

Larger distribution ranges of seagrasses towards the equator

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Abstract

Aim: The description of species' ranges provides biogeographical information to explain fundamental macroecological and evolutionary processes. In this study, we investigated the Rapoport's rule for the world's seagrasses, that is, whether the range extent of seagrasses increases from the tropics to the poles.

Location: Global.

Taxon: Seagrasses.

Methods: We examined whether four range geographical metrics: the extent of latitudinal and longitudinal ranges, total distribution area (Km²) and the number of marine ecoregions encompassed by seagrass species, changed according to their latitudinal distribution midpoints.

Results: Seagrasses have larger distribution ranges, as indicated by all geographical metrics, close to the equator in both hemispheres, supporting the inverse of the Rapoport's biogeographical pattern.

Main Conclusions: The larger distribution ranges of seagrasses towards equatorial regions may be attributed to their origins during warm geologic periods, and the subsequent longer climatic stability in tropical areas leading to climate niche conservatism constraining seagrass evolution.

KEYWORDS

evolution, latitude, macroecology, macroevolution, marine angiosperms, Rapoport's rule

1 | INTRODUCTION

The study of species' geographic ranges, that is, the spatial area where species occur, has long attracted the attention of ecologists and evolutionary biologists. Unravelling the evolution of ranges provide responses to key questions in ecology, conservation and evolution, including topics such as species' response to climate change (Jablonski et al., 2006; Pie et al., 2021; Sheth et al., 2020). Biogeographical information on species' ranges provides key information to explain fundamental macroecological and evolutionary processes, such as adaptation and dispersal (Di Marco & Santini, 2015; Gaston, 2009; Sheth et al., 2020). Within a conservation context, examining the

extent of species' ranges is valuable to predict extinction risks, rarity and invasiveness and to optimize conservation decisions.

Geographic ranges depend on the place and time where a species and their ancestors originated, and the evolutionary history of the species, with species' ranges rather dynamic (expansions and contractions) through geological time scales from millennia to millions of years (Gaston, 2009). Species' life-history traits (e.g. dispersion abilities, Lester et al., 2007; Sunday et al., 2015) and biotic interactions (Hellmann et al., 2012; Pigot & Tobias, 2013) affect species' capabilities to respond and adapt to climate alterations through geological eras (Lenoir & Svenning, 2015), ultimately contributing to explain shifts in species' distribution ranges.

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One of the best known, but also controversial, rules in macroecology is the Rapoport's pattern, which predicts that the mean latitudinal range size of species decreases towards the tropics, so there are smaller range sizes in tropical than in temperate realms (Rapoport, 1982). Under this theory, Stevens (1989) proposed the 'climatic variability' or 'seasonal variability hypothesis', which postulates that individuals at higher latitudes have to withstand considerable temporal variability in climatic conditions relative to organisms at lower latitudes. Consequently, species at high latitudes occupy larger latitudinal extents and therefore have more ample distribution ranges, than their low-latitude counterparts. However, this rule does not always apply, or only partially occurs in certain regions (Gaston & Chown, 1999; Pintor et al., 2015; Rohde, 1996), while there is sparse support for marine organisms (Pie et al., 2021; Pintor et al., 2015).

In the marine realm, an inverse of the Rapoport's pattern has been reported for some groups, such as fishes (Pie et al., 2021) and invertebrates (Roy et al., 1998; Tomašových et al., 2015), related to the fact that species' ranges result from both evolution in dispersal and niches and range limits can be either dispersal or niche-limited (Wiens & Graham, 2005). Niche-limited range limits are typical for species that originated in the tropics, and have undergone phylogenetic conservatism in their thermal niche, that is, 'tropical/climatic niche conservatism' hypothesis (Wiens & Donoghue, 2004). Because tropical regions are characterized by shallower thermal environments, species can occupy larger geographical extents, even when they are thermal specialists (Tomašových & Jablonski, 2017). In contrast, steeper thermal environments in temperate regions prevent species of tropical origin to occupy extratropical regions over geological timescales, because of constraints in their thermal niche (Wiens et al., 2010).

