LS hab.	MWU	$p = .0076$	
Shelf width	Species richness	MWU	$p = .0004$ ([†] 0.049)	There are more fish species on narrow shelves than wide shelves.
Seafloor age, tectonic setting, shelf width	HS hab.	GLM	Model $p < .0001$ <i>Tectonic setting $p = .005$</i> <i>Shelf[†]tectonics $p = .005$</i> <i>Shelf[†]seafloor $p = .031$</i> <i>Seafloor age $p = .034$</i> <i>Shelf width $p = .091$</i>	The physical/geologic processes of a region shape habitat abundance.

so this area was excluded from our study (Fig. S9). Overall, we do not believe the effects of uplift would bias our overarching conclusions, but these considerations would be important for local interpretations in some areas.

Third, we do not account for many environmental or climatic processes that are known to influence the distribution of species (Jacobs et al., 2011; Kench, 1999; Wolfe and Kjerfve, 1986). It was previously noted that because estuaries have highly variable abiotic properties (salinity, temperature, pH, turbidity, dissolved oxygen, dissolved organic matter, etc.), that not only is it likely that their inhabitants can sustain a range of abiotic conditions, but also it is not possible to include this abiotic detail in our models. Regional upwelling may also affect the species richness estimates and was not accounted for. Also, the degree of wave or tidal influence in an area will change as the coastal configuration changes during sea level oscillations. Our simplifying assumption is that the present-day oceanographic properties (i.e. via the ternary classification) accurately reflect these attributes for the coast at lowstand as well.

Fourth, tests for spatial autocorrelation are significant (see Supporting Data) as expected because our analysis does not facilitate random sampling and samples (coastal regions) are not independent of one another because tectonic, sediment, and oceanographic processes operate on larger spatial scales than our variable of interest (habitat). This means that neighboring coastal regions are more likely to share these processes than distant regions. The effect of spatial autocorrelation is to inflate the significance of correlations and the likelihood of Type I errors ('false positives'). Most results found here to be statistically significant would remain so even after making the significance threshold more stringent to account for this (e.g., to 0.001), but it is important to consider this bias when interpreting the strength of relations.

Fifth, we use 130–140 mbsl as the lowstand depth bin. Some sea-level curves for the LGM and preceding lowstands 0.8–0.0 Ma (i.e. the period that post-dates the Mid-Pleistocene Transition; Chalk et al., 2017) show shallower lowstand maxima (e.g., ~120 mbsl). We chose the –140 m convention: 1) to fit with previous studies (e.g., Dolby et al., 2018; Dolby et al., 2016), and 2) so our results are able to be extrapolated to the older, deeper lowstand events that preceded the LGM. We spot-checked the effect this choice could have on our interpretations by running some of the same statistical tests using the 110–120 depth bin and results were always equivalent to the results shown (data not shown).

Finally, there can be bias introduced by our approach of manually sub-setting coastlines into coastal regions, as well as the classification scheme used to categorize tectonic settings (Nyberg and Howell, 2016). Coastlines are inherently heterogeneous and variable (Figs. 2, S1, S10)

and so coastal region sizes vary between continents (Fig. S9), which is why we normalized by region size. For example, wide margins will inherently have larger (wider) coastal regions to include the 0-m and –140-m isobaths than narrow margins. Also, the coastline in some regions is more intricate than a simple classification scheme can easily capture and may not be well represented by a single tectonic classification (e.g., Japan is small but encompasses a variety of tectonic interactions, including a complex history of evolving triple junctions; Osozawa, 1992).

While the above complications are important to consider we do not think they strongly bias our overall interpretations. That said, any studies focusing on a local-to-regional scale need to consider how these factors would affect their methods and results as some of these considerations can be accounted for when working on a smaller scale.

3. Results

3.1. Statistical relations

Our GIS analysis produced habitat abundance estimates for 14 depth bins in each of 277 manually curated coastal regions (Fig. 3). The habitat data were overdispersed based on a Pearson Chi Square test that yielded a value of 2.3; overdispersion was therefore accounted for in the GLMs. Broadly, we found several significant correlations between habitat abundance and coastal characteristics (summarized in Table 2). MWU tests revealed significantly greater habitat abundance on wide shelves (≥ 75 km) than narrow shelves (≤ 25 km) at both highstand and lowstand (Fig. 4, Table 2) as well as significantly greater habitat abundance on tectonically passive margins than fore-arc settings. More habitats occurred in wave-dominated oceanographic regions than tide-dominated regions and the largest present-day habitats tended to change in size the most from highstand to lowstand (Fig. 5). Most present-day tide-dominated habitats are large, whereas the smallest present-day habitats tended remained a constant size from highstand to lowstand and are almost all wave-dominated (Fig. 5). Contingency analysis showed that fore-arc settings significantly associate with narrow shelves, while mid and wide shelves associate with passive margins (Figs. 6; S3). When this comparison excluded foreland settings, there was strong association between shelf width and tectonic setting ($\gamma = 0.83 \pm 0.17$).

A GLM showed a positive relation between habitat abundance and passive margin age, but this relation was not significant at highstand ($p = .054$) or lowstand ($p = .78$; Figs. S4B, S4C, S5). A multivariate GLM that assessed the relative importance of different variables on habitat abundance produced a significant model ($p < .0001$; Table 2). The FDR-controlled variable-specific p values and log worth values

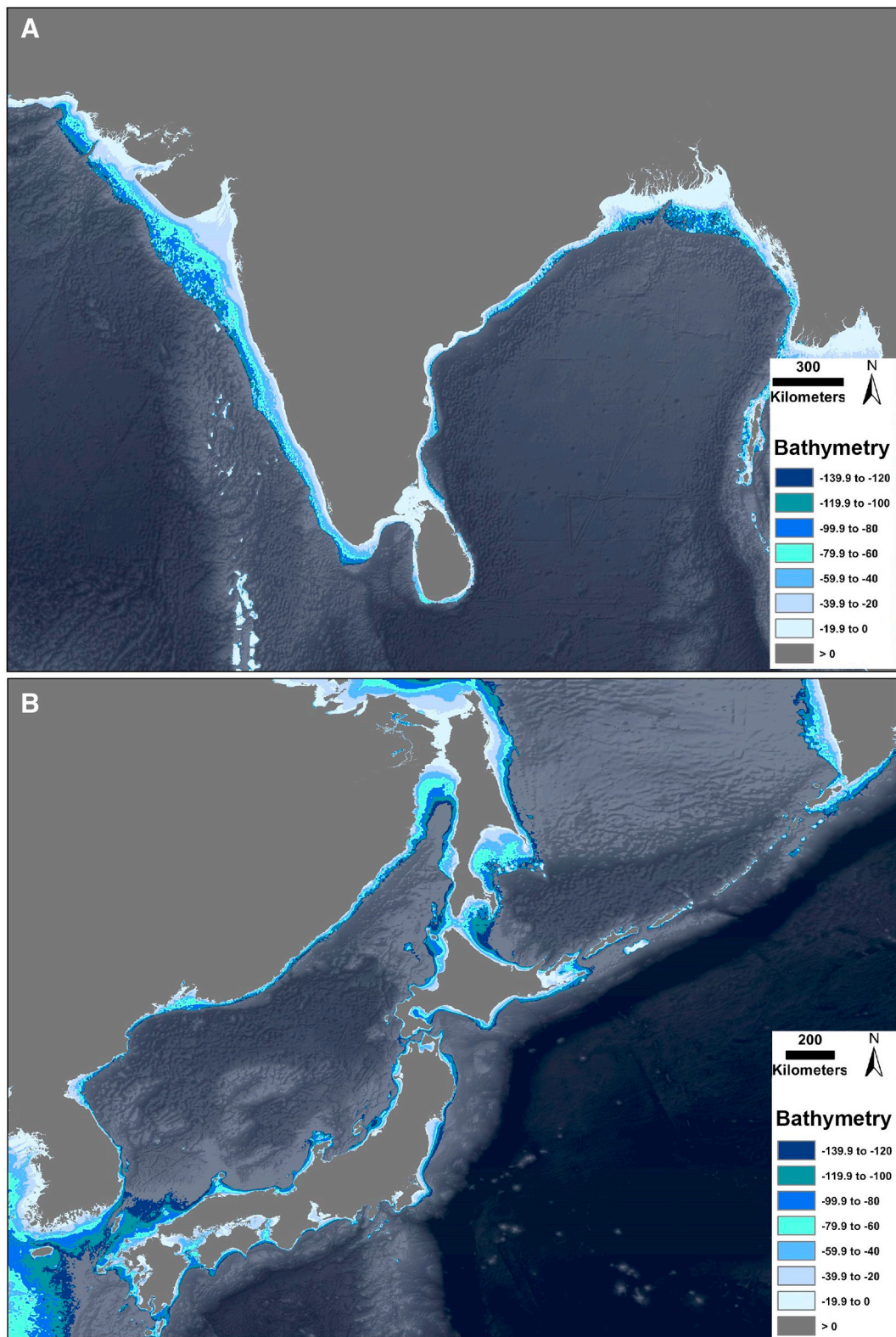


Fig. 2. Maps of lands studied that depict the area exposed during glacial-induced sea level fluctuations (light blues, 0–0.8 Ma, 0–140 mbsl). Lands are India (top) and Japan (bottom).