Seagrasses are a polyphyletic group of key ecosystem engineers, distributed across tropical, sub-tropical and temperate coasts of the world (Daru et al., 2017; Short et al., 2007; Waycott et al., 2014). Currently, up to 72 species of seagrasses create habitats of paramount ecological, socio-cultural and economic relevance, which are of considerable conservation interest (McKenzie et al., 2020; Short et al., 2007). Seagrasses evolved from terrestrial relatives, which diverged around 140 million years ago during the Cretaceous (Lee et al., 2018). Ancient seagrasses entered in the ocean and evolved in different parallel events (Lee et al., 2018; Les et al., 1997; Wissler et al., 2011). Although the fossil record of seagrasses is limited, ancient seagrasses established under warm conditions (Lee et al., 2018; Vélez-Juarbe, 2014). By the early Eocene (55–50 million years ago), for example, tropical conditions extended to latitudes as high as 50° in western Europe (Zachos et al., 2001). Climatic cooling during the early Oligocene seemed to have limited the extent of seagrasses, although seagrasses further diversified and expanded their distributions by the late Oligocene following ocean warming (Vélez-Juarbe, 2014). Legacies of past climatic periods, hence, have influenced the current distribution and biology of certain seagrass species (Daru et al., 2017; Duffy et al., 2022; Martínez-Abraín et al., 2022).

Macroecological studies of seagrasses are scarce, despite key recent advances such as a phylogenetic regionalization of the world's

Significance Statement

We demonstrate seagrasses have larger distribution ranges near the equator in both hemispheres, supporting the inverse of the Rapoport's biogeographical pattern, and suggesting that climate niche conservatism has governed seagrass evolution.

coasts that demonstrated close evolutionary affinities among separate temperate seagrass assemblages (Daru et al., 2017). It has also been modelled seagrass distributional responses to future climate change scenarios, which showed both range contractions and expansions (Daru & Rock, 2023).

In this study, we explored the Rapoport's rule for the world's seagrasses. Specifically, we investigated whether the range extent of the world's seagrasses change with their mean latitudinal point, using four species' range metrics: the latitudinal and longitudinal range, total distribution area (Km²) and the number of marine ecoregions encompassed. We hypothesized that, because of their tropical origin and likely pattern of thermal niche conservatism, geographic range extent in seagrasses would be inversely related to latitude. Our study provides fundamental information on seagrasses' biogeographical distributions to boost our understanding on the macroecology of their geographical ranges.

2 | MATERIALS AND METHODS

2.1 | Data source

Biogeographic distributional information for a total of 61 out of 72 of the world's seagrass species (16 species within the Cymodoceaceae, 19 within the Hydrocharitaceae, 7 within the Posidoniaceae and 19 within the Zosteraceae) was collected (<https://github.com/ftuya/seagrass-ranges>) from the International Union for the Conservation of Nature (IUCN) red list portal (www.iucnredlist.org). A total of 32 temperate and 29 tropical species were here considered according to Rolland et al. (2014) criteria (−23.4° and 23.4° as the threshold latitudes defining the tropics). Although these are broad-scale approximations of seagrass distributions, they provide a reliable approximation to model distributions of seagrasses (Daru & Rock, 2023); because the IUCN periodically updates these distribution maps, this is the most accurate source of seagrass distribution (Daru et al., 2017).

We initially downloaded a shapefile (i.e. polygons) for each of the current 72 seagrasses with their current known distributional range. We then excluded those more typical of brackish waters (e.g. *Ruppia* spp.), while those with uncertainties in either their taxonomy or geographical distributions were also discarded (Rock & Daru, 2021). Taxonomic validation of scientific names followed the WORMS (www.marinespecies.org) and the World Flora Online (www.worldfloraonline.org) utilities.

2.2 | Calculations of species' ranges

Biogeographers and macroecologists have accounted for range size through their latitudinal or longitudinal extent, the extent of occurrence, and/or the area of occupancy (Gaston & Chown, 1999). In this study, we focused on four attributes (metrics) of seagrasses' ranges: the latitudinal and longitudinal range extent, the total distribution area (Km²) and the number of marine ecoregions encompassed by each seagrass species. The maximum and minimum latitude and longitude of the species' ranges were extracted, and the latitudinal midpoint (mean latitude) was calculated. The total area (in Km²) of the range of each species was calculated using the function 'st_area' of the 'sf' R package (Pebesma, 2018), which assumes that the coordinates are planar, that is, a flat Earth model. To explore in which and in how many marine ecoregions each seagrass species occurred, we downloaded the marine ecoregions of the world (Spalding et al., 2007), and then we used the 'intersect' function of the 'raster' R package. Ecoregions, that is, areas of relative ecological homogeneity (similar ecological structure, function and composition, Loveland & Merchant, 2004), represent a formal tool for conservation decisions (Olson et al., 2001). Prior to this step, we transformed our 'polygon' ranges into a 'spatial polygons data frame', using the 'as_Spatial' function of the 'sf' R package.