were: *tectonic setting* ($p = .005$, 1.9), *shelf width * tectonic setting* interaction ($p = .005$, 1.9), *shelf width * margin age* interaction ($p = .031$, 1.37), *margin age* ($p = .034$, 1.37) and *shelf width* ($p = .091$, 1.04)—revealing that tectonic setting and shelf width best predict habitat abundance.

For biological patterns, we found significantly greater species richness (number of fish species) on narrow shelves than wide shelves (Fig. 7B). This pattern was evident with (MWU, $p = .0004$) and without (MWU, $p = .049$) the 65 reef-associated coastal regions. Species richness was significantly negatively correlated with shelf area (Fig. 8) with

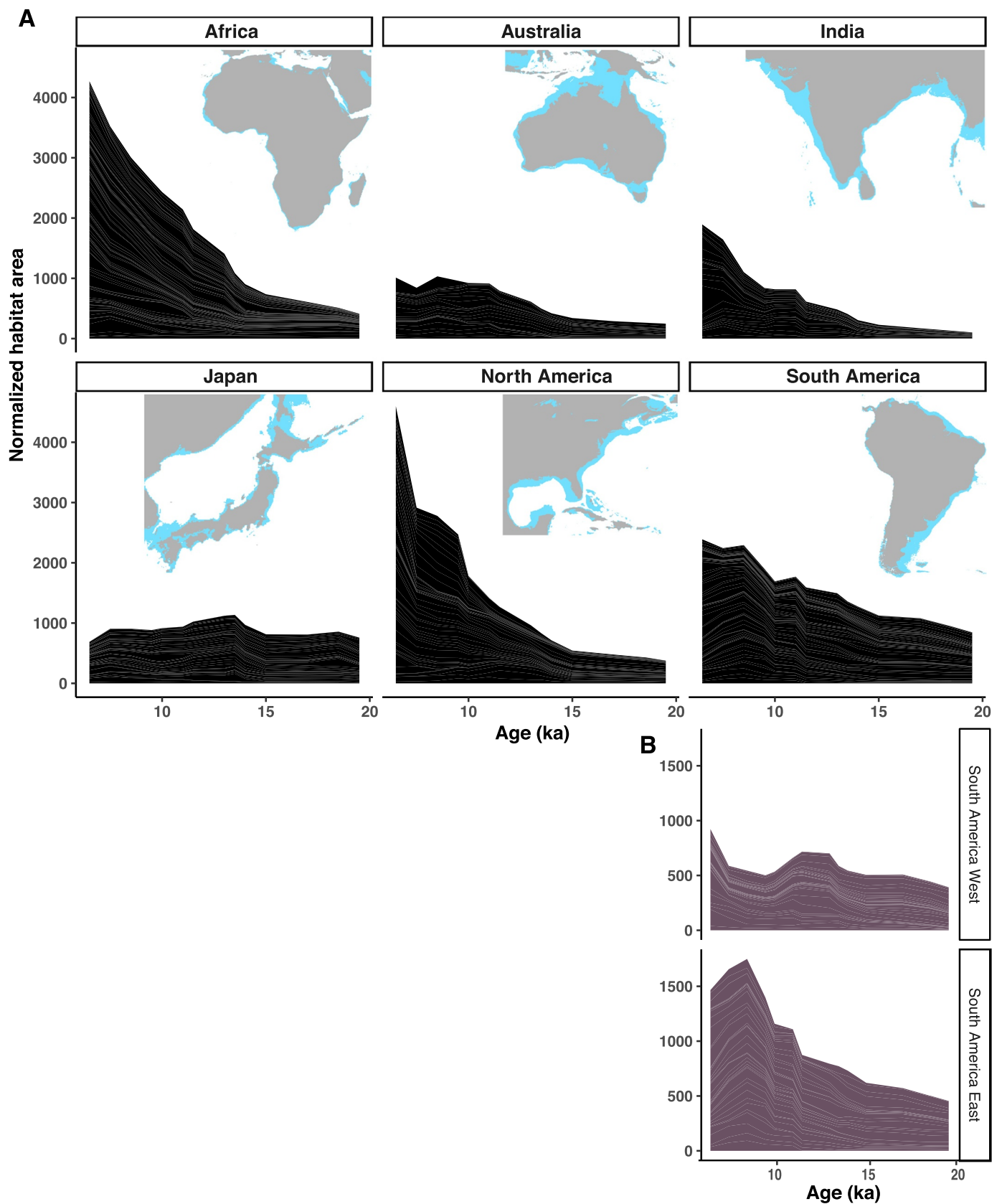


Fig. 3. Putative estuarine habitat area through time A) for each landmass surveyed in the present study. At each timepoint, the stacked area is a summation over all coastal regions of that landmass. Area is calculated as area (km²) of the DEM that is low-grade ($\leq 3.5\%$) in 10-m depth bins that correlate with age based on a sea-level curve. Japan is used as a counterexample; it is the only land studied that has an intricate archipelago coastline as opposed to large, contiguous and simple coastline. Outline of landmass (grey) is shown above the habitat-area curve for each continent where blue is bathymetry is highlighted in blue (0–140 mbsl) and deeper water is white (lands are not to scale). B) South American habitat through time separated into the fore-arc, narrow shelf setting of the western margin (top) and the tectonically passive and broad east margin (bottom).

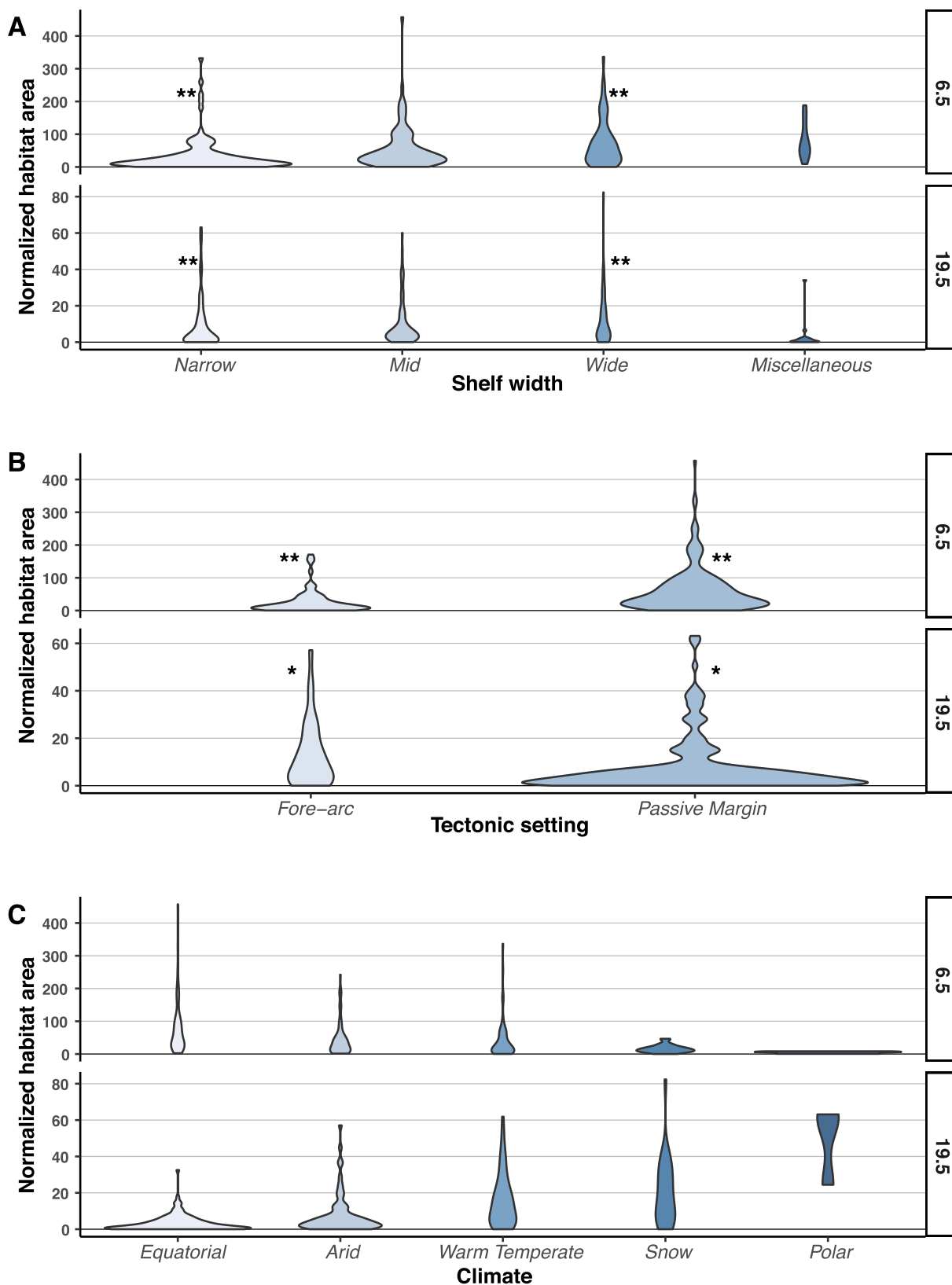


Fig. 4. Putative habitat area versus coastline characteristics at highstand (6.5 ka, top rows) and lowstand (19.5 ka, bottom rows). Physiographic comparisons include habitat versus: A) Shelf width (narrow less than or equal to 25 km, mid 26–75 km, and wide greater than or equal to 75 km, miscellaneous settings are mostly epicontinental seas). There is more habitat on wide shelves; B) Tectonic setting based on the two settings with the most observations and which represent opposing compressive versus extensive forces. There is greater habitat on passive margins (see Figures 5, S3). C) Climate (note there are few observations for polar and snow regions). Individual violin width is proportional to number of observations (i.e. count) for panels a and b (meaning they can be compared), but panel C is not scaled because there are limited observations for polar and snow regions, which are found in South America and Japan. Comparisons that were statistically evaluated were each significant at the (*0.05 level or **0.0001 level; see Table 1).

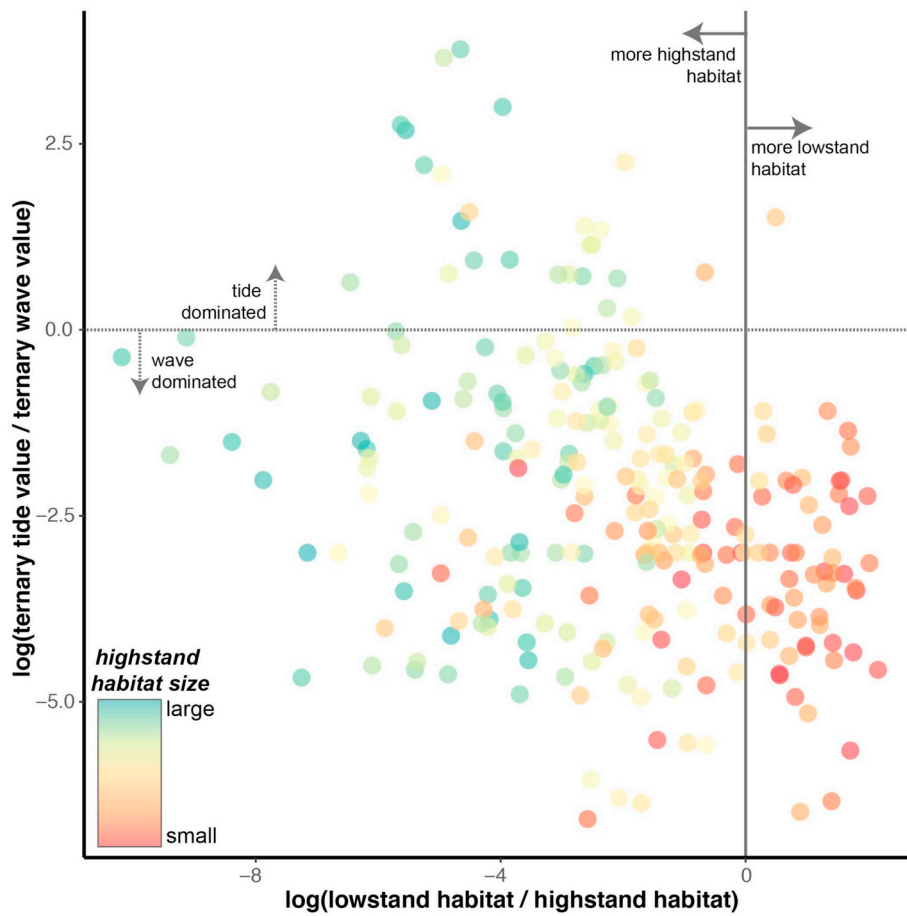


Fig. 5. Change in habitat abundance from highstand to lowstand related to oceanographic setting. Habitat (individual dots) in tide-dominated regions (above the dashed line) tend to be large at highstand (blue) and decrease dramatically at lowstand (left of solid line). In contrast, habitats that are small at highstand (red dots) tend to occur in wave-dominated regions (below dashed line) and they change in size minimally or increase in size comparing highstand to lowstand habitat abundance ($x \geq 0$). These data are log transformed to better visualize the patterns. The vertical $x=0$ line is where highstand habitat abundance and lowstand habitat abundance are equal (i.e. habitat size does not change); the horizontal $y=0$ line is where a region would have equal tide and wave scores according to the ternary classification scheme of Nyberg and Howell (2016). Fluvial ternary aspect is not shown due to limited non-zero observations.

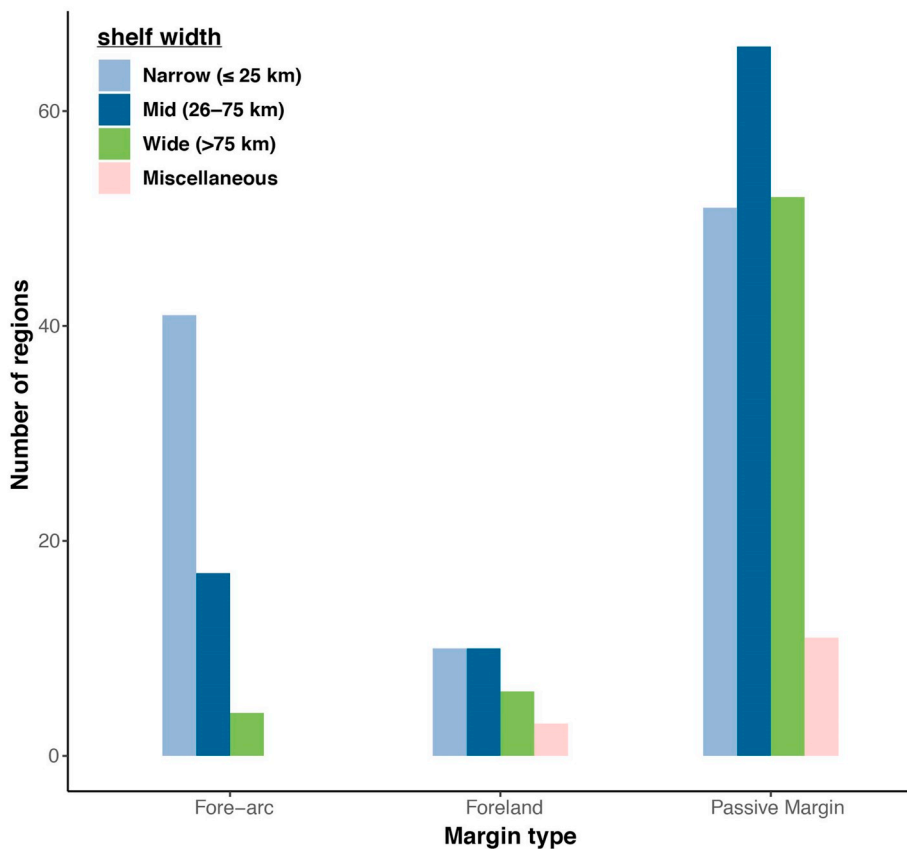


Fig. 6. Number of coastal regions found within fore-arc, foreland, and passive margin settings, colored by shelf width. Most regions within wide margins (green bars) are within passive margins. Note that the y-axis is the number of regions with a particular shelf profile and this is not normalized by length of coastline (i.e. there are the greatest number of observations (number of coastal regions) on passive margins).

or without reef-associated regions (Fig. S6). Finally, new world (western hemisphere) species richness is lower than on eastern hemisphere continents (Figs. 7A; S7) and is higher in equatorial settings (Fig. S8).