2.3 | Statistical analysis

To test if the latitudinal midpoint of seagrass species contributed to explain their distribution extent, in terms of the four biogeographic metrics, we fitted generalized additive models (GAMs), using the 'mgcv' R package (Wood, 2011). All models were fitted through a 'Poisson' family error structure and a 'log' link function, with the basis dimensions of the smooth terms (thin plate regression splines) limited to 5 knots to avoid overfitting and ensure monotonic relationships. We checked for normality and homoscedasticity of models residuals through visual examination.

3 | RESULTS

Seagrass latitudinal midpoints varied between +51° and -41° (Figure 1a). *Zostera marina* showed the northern maximum latitudinal point of all ranges (+74.1°), and *Zostera tasmanica* the southernmost point (-37.8°). The maximum latitudinal range was between 60 and 70° for several seagrass species (Figure 1b). The maximum longitudinal range was >290° for two species (*Zostera marina* and *Halophila decipiens*) (Figure 1c). While most species have small geographic ranges (<10 e⁵ Km²), a small number of species have large geographic ranges (>100 e⁵ Km²), which resulted in a right-skewed distribution of seagrass ranges according to their total distribution area (Figure 1d). A similar pattern was observed for the number of marine ecoregions encompassed by seagrasses (Figure 1e), with most of species found on less than 20 ecoregions.

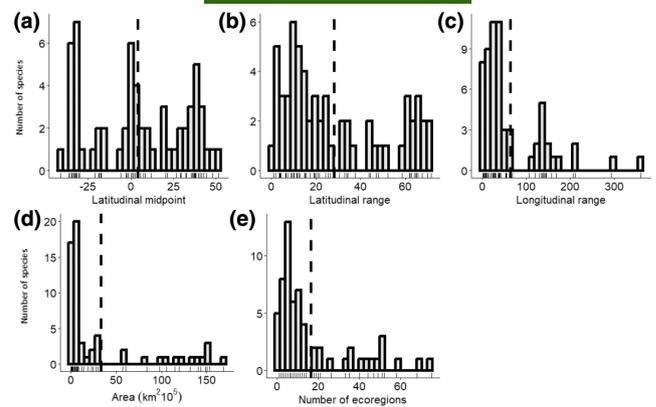


FIGURE 1 Histograms of geographical range metrics for the world's seagrasses, including (a) the latitudinal midpoint, (b) the latitudinal range, (c) the longitudinal range, (d) the total distribution area and (e) the number of marine ecoregions encompassed by seagrasses. The mean for each metric is included as a vertical dashed line.

Seagrasses' geographical extent, as represented by all range metrics, peaked at low latitudes, that is, towards to the equator (Figure 2). Therefore, wider ranges across a more ample number of ecoregions were observed at low latitudes, as opposed to the Rapoport's rule. In other words, those species with latitudinal midpoints towards temperate environments are more restricted in their ranges, particularly in the southern hemisphere. All tested models (Table 1) showed low *p*-values (<2·10⁻¹⁶), so the explanatory variable (latitudinal midpoint) statistically explained a considerable amount of variation (>50% in terms of deviance explained) in the four range metrics (Table 1).

4 | DISCUSSION

Our results have demonstrated that the global distribution of seagrasses follows the inverse of the Rapoport's rule, that is, there is an overall negative relationship between latitude and range size. This inverse biogeographical pattern has been reported for other marine organisms, from molluscs (Roy et al., 1998; Tomašových et al., 2015) to reef fishes (Macpherson & Duarte, 1994; Pie et al., 2021), but contrast with recent support for this biogeographical pattern for terrestrial plants (Huang et al., 2021). An interplay between temperature stability across the oceans' latitudes, that is, reduced temperature changes from the equator to both poles relative to terrestrial ecosystems, altogether with large environmental heterogeneity and varying dispersal capacities of marine species, have been considered to explain the inverse of the Rapoport's rule for varying clades of marine organisms (Pie et al., 2021; Pintor et al., 2015; Tomašových et al., 2015). In this sense, expected larger thermal instability towards higher latitudes is minored and so the principle of the rule is difficult to be tested. The mid-domain effect does not seem here to play any effect, because some seagrass species with wide ranges have their latitudinal midpoints at high latitudes, and seagrasses are

not found at polar latitudes where they potentially could expand (Daru & Rock, 2023).