3.2. General habitat patterns

Globally, we find an 82% reduction of estuarine habitat abundance at lowstand (19.5 ka) relative to highstand (0–6.5 ka; Fig. 3A). This difference was greater on wide shelves (83% reduction) than narrow shelves (73% reduction; Fig. 4A). Africa and North America have the largest amount of highstand habitat and the greatest change in habitat area relative to lowstand (Fig. 3A). Most landmasses follow a near-exponential increase in habitat from lowstand to present except Australia, which flattens out at approximately 12 kya, as well as Japan, whose habitat remains nearly flat over time (Fig. 3A). Some types of regions exhibit complicated or ‘reverse-trend’ patterns such as continental shelf areas classified as miscellaneous (mostly epicontinental seas), which have an abundance of mid-depth habitat area. They do not show the near-exponential habitat abundance curve typical of other areas (Jablonski, 1985; Vermeij, 1978).

4. Discussion

We performed a GIS analysis to estimate putative estuarine habitat abundance through time as a function of sea level change and continental shelf geomorphology across continents with different tectonic, sediment, climatic, and oceanographic properties (North America, South America, Africa, India, Australia, and Japan; Figs. 1–2). Results show on average there is 82% less estuarine habitat at sea-level lowstand (140 mbsl; 19.5 ka) relative to present-day sea level (0–6.5 ka; Fig. 3). Recent results proposed that the reduction of habitat availability particularly on narrow continental shelves can physically isolate estuarine populations and lead to the formation of genetically distinct groups (Dolby et al., 2018; Dolby et al., 2016). Supporting these prior results, we find on this larger, global scale that there is lower habitat abundance on narrow margins than wide margins (Fig. 4A; Table 2), less habitat in fore-arc settings than passive margins (Fig. 4B), that fore-arc settings significantly associate with narrow shelves (Figs. 6, S3), and there is a weak positive, nonsignificant relationship between habitat abundance and passive margin age (Fig. S4).

Richness data of 1721 fish species show there are more fish species inhabiting narrow margins than wide margins (Fig. 8), a finding which violates conventional species-area relation that is based on richness patterns of terrestrial islands (Losos, 1996; Losos and Schluter, 2000). A pattern of greater richness on narrow margins could be explained: (1) If narrow margins facilitate in situ speciation through the physical isolation of populations during sea level change and/or over deeper time (Figs. 7–9); or (2) If there is a greater diversity of habitat types or greater habitat heterogeneity on narrow shelves than wide shelves (Figs. 7B, 8; Connor and McCoy, 1979; Eadie et al., 1986); or (3) If the stability of habitat abundance on narrow margins acts to preserve biota and the large habitats that inhabit wide margins cause population bottlenecks and extirpations (‘areal restriction’, Figs. 3B, 5; Olsson, 1961; Vermeij, 1989). We detail the significant findings and their implications below.

4.1. Controls on habitat abundance and species richness

4.1.1. Habitat abundance

Several predictions exist about the relation between sea-level change, habitat abundance, and biological evolution (Dall, 1890; Dolby et al., 2018; Dolby et al., 2016; Olsson, 1961; Stanley, 1986; Stanley, 1984; Vermeij, 1978; Vermeij, 1989). These predictions differ widely. They include sea-level change leading to regional extinctions through ‘areal restriction’, sea-level change having little-to-no impact on organismal evolution, and sea-level change driving genetic diversification

through isolation of populations. The strongest pattern found in our global analysis is that tectonic setting and shelf width are the foremost predictors of habitat abundance and that narrow shelves and fore-arc setting host significantly less estuarine habitat abundance than wide shelves and passive margins (Fig. 4, Table 2). These together are more predictive than age of margin. We find fore-arc settings are associated with narrow shelves (≤ 25 km width) while passive margins associate with mid and wide shelves (Figs. 6, S3). Fore-arc margins are dominated by compressional tectonics; examples include the western coast of South America and eastern coast of Japan. They have lower habitat abundance relative to passive margins, such as the eastern coast of North America, eastern coast of South America, and much of Africa and Australia (Fig. 3). South America provides a natural microcosm of this where its western margin is a fore-arc setting (i.e., subduction zone) with a narrow shelf that hosts less habitat (as well as less change in habitat abundance) at all timepoints compared to its eastern coast (Fig. 3B), which is a wide, passive margin.

Over this global setting, our findings uphold the documented causal relation of regional tectonic processes shaping shelf width (Algeo and Wilkinson, 1991; Burk and Drake, 2013; Nyberg et al., 2018; Nyberg and Howell, 2016) as well as their combined control on estuarine habitat abundance (Dolby et al., 2018; Hannisdal and Peters, 2011). The simplest interpretation of the combined results is that shelf width is the proximal causal mechanism controlling habitat abundance and factors that shape shelf width (e.g., tectonic setting) act as ultimate causal mechanisms to control habitat abundance through the intermediary of shelf width (Fig. 9). Based on this logic and previous literature, we expected old passive margins to be wider on average than younger passive margins because they would have more time for shelf-building processes to occur, such as sediment progradation/aggradation or carbonate platform growth, leading to higher habitat abundance. This relation was previously documented based on overall shelf area and margin age (Algeo and Wilkinson, 1991). However, while we found a positive relation between habitat abundance and seafloor age along passive margins, the relation is extremely weak (Figs. S4, S5). It is unclear why there is no clear relation between the age of a passive margin and habitat abundance. Perhaps the influence that age and sedimentation exert on shaping shelf width are less important than first-order tectonic processes (e.g., Fig. 23 in Nyberg and Howell, 2016). Additional factors not analyzed here that could be influential include drainage basin size and sediment flux.

4.1.2. Species richness

Previous work evaluated genetic differentiation and connectivity of estuarine species within the framework outlined in Fig. 9. Here, we use richness data of 1721 extant fish species to test the areal restriction hypothesis. Species distributions are affected by origination (speciation) events, extinction events, dispersal, biotic interactions, and ecological niche breadth and type. There is an expectation that genetic differentiation of populations within a species can, given enough time, manifest into a pattern of higher richness and diversity. This led us to postulate that narrow margins could facilitate the formation of new species over time through the physical isolation imposed by patchy coastal habitats.

Consistent with the above prediction, we find greater species richness on narrow margins than wide margins (Fig. 7B) and a weak but significant negative relation between *total shelf area* and richness (Fig. 8). These results use overall shelf area (between 0 and –140 m isobaths) within coastal regions and *not* habitat abundance to test these relations. The results are equivalent with or without putatively reef-associated coastal regions (Table 2; Fig. S6). These patterns, while previously predicted (Dolby et al., 2018), are nonetheless surprising as they violate the canonical species-area relation, which intuitively predicts greater area leads to more species (Lomolino, 2000; Losos, 1996; Losos and Schluter, 2000; Tjørve, 2009; Triantis et al., 2012). Considering South America again, species richness levels are not