The general decrease in the distribution range extent of seagrasses, from the equator towards high latitudes, is consistent across both hemisphere, but likely because of different causes. The southern hemisphere has been less affected by recent glaciations in the Pleistocene, including the Last Glacial Maximum, relative to the northern hemisphere (Ehlers & Gibbard, 2007), so seagrasses have had more time to expand their distributions and speciation to occur (Waycott et al., 2014). However, in the southern hemisphere, there is comparatively less effective area (i.e. terrestrial masses) to colonize/disperse into, which has been already pointed out to call attention on limitations for the persistence of marine vegetation, such as kelp, in southern waters (Wernberg et al., 2019). Isolation and climatic stability have favoured the existence of a considerable number of temperate seagrasses from south Australia, in particular endemics within the genus *Posidonia* and *Amphibolis* and even a unique species of *Halophila* (*H. australis*) (Larkum et al., 2018). In this sense, the evolutionary distinctiveness of seagrasses is maximum here and in temperate south America and southern Africa (Daru et al., 2017). The large tectonic stability, since the Late Cretaceous, of the continental shelf along these western and southern continental margins, is a plausible explanation for these observations.

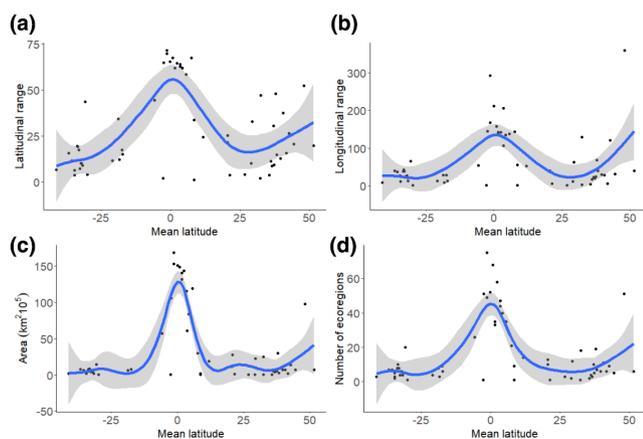


FIGURE 2 Relationship between the latitudinal midpoint in the geographic distribution of the world's seagrasses and their (a) latitudinal range (in degrees), (b) longitudinal range (in degrees), (c) range area and (d) the number of marine ecoregions encompassed. The blue line represents the fitted (smooth) GAM function, and the grey shade area is the 95% confidence level interval.

Environmental gradients, historical processes, species interactions and evolutionary factors, all play crucial roles in determining species distributions, range sizes and richness patterns (Wiens & Graham, 2005). For seagrasses, a larger species richness is observed towards the tropics (Short et al., 2007), and the total areal extent of seagrass is also larger in tropical areas, while decreasing towards temperate environments (Jayatilake & Costello, 2018; McKenzie et al., 2020). Despite the limited presence of seagrass material in the fossil record, the likely ancestral tropical origin of seagrass lineages (Lee et al., 2018; Vélez-Juarbe, 2014; Wissler et al., 2011) has been advocated to explain these patterns. At the same time, it seems to have contributed to imprint their current-day geographical ranges, in particular with larger ranges towards the equator. When a clade has a tropical origin (i.e. originated in warm climates), 'Climate Niche Conservatism' (CNC) is a notable process behind the maintenance of the latitudinal richness gradient (Smith et al., 2012; Wiens & Donoghue, 2004). CNC, that is, the inclination of species to retain traits of their climatic niche over evolution (Wiens & Graham, 2005), considers that the ancestral niche determines regions and habitats that members of particular a clade can colonize (Wiens & Donoghue, 2004), and it has been already proposed to govern the evolution of seagrasses (Daru et al., 2017). Near the centre of a clade's origin, there is often a longer history of adaptation and tolerances to environmental conditions, so species may have larger ranges compared to species with more restricted tolerances, not moving far from the optimum niches (Donoghue, 2008). If corridors for dispersal are accessible, new habitats are colonized, broadening species' ranges. The 'out of the tropics' hypothesis, according to which lineages mostly originate in the tropics and then disperse to temperate latitudes without losing their tropical presence (Jablonski et al., 2006), seems also to have concurrently explained seagrass macro-evolution.

Seagrasses rely on various mechanisms for long-distance dispersal, with vegetative fragments drifting in ocean currents being particularly important (Kendrick et al., 2012). However, across the planet's oceans, only few seagrass lineages have successfully diversified and colonized temperate latitudes. For seagrasses, environmental gradients that delimitate temperate regions seem to limit dispersal, reinforcing the idea that CNC has constrained seagrass evolution (Daru et al., 2017).

Compared with other foundation species creating marine habitats (e.g. corals and kelps), predictions on the future distribution of seagrasses remain majorly unknown. Recently, it has been forecasted both contractions and expansions of seagrass ranges under climate change scenarios (Daru & Rock, 2023). Recent calls have advocated

Biogeographical metric	Estimate	Standard error	Z value	p	Deviance explained (%)
Latitudinal extent	3.15	0.03	110.1	$<2 \cdot 10^{-16}$	56.8
Longitudinal extent	3.85	0.02	183.6	$<2 \cdot 10^{-16}$	57.8
Area	14.19	0.00	104712.0	$<2 \cdot 10^{-16}$	79.9
Number of ecoregions	2.43	0.04	57.1	$<2 \cdot 10^{-16}$	70.5

TABLE 1 Summary of fitted GAMs to metrics depicting distribution ranges of the world's seagrasses according to their latitudinal midpoint.

the evolutionary context in the origin of species, seagrasses in particular (Martínez-Abraín et al., 2022), to not exclusively rely on spatial distribution models (SDMs) to predict future distributions. In this sense, the identification of biogeographical patterns and underlying evolutionary hypotheses for species' ranges across the globe can better inform conservationists, under the warming trend of the planet's oceans, to better interpret the future of species' distributions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data and R code are available at <https://github.com/ftuya/seagrass-ranges>.