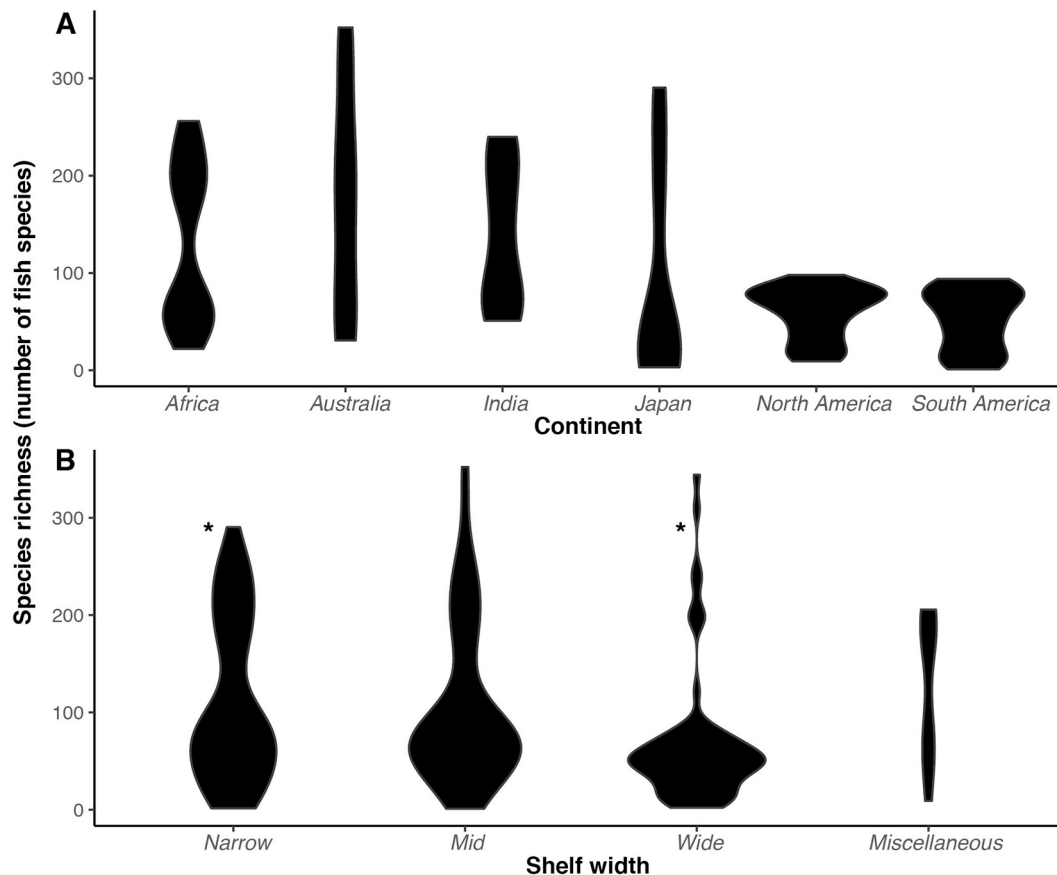


Fig. 7. Species richness A) per continent, and B) per shelf width. In panel A, violin width is not scaled by number of observations (i.e. all violins have the same area), emphasis is on number of species (y axis) and the distribution of species richness; violin width in panel B is scaled to number of observations (i.e. there are fewer observations for miscellaneous regions than others). Narrow shelves have higher species richness than wide shelves (* $p = 0.0004$) based on 1,721 fish species. Overall, there is lower diversity in the Americas. Note these fishes are not exclusive to estuaries.

significantly different between the narrow western margin and broad eastern margin. The fact that they have similar richness itself violates the conventional species-area relation because the eastern margin has much greater area and should therefore have more species. There is no a priori reason why terrestrial and marginal marine species would be governed by different relationships. Many marine species have high dispersal capacity (Kelly and Palumbi, 2010; Marko, 2004), but the same positive species-area relation has been demonstrated in coral reef habitats (Belmaker et al., 2006; Chittaro, 2002).

A first interpretation of this pattern is that a ‘habitat-diversity’ model (Connor and McCoy, 1979; Eadie et al., 1986) may fit, in which increasing the types of different habitats or abiotic conditions increases richness by representing different types of species. Probabilistically, this can occur as greater area is sampled there is a greater probability of encountering a different habitat type, but marginal marine systems may pose a special case. Estuaries, like other coastal habitats, occur in discrete patches along what can be considered a one-dimensional (linear) space, which is inherently different from island systems where area (and therefore habitat) increases in two dimensions. As we note that estuarine habitats are smaller on narrow margins than wide margins, and because different coastal habitats occur under different physical settings (think rocky intertidal vs. sandy beach), it may be that the smaller those habitat patches, the more habitat heterogeneity fits into a linear coastline, and therefore a higher species richness. This would be in contrast to wide coasts that have either larger habitats or fewer habitat types. For example, wide margins are less likely to have rocky shore communities (consider the western versus eastern coast of North America).

A second explanation is that narrow margins produce new species in

situ through the physical isolation of populations. Here we are studying estuarine habitat, but this likely applies to other coastal habitats as well because these habitat types also occur as discrete, isolated patches along the one-dimensional coastline. Because there is less estuarine habitat on narrow shelves than wide shelves not only at lowstand—but at highstand as well—this narrow-margin-isolation mechanism could apply not only during times of sea-level change, but potentially over the lifespan of the margins themselves—up to a hundred million years or more for some regions studied here (Fig. S4). While it is unlikely diversification of estuarine lineages can explain the negative area-richness pattern alone (it is an aggregate pattern), if the same set of processes applies to other habitat types as well then this could account for higher overall origination rates on narrow margins. Indeed, previous work showed that high in situ speciation rates can cause a negative species-area effect (Algar and Losos, 2011). The fact that habitat size on old margins and young margins is not appreciably different (Table 2; Figs. S4, S5) suggests that a narrow margin remains so (at least relative to wide margins) despite the effects of long-term sediment and erosional processes. In other words, a narrow margin may be a habitat-limited setting over very deep time, providing adequate time for long-term isolation and origination to take place. Additionally, processes that drive populational divergence within a species also increase the genetic diversity of the species overall, which mitigates against extinction risk (Birand et al., 2012; Purvis et al., 2000).

A third and final interpretation is that the size-stability of habitats on narrow margins allows for the accumulation and retention of species relative to wide margins. This is essentially equivalent to the ‘museum’ hypothesis proposed for why the neotropics are so speciose (Moreau and Bell, 2013; Rull, 2011) combined with Olsson’s ‘areal restriction’

hypothesis (Olsson, 1961), which predicts extinctions during sea-level change in regions with large amounts of shallow shelf area. Because large present-day habitats are predominantly on wide margins, and large habitats change in size the most from highstand to lowstand, this could lead to bottlenecks or extinction on wide margins as habitats radically change. Indeed, it has been proposed that the Pliocene to Quaternary transition eliminated significant shallow-sloping shelf fauna on the eastern coast of North America, yielding reduced shelf diversity (Blackwelder, 1981; Stanley and Campbell, 1981; Vermeij, 1978). Considering from above that narrow margins seem to remain so over deep time suggests a species accumulation model would have ample time to work over Pleistocene and earlier sea level oscillations, and might then host relictual (old) lineages.

Of course, species distributions are not immutable over deep time, but without delving into evidence from the fossil record, which is beyond the scope of this study, there is little that can be said for how long these species have inhabited their present-day distributions. One could address this with phylogenetics and divergence ages because lineages speciating in situ during sea level change would have a strong phylogenetic signal as opposed to the accumulation of lineages that have simply gone extinct elsewhere. The notion that long-term physical isolation could lead to formation of new species is commonplace from the population genetics perspective, but we note that our interpretation here is in direct opposition to previous literature which interpreted that eustatic regressions lead to extinctions. It is plausible that fossil evidence associating regressive periods with extinction events occur partly from sampling issues (Holland, 2012; Peters and Foote, 2001; Sepkoski Jr, 1976). For example, if estuarine habitat area reduced ~85% at lowstand relative today and many habitats were extirpated, one can imagine how that habitat reduction would manifest in the fossil record, particularly if the record is exposed only locally and if the exposed pieces themselves do not record all living organisms (which is common). What makes the genetic perspective here useful is it tells us that even with habitat dramatically reduced to small, isolated pockets, populations can still persist and give rise to a more contiguous distribution when sea level rebounds (Dolby et al., 2018; Dolby et al., 2016). Yet, if the fossil record from that reduced-habitat period was assessed, the probability of sampling one of the few refugia for a given species would be low and could lead to the estimation that a given species had been extirpated. Preservation bias may be particularly relevant on the Pacific coast of North America where preserved material from the mid-to-late Pleistocene generally only reflects highstand periods.

The genetic consequence of habitat reduction on wide margins during sea-level change may be significant. Reducing or extirpating populations reduces genetic diversity of that species overall (i.e. 'bottleneck') and when the population size of that species rebounds it still reflects the small pool of genetic material it came from, meaning that those individuals are much more similar genetically than would be expected in a population of that size (i.e. they have a low effective population size, N_e). It takes many generations in a recovered population for mutations to 'catch up' and yield the amount of genetic differences expected from a population of that larger size. In the meantime, low genetic diversity and low N_e are risk factors for extinction.