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REFERENCES

- Daru, B. H., Holt, B. G., Lessard, J. P., Yessoufou, K., & Davies, T. J. (2017). Phylogenetic regionalization of marine plants reveals close evolutionary affinities among disjunct temperate assemblages. *Biological Conservation*, 213, 351–356.
- Daru, B. H., & Rock, B. M. (2023). Reorganization of seagrass communities in a changing climate. *Nature Plants*, 606, 75–1043.
- Di Marco, M., & Santini, L. (2015). Human pressures predict species' geographic range size better than biological traits. *Global Change Biology*, 21, 2169–2178.
- Donoghue, M. J. (2008). A phylogenetic perspective on the distribution of plant diversity. *Proceedings of the National Academy of Sciences*, 105, 11549–11555.
- Duffy, E., Stachowicz, J. J., Reynolds, P. L., Hovel, K. A., Jahnke, M., Sotka, E. E., Boström, C., Boyer, K. E., Cusson, M., Eklöf, J., Engelen, A. H., Eriksson, B. K., Fodrie, F. J., Griffin, J. N., Hereu, C. M., Hori, M., Hughes, A. R., Ivanov, M. V., & Jorgensen, P., ... Olsen, J. L. (2022). A Pleistocene legacy structures variation in modern seagrass ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, 119, 1–8.
- Ehlers, J., & Gibbard, P. L. (2007). The extent and chronology of Cenozoic global glaciation. *Quaternary International*, 164–165, 6–20.
- Gaston, K. J. (2009). Geographic range limits of species. *Proceedings of the Royal Society B: Biological Sciences*, 276, 1391–1393.
- Gaston, K. J., & Chown, S. L. (1999). Why Rapoport's rule does not generalise. *Oikos*, 84, 309–312.
- Hellmann, J. J., Prior, K. M., & Pelini, S. L. (2012). The influence of species interactions on geographic range change under climate change. *Annals of the New York Academy of Sciences*, 1249, 18–28.
- Huang, E., Chen, Y., Fang, M., Zheng, Y., & Yu, S. (2021). Environmental drivers of plant distributions at global and regional scales. *Global Ecology and Biogeography*, 30, 697–709.
- Jablonski, D., Roy, K., & Valentine, J. W. (2006). Out of the tropics: Evolutionary dynamics of the latitudinal diversity gradient. *Science*, 314(5796), 102–106.
- Jayatilake, D. R. M., & Costello, M. J. (2018). A modelled global distribution of the seagrass biome. *Biological Conservation*, 226, 120–126.
- Kendrick, G. A., Waycott, M., Carruthers, T. J. B., Cambridge, M. L., Hovey, R., Krauss, S. L., Lavery, P. S., Les, D. H., Lowe, R. J., Vidal, O. M., Ooi, J. L., Orth, R. L., Rivers, D. L., Ruiz-Montoya, L., Sinclair, E. L., Statton, J., Van Dijk, J. L., & Verduin, J. J. (2012). The central role of dispersal in the maintenance and persistence of seagrass populations. *Bioscience*, 62, 56–65.
- Larkum, A. W. D., Waycott, M., & Conran, J. G. (2018). Evolution and biogeography of seagrasses. In *Seagrasses of Australia: Structure, Ecology and Conservation* (pp. 3–29). Springer.
- Lee, H., Golicz, A. A., Bayer, P. E., Severn-Ellis, A. A., Chan, C. K. K., Batley, J., ... Edwards, D. (2018). Genomic comparison of two independent seagrass lineages reveals habitat-driven convergent evolution. *Journal of Experimental Botany*, 69, 3689–3702.
- Lenoir, J., & Svenning, J. C. (2015). Climate-related range shifts—a global multidimensional synthesis and new research directions. *Ecography*, 38, 15–28.
- Les, D. H., Cleland, M. A., & Waycott, M. (1997). Phylogenetic studies in alismatidae. II: Evolution of marine angiosperms (seagrasses) and hydrophily. *Systematic Botany*, 22, 443–463.
- Lester, S. E., Ruttenberg, B. I., Gaines, S. D., & Kinlan, B. P. (2007). The relationship between dispersal ability and geographic range size. *Ecology Letters*, 10, 745–758.
- Loveland, T. R., & Merchant, J. M. (2004). Ecoregions and ecoregionalization: Geographical and ecological perspectives. *Environmental Management*, 34, 1–13.
- Macpherson, E., & Duarte, C. M. (1994). Patterns in species richness, size, and latitudinal range of East Atlantic fishes. *Ecography*, 17, 242–248.
- Martínez-Abraín, A., Castejón-Silvo, I., & Roiloa, S. (2022). Foreseeing the future of *Posidonia oceanica* meadows by accounting for the past evolution of the Mediterranean Sea. *ICES Journal of Marine Science*, 79, 2597–2599.
- McKenzie, L. J., Nordlund, L. M., Jones, B. L., Cullen-Unsworth, L. C., Roelfsema, C., & Unsworth, R. K. F. (2020). The global distribution of seagrass meadows. *Environmental Research Letters*, 15, 074041.
- Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'Amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P., & Kassem, K. R. (2001). Terrestrial ecoregions of the world: A new map of life on earth. *Bioscience*, 51, 933–938.
- Pebesma, E. (2018). Simple features for R: Standardized support for spatial vector data. *R Journal*, 10, 439–446.
- Pie, M. R., Divieso, R., Caron, F. S., Siqueira, A. C., Barneche, D. R., & Luiz, O. J. (2021). The evolution of latitudinal ranges in reef-associated fishes: Heritability, limits and inverse Rapoport's rule. *Journal of Biogeography*, 48, 2121–2132.
- Pigot, A. L., & Tobias, J. A. (2013). Species interactions constrain geographic range expansion over evolutionary time. *Ecology Letters*, 16, 330–338.
- Pintor, A. F. V., Schwarzkopf, L., & Krockenberger, A. K. (2015). Rapoport's rule: Do climatic variability gradients shape range extent? *Ecological Monographs*, 85, 643–659.
- Rapoport, E. H. (1982). *Areography: geographical strategies of species*. Pergamon.
- Rock, B. M., & Daru, B. H. (2021). Impediments to understanding seagrasses' response to global change. *Frontiers in Marine Science*, 8, 1–15.
- Rohde, K. (1996). Rapoport's rule is a local phenomenon and cannot explain latitudinal gradients in species diversity. *Biodiversity Letters*, 3, 10–13.
- Rolland, J., Condamine, F. L., Jiguet, F., & Morlon, H. (2014). Faster speciation and reduced extinction in the tropics contribute to the mammalian latitudinal diversity gradient. *PLoS Biology*, 12, 1001775.