Recent work discovered a diversification 'pump' biased toward higher latitudes, and thus toward biotas with cold-water affinities (Rabosky et al., 2018). We find that the majority of habitat at present-day is found in equatorial settings (Fig. 4C), which simply results from Earth's present landmass configuration. If narrow margins actually generate species, then as landmass configurations change over geologic time, it would affect different regional faunas. Studies to understand extrinsic controls on origination rates include: diversity-based diversification (Rabosky, 2013); high-latitude driven diversification (though the proximal causal mechanism (light, temperature, UV) is undetermined; Rabosky et al., 2018); climatic stasis (Cronin, 1985; Cronin and Schneider, 1990); and rapid supply of new niche space (Peters, 2005)—though this may impact extinction rather than origination

patterns (Peters et al., 2013). While unlikely to account for large-scale extinction events (Jablonski, 1985), isolation on narrow margins could be an unappreciated influence on speciation processes of marginal marine communities.

4.2. Controls on shelf width and gradient

The width and gradient of a continental shelf is controlled by several tectonic and sedimentary factors over its lifespan. Some factors are ingrained early on in its tectonic history, millions of years in the past, and can continue to evolve over million-year time scales. Whereas, other surficial and sedimentary processes modify margin morphology over thousand-year timescales.

Shelf width is controlled by different tectonic factors at convergent (e.g., fore-arc) and divergent (e.g., passive) plate margins. Accretion of sediment and other crustal imperfections scraped off the incoming oceanic plate is an important process at some convergent margins. The off-scraping and accretion of such material commonly increases the width of the continental shelf, where models of steady-state accretion suggest that longer-lived subducting plate margins will progressively grow in width between the arc and the trench (Dickinson, 1971) and potentially host wider and lower gradient continental shelves. Other convergent margins are characterized by subduction erosion, where slivers of the overriding plate are tectonically removed and carried down the subduction zone. This commonly occurs where sedimentary cover is relatively thin (< 1 km) and convergence rates are relatively high (Clift and Vannucchi, 2004). Subduction erosion can lead to landward retreat of the trench and may help form narrower and steeper-gradient continental shelves.

At divergent margins, several factors control whether rift-related faulting is focused in a narrow zone or is distributed over a wider area, including crustal thickness (Buck, 1991), strain rate (England, 1983), sediment cover (Bialas and Buck, 2009; Lavier and Steckler, 1998), and the obliqueness of divergent plate motion (Bennett et al., 2013; Bennett and Oskin, 2014). After continental breakup and evolution to sea-floor spreading, areas of extensional faulting commonly subside and are buried by thick marine sediments that form the continental shelf. Asymmetric rifting, where one margin is characterized by a wide zone of faulting and faulting at its conjugate margin is more spatially concentrated (e.g., Brune et al., 2014), can lead to conjugate passive margins with unequal shelf widths (e.g., the Gulf of California). This rift asymmetry was previously shown to have a marked effect on the distribution of estuarine habitat (Dolby et al., 2018). Thus, the early history and style of rifting strongly controls the shape, width, and form of the nearshore, shelf-building sedimentary systems and plays an important role in the eventual width of the continental shelf at a passive margin. One can imagine applying our understanding of rift dynamics to deep-time continents to estimate their effects on habitat abundance and marginal marine species richness.

Incised river valleys or canyons can also affect the morphology of continental shelves. First, these channels can bypass the shelf and export terrigenous sediment farther offshore, preventing the shelf from building up or outwards. Additionally, channels and canyons are steeper than the typical grade of the shelf and in high densities generate large gaps along the shelf front—up to 20–40% gaps calculated for some regions of the west African margin (Seibold and Hinz, 1974).

Exposure to wave energy and resultant erosion, combined with the resistance strength of the underlying bedrock, are also critical factors shaping shelves (Masters, 2006; Masters, 2003). Wave energy is largely the product of long period waves produced by polar-front storms which are currently strongest and emanate from circum-Antarctic polar front for much of the year. These have significant impacts on the south-facing coastlines of Australia and Africa. Strong seasonal polar front storms generate significant wave energy in the North Pacific and North Atlantic basins. Clearly these and other erosional processes need time to operate. So, the time since the last major tectonic event should be impactful.

4.2.1. Emergent lands & 'reverse-trend' regions

Within our results are 'reverse-trend' regions that disobey the pattern of reduced habitat at lowstand. The Japanese archipelago is used here as a counterexample to the other landmasses and, unlike other continents, does not increase habitat abundance from lowstand to highstand (Fig. 3A). Overall there is little low-relief shelf area and little estuarine habitat abundance across Japan. However, the relative constancy of Japan's habitat abundance over time suggests it may be a rare example of habitat stasis. Because this is the only archipelago in our study, it will require more work to determine whether these findings are due to Japan's old and tectonically complex history (western South America has a somewhat similar pattern; Fig. 3B) or is characteristic of archipelagos in general.

The conic shape of many oceanic islands, particularly those of volcanic origin, yields equal or greater habitat area at lowstand than highstand (Jablonski, 1985). Such islands are therefore of interest because they exhibit reverse-trend habitat abundance patterns as they have more coastline and potentially more habitat and shelf area at lower sea levels. Epicontinental seas also provide anomalous trends as they have dramatically large mid-to-highstand area and minimal-to-no lowstand area. These flooded continental regions can originate due to extension of continental crust associated with rifting. Examples of reverse-trend areas in this study include the Bass Strait (between Tasmania and Australia), the Palk Strait (between Sri Lanka and India), the region surrounding the Malvinas Islands (Falklands, South America), and the Seychelles (Africa). Others are the product of thrust-loading associated with arc-continent or continent-continent collisions, for example the Persian Gulf, the Arafura Sea (between Papua New Guinea and Australia, not studied here), and the Formosa (Taiwan) strait (between Taiwan and China). It should be noted that while these regions have an excess of mid-depth bathymetry, many if not most of these regions are likely fully subaerially exposed with estuarine fauna extirpated at lowstand (see Miscellaneous category in Fig. 4A). Extirpation at any depth requires recolonization if that region is to rejoin a species' range, so these areas may be very biologically dynamic during periods of sea level change.

4.3. Dynamics of sea level change & biological consequences

4.3.1. The role of cyclicity

As with most sea level papers, this study compares highstand habitat distributions (0–6.5 ka) with those at glacial lowstand (19.5 ka), focusing on the LGM because its impacts are most recent. However, the history of sea level is one of *cyclicity*, particularly during the Pleistocene. Between ~2.5 and ~0.8 Ma sea level oscillations were dominated by 41-kyr periodicity and were of smaller amplitude, reaching on average only ~30–60 mbsl (Fig. 10). The Mid Pleistocene Transition (MPT) between 1.1 and 0.7 Ma (Chalk et al., 2017; Clark et al., 2006; Willeit et al., 2019) marked the shift to high-amplitude (up to 120–140-m) sea level oscillations paced by longer ~100-kyr periods (Fig. 10A). Therefore, glacial cycles have been an ongoing process of varying strength for much longer than the ~20-kyr timeframe that is typically studied.

Additionally, not only is the rate of postglacial sea-level rise not uniform (and therefore the pace of habitat growth/reduction not constant; e.g., Chaytor et al., 2008; Lambeck et al., 2002), but most (about 80%) of any given 100-kyr glacial cycle is spent in the regressive (ice-growing) phase, with only ~20 kyrs spent in the transgressive (ice-melting) phase (Miller et al., 2005). The importance of these asymmetries is twofold. First, the present sea level configuration is only a snapshot of a continuous process that has been happening in earnest over the past ~2.5 million years (Fig. 10). In fact, the 6.5 ka to present sea level (and habitat) configuration accounts for only ~6.5% of post-MPT-time (~52 kyrs total since ~0.8 Ma). Since the MPT, the average sea level has been ~64 mbsl based on data from Miller et al. (2005). This summary of sea level history is to say that the genetic connectivity

imposed by habitat configurations at mid-depths (e.g., 30–80 mbsl) are much more the norm than the population connectivity that we see today or than populations experienced during 120–140 mbsl lowstand, although the habitat reduction imposed at lowstand, however short, is surely impactful.

Second, it means the relevant timeframe to understand the genetic consequences of sea-level change is not LGM to present (i.e., the past ~20 kyrs), though this is the easiest to study, but is actually ~0.8 Ma to present—the duration of highest-amplitude Pleistocene glaciations. A reasonable way to think of this may be to extrapolate the genetic effects of LGM to present eight-fold to account for the effects of repeated glaciations. It also means that whatever model of isolation and post-glacial admixture best describes genetic patterns from LGM to present ignores the cyclical, longer-term nature of these phenomena (Fig. 10), and evolutionary findings from LGM to present are patterns that come on the heels of and are superimposed on previous cycles. Whether the available genetic modeling approaches (e.g., Approximate Bayesian Computation) and genetic data are sufficient to tease apart recent from previous glacial effects is so far untested.

4.3.2. Deep-time biodiversity predictions

One can imagine that putting all these points together leads us to a sort of 'extirpation game'. If the populations of a species are pushed into isolation during regression, it can promote diversification or speciation, which in turn fosters resiliency or biodiversity—but if pushed slightly too far—it can lead to bottlenecks, extirpations, or extinctions. Tipping points are an intrinsic part of many Earth systems, such as the link between ice volume, obliquity, insolation and greenhouse gasses; or ecosystem functions, community richness, and nutrient cycling. Considering isolation on narrow margins to have a 'tipping point' component may be useful, but it also complicates the ability to make deep-time predictions unless that threshold is better understood across species and habitat types.

It is difficult to know over the long term whether narrow margin isolation causes extinction or diversification (Jansson and Dynesius, 2002), but results from this and previous studies (Dolby et al., 2018; Dolby et al., 2016) support the idea that narrow margins are a diversification pump, and/or they accumulate species over time. Extending this scenario over deep-time tectonic processes is an obvious next step. Compressional/tensional tectonics between oceanic and continental lithospheric plates (e.g., fore-arc settings) produce narrow, biodiversity-promoting settings. But continent-continent collisions instead lead to the closure of seaways (e.g., Tethys Sea) and destruction of coastal habitats in the path of the colliding margin.

Over geologic time we would predict that diversification of estuarine species (and perhaps those of other coastal habitats) should be highest when the cumulative global length of coastlines is high and when most of those coasts have narrow shelves. With this logic, after supercontinent formation (Wilson Cycles, e.g., Pangea) there is less available coastline and many coastal habitats are eliminated (Martin, 2003). Rifting processes that subsequently break up a supercontinent would create a large amount of coastline along the newly formed passive margins that, based on this study, would in all likelihood host the wide shelves and high habitat abundance (Algeo and Wilkinson, 1991; Holland, 2012; Martin, 2003) that promotes genetic connectivity instead of diversification. So, diversification of estuarine species should be low during the supercontinent formation phases (Wilson, 2005), and should be high when there is a large amount of oceanic coast being subducted globally.

4.4. Directions for future work

There are four main areas of future work to expand on and refine the results produced here. The first is to ground-truth the habitat models used in this study to ascertain their validity in different geomorphic contexts. Work is particularly needed in strike-slip (transform) coastlines,

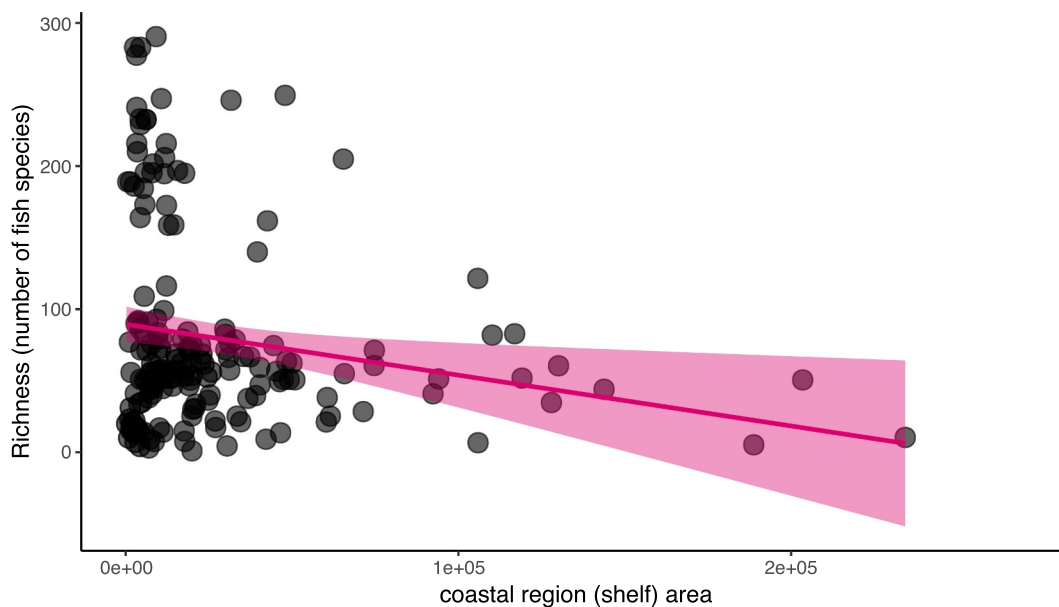


Fig. 8. Species richness as a function of shelf area. Total number of species displayed as a function of total shelf area between 0 and 140 mbsl (i.e. not habitat area). Putatively reef-associated regions are excluded, although the trend is equivalent when including reef-associated regions (Figure S6B). This weekly negative relationship violates the canonical species-area expectation of greater species richness with greater area.

which we expect to exhibit narrow shelves similar to fore-arc settings. While it is established that estuaries predominantly inhabit low-gradient regions (Jacobs et al., 2011), measuring the sensitivity and specificity of these models on present-day habitat could develop more sophisticated paleo-estuarine models as well as modeling approaches for other types of coastal habitats. Detailed seismic stratigraphy data could be used to ground-truth such estimates (Bastos et al., 2015; Berton et al., 2019; Lee et al., 2017; Roach, 2017; Zaremba et al., 2016).

Second, projecting our models into the future to predict estuarine habitat abundance (and biological implications) over projected scenarios of anthropogenic sea-level rise would be useful. In particular, understanding which regions will be subject to the greatest habitat changes is valuable information. However, this includes extrapolating over highly modified coastlines, and whether our modeling techniques will work effectively over industrialized landscapes is untested.

Third, the framework we outline provides clear, testable predictions about patterns over deeper time. For example, using information about times of great sea-level change or major reorganizations of global landmasses would enable a detailed set of predictions that can be tested genetically. The advent of high-throughput genomic sequencing provides an opportunity to look in great detail at the evolutionary history of lineages, including: 1) the diversification rate of estuarine families during periods of predicted environmental or tectonic change, 2) the origination age of lineages on narrow margins to determine if they are relictual or recent, and 3) the origination age of specific genes or gene pathways that enable ecological adaptations that could be expected to occur during periods of habitat reorganization (e.g., paleogenomics; Bottjer, 2017; Thompson et al., 2017). These can be compared against the fossil record and computer simulations that integrate paleo-geographic estimates with origination-extinction models. Together they

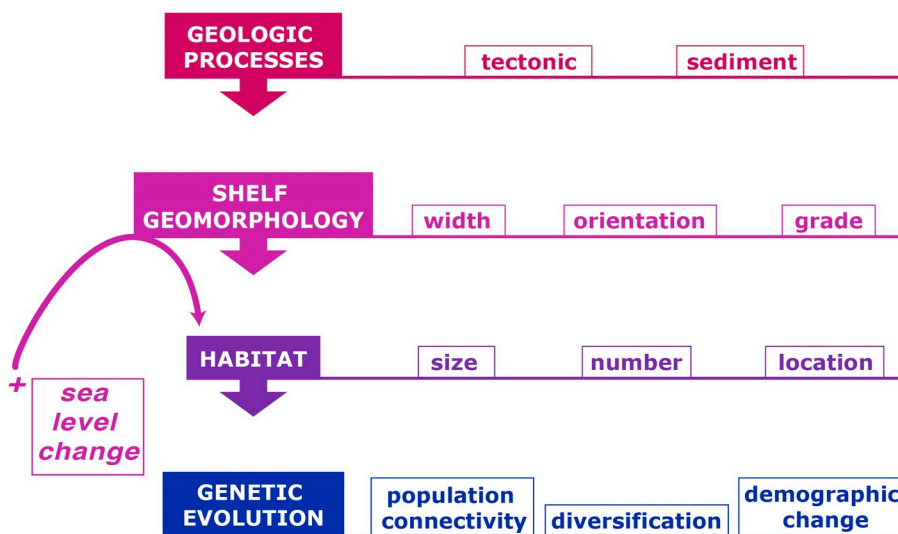


Fig. 9. Schematic that outlines the top-down physical control on evolutionary genetic processes related to estuarine habitat and sea-level change.