- Roy, K., Jablonski, D., Valentine, J. W., & Rosenberg, G. (1998). Marine latitudinal diversity gradients: Tests of causal hypotheses. *Proceedings of the National Academy of Sciences of the United States of America*, 95, 3699–3702.
- Sheth, S. N., Morueta-Holme, N., & Angert, A. L. (2020). Determinants of geographic range size in plants. *New Phytologist*, 226, 650–665.
- Short, F., Carruthers, T., Dennison, W., & Waycott, M. (2007). Global seagrass distribution and diversity: A bioregional model. *Journal of Experimental Marine Biology and Ecology*, 350, 3–20.
- Smith, B. T., Bryson, R. W., Houston, D. D., & Klicka, J. (2012). An asymmetry in niche conservatism contributes to the latitudinal species diversity gradient in New World vertebrates. *Ecology Letters*, 15, 1318–1325.
- Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdaña, Z. A., Finlayson, M., Halpern, B. S., Jorge, M. A., Lombana, A., Lourie, S. A., Martin, K. D., McManus, E., Molnar, J., Recchia, C. A., Robertson, J. (2007). *Marine ecoregions of the World: a bioregionalization of coastal and shelf areas*.
- Stevens, G. C. (1989). The latitudinal gradient in geographical range: How so many species coexist in the tropic. *The American Naturalist*, 133, 240–256.
- Sunday, J. M., Pecl, G. T., Frusher, S., Hobday, A. J., Hill, N., Holbrook, N. J., Edgar, G. J., Stuart-Smith, R., Barret, N., Wernberg, T., Watson, R. A., Smale, D., Fulton, E. A., Slawinski, D., Feng, M., Radford, B. T., Thomson, P. A., & Bates, A. E. (2015). Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecology Letters*, 18, 944–953.
- Tomašových, A., & Jablonski, D. (2017). Decoupling of latitudinal gradients in species and genus geographic range size: A signature of clade range expansion. *Global Ecology and Biogeography*, 26, 288–303.
- Tomašových, A., Jablonski, D., Berke, S. K., Krug, A. Z., & Valentine, J. W. (2015). Nonlinear thermal gradients shape broad-scale patterns in geographic range size and can reverse Rapoport's rule. *Global Ecology and Biogeography*, 24, 157–167.
- Vélez-Juarbe, J. (2014). Ghost of seagrasses past: Using sirenians as a proxy for historical distribution of seagrasses. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 400, 41–49.
- Waycott, M., McMahon, K., & Lavery, P. (2014). *A guide to southern temperate seagrasses* (p. 108). CSIRO Publishing.
- Wernberg, T., Coleman, M. A., Babcock, R. C., Bell, S. Y., Bolton, J. J., Connell, S. D., Hurd, C. L., Johnson, C. R., Marzinelli, E. M., Shears, N. T., Steinberg, P. D., Thomsen, M. S., Vanderklift, M. A., Vergés, A., & Wright, J. T. (2019). Biology and ecology of the globally significant kelp *Ecklonia radiata*. *Oceanography and Marine Biology: An Annual Review*, 57, 265–324.
- Wiens, J. J., Ackerly, D. D., Allen, A. P., Anacker, B. L., Buckley, L. B., Cornell, H. V., Damschen, E. I., Davies, T. J., Grytnes, J. A., Harrison, S. P., Hawkins, B. A., Holt, R. D., McCain, C. M., & Stephens, P. R. (2010). Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters*, 13, 1310–1324.
- Wiens, J. J., & Donoghue, M. J. (2004). Historical biogeography, ecology and species richness. *Trends in Ecology and Evolution*, 19, 639–644.
- Wiens, J. J., & Graham, C. H. (2005). Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics*, 36, 519–539.
- Wissler, L., Codoñer, F. M., Gu, J., Reusch, T. B. H., Olsen, J. L., & Procaccini, G. (2011). Back to the sea twice: Identifying candidate plant genes for molecular evolution to marine life. *BMC Evolutionary Biology*, 11, 8.
- Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society B*, 73, 3–36.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E., & Billups, K. (2001). Trends rhythms and aberrations in global climate 65 ma to present. *Science*, 292, 686–693.

BIOSKETCH

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