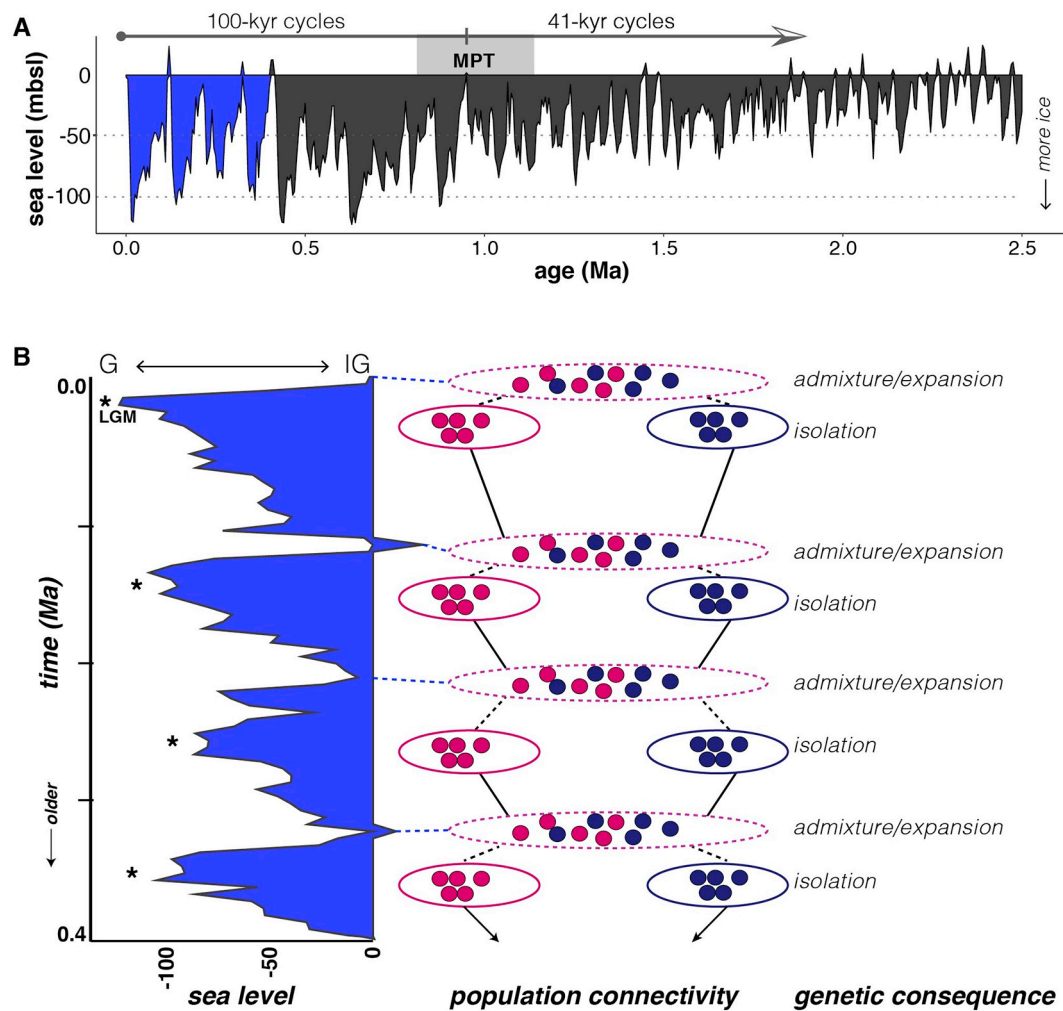


Fig. 10. Schematic of changes in periodicity and amplitude of sea level oscillations. Sea level data is adapted from Miller et al. (2005) and shows A) transition from 100-kyr glacial cycles of higher amplitude to 41-kyr cycles at the Mid Pleistocene Transition (MPT). B) Most recent glaciations (blue part of panel A) are redrawn in detail with estimated biological effects. Periods of isolation in refugia (solid lines) during glacial (G) periods and periods of recolonization (dotted lines) during interglacial (IG) times. Asterisks denote glacial maxima. Small circles represent individuals where color represents genetic identity; ovals represent populations (boundaries of gene exchange). Most biological studies focus isolation and recolonization from LGM to present; this graphic emphasizes the cyclical nature of Pleistocene sea level change. Note, the colors of individuals do not change through time for illustration purposes, in reality the admixture period would result in gene flow between red and blue individuals.

can determine whether there is evidence for diversification that can be explained by the framework outlined here, and whether it explains why evidence for biodiversity and sea-level change in the fossil record has been mixed.

Finally, genomic tools enable fine-scale whole-genome assessments of how isolation, extirpation, recolonization processes impact species evolution, and in particular what genetic signals of these are retained over repeated glaciations. We anticipate lowstand isolation to be inversely correlated with species dispersal ability, such that very high-dispersing species would not be isolated even on narrow margins during the deepest lowstands (Jablonski, 1986). Whole-genome comparative approaches can be used to investigate whether there is a threshold dispersal ability at which lowstand isolation is no longer applicable. These approaches could also help determine how common differential adaptation is during periods of lowstand isolation and may also be applied to organisms in the fossil record to better understand the controls on their evolution and distribution through time. Overall, it appears there is much to be gained by integrating geological evidence with population genomic and species richness data, particularly when developing conceptual frameworks that can be broadly applied over recent and deep time.

5. Conclusions

Nearly 60 years after Olsson (1961) proposed the areal restriction hypotheses to explain regional extinctions in the fossil record, we provide global evidence drawn from geological and biological records to tentatively suggest that tectonic setting directly controls the physical size and distribution of marginal marine habitats on coastlines worldwide, and that habitat abundance decreases during sea level regression.

We find fore-arc settings produce narrow continental shelves that limit estuarine habitat availability, a phenomenon that probably also occurs at strike-slip margins (though this requires more data). The small habitats on narrow margins are more size-stable during sea level change than large habitats. Narrow margins are associated with higher species richness based on data of 1721 fish species. This negative relation defies the canonical species-area relation but can be explained: 1) if narrow margins generate new species in situ by imposing physical isolation on populations over deep time; 2) if narrow margins retain species because small habitats are less variable in size during sea-level change and therefore are less affected by extirpations; or 3) if narrow margins have higher habitat heterogeneity that leads to greater richness (habitat diversity hypothesis). The concept of narrow margins as a diversification

pump is in opposition to previous paleontological literature that generally argued areal restrictions were not important and/or regressions led to extinctions.

While differing from previous interpretations, our framework is more in line with the basic tenets of population genetics and our results support Holland (2012) who found that the complex and idiosyncratic relation between habitat and sea-level change depended on the inherent geomorphic properties of the coastline (Holland, 2012; Paulay, 1990). The juxtaposing viewpoint offered here is based on 1) population genetic theory that population isolation can lead to genetic divergence and promote species diversification and 2) our new findings that narrow margins have more fish species. Our results regarding hierarchical physical controls on genetic connectivity and richness of populations yields a predictive, testable, and systematic understanding of sea-level change and recent evolution that can be advanced using tools from whole-genome sequencing and seismic stratigraphy. Whether this framework can predict macroevolutionary diversification rates of marginal marine biota on deeper geologic timescales remains to be tested.

Author contributions

GAD and DKJ co-conceived of this project. AMB and GAD performed GIS analyses, GAD performed statistics and drafted the paper. DKJ and SEKB contributed to the paper and all authors gave final approval.

Data availability & appendices

Third part data sources are cited in the methods. All other products associated with this study are bundled in a Harvard's Dataverse: <https://dataverse.harvard.edu/dataverse/DolbyGPC>. Products include: spreadsheet of all habitat data with spatial join data, KML layers, html archiving of spatial autocorrelation and JMP statistical results.

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Declaration of Competing Interest

We have no conflicts of interest to declare.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gloplacha.2020.103128>.

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