Research article

Shallow coverage in shallow waters: the incompleteness of intertidal species inventories in biodiversity database records

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The availability of online biodiversity data has increased in recent decades, aiding our understanding of diversity patterns and species richness–environment relationships across temporal and spatial scales. However, even the most exhaustive databases are prone to sampling biases, which create knowledge gaps in species distributions and increase uncertainty in model predictions. Regarding marine environments, intertidal zones are globally distributed and considered early warning systems for climate change impacts and species' range shifts. Owing to their relative accessibility, intertidal records should – supposedly – be less incomplete and biased compared to open-ocean and deep-sea areas. Yet, the extent and coverage of intertidal records available in global biodiversity databases remains unknown. In this study, we used a high-resolution world-wide tidal flat map to identify intertidal records of 11 563 benthic species from the OBIS (Ocean Biodiversity Information System) portal. Following a thorough data-cleaning process, we evaluated geographic patterns in observed species richness, site accessibility, sampling effort, and inventory completeness across latitudes. We demonstrate that observed species richness has mid-latitudinal peaks while the tropics accumulate species with missing records, similar to patterns described for the entire marine realm. These patterns correlate with disproportionate mid-latitude sampling efforts and poor tropical sampling coverage. Sixty-five percent of the mapped intertidal sites are located within 3 hours of a city, but sampling records remain almost absent along African Atlantic, South American Pacific, and Indo-Pacific coasts. Thus, even for the accessible and well-studied intertidal shorelines, database records are not free from geographical biases and their associated implications for biodiversity estimates. Our results highlight the need for a better data-sharing culture, and we hope to encourage

initiatives promoting more and better-distributed research efforts on intertidal biodiversity, which could improve global scale detection and prediction of climate change impacts at regional and global scales.

Introduction

Over the last several decades, availability of online biodiversity data has increased by orders of magnitude, providing access to millions of occurrence records (Nelson and Ellis 2019), along with genetic, functional, and ecological information across multiple taxonomic groups, from bacteria to vertebrates (Kattge et al. 2011, Benson et al. 2012, Poelen et al. 2014). Free access to globe-spanning biodiversity data offers an unprecedented source of information for describing species distribution patterns across temporal and spatial scales. This effort has driven a dramatic increase in the development and use of species distribution modelling (Elith and Leathwick 2009, Franklin 2010, Ball-Damerow et al. 2019, Heberling et al. 2021), which has contributed significantly to describing the impacts of human activities and climate change on biodiversity patterns, and improved predictions of species extinction and geographic range shifts (Molinos et al. 2016, Levin et al. 2022). The results of such studies can be used to inform stakeholders and rights holders of potential threats to biodiversity, which is essential for companies, agencies, and governments regarding land- and invasive species management, allocation of protected areas, human health, and biodiversity conservation (Gray et al. 2016, Longbottom et al. 2018, Di Marco et al. 2019). For instance, the Global Invasive Species Database (GISD; http://www.iucngisd.org) has been used to pinpoint in which regions native vertebrates are most threatened by invasive species (Bellard et al. 2016), and the Global Biodiversity Information Facility (GBIF; https://www.gbif.org) and the Ocean Biogeographic Information System (OBIS; https://www.obis.org) databases have been used to identify suitable areas for protection (Zhao et al. 2020). Biodiversity databases have supported thousands of scientific publications and play an important role across many different disciplines (Heberling et al. 2021). Given their importance and widespread use, we must remain cognizant of the limitations of the data they contain. A major limitation is that online database records are usually incomplete and spatially biased, with most species' distributions still poorly known (Lomolino 2004, Beck et al. 2014).

Biases in database records are pervasive across taxonomic, temporal, and spatial dimensions. While 2% of species account for more than 50% of the records, a significant proportion of species is represented by only a single record or may have no record at all (Hughes et al. 2021). In some poorly sampled regions, no new records have been registered for decades (Stropp et al. 2016). Moreover, occurrence records are commonly biased towards easily accessible locations, e.g. on land, roadsides, walking paths, and urban areas

(Hughes et al. 2021, Petersen et al. 2021). For instance, in the Arctic, data from terrestrial ecosystems originate primarily from the vicinity of research stations, with areas within 50 km of only two of these stations accounting for 13% of all Arctic sites surveyed (Metcalfe et al. 2018). At a large scale, the majority of marine and terrestrial records are located in mid-latitudinal regions, while the tropics are generally undersampled (Magurran 2017, Menegotto and Rangel 2018, Hughes et al. 2021, Thyrring and Peck 2021). These sampling biases create spatial and temporal gaps in the knowledge of species distributions (Menegotto and Rangel 2018), increasing uncertainty in subsequent distribution models, like those investigating global-scale biotic responses to climate change (Wisz et al. 2015), as well as in other macroecological inferences (Yang et al. 2013).

In the marine realm, where changes in species distribution and biodiversity reorganization have been reported to be faster than in the terrestrial realm (Blowes et al. 2019, Lenoir et al. 2020), sample coverage is notably lower. Consequently, the geographic distribution of most marine species remains uncertain, especially in the tropics (Menegotto and Rangel 2018), a region with severe environmental changes and where the capacity of species to resist changes is among the lowest (Nguyen et al. 2011). More so, distribution records also decrease from the shoreline to the deep sea (Hughes et al. 2021). Thus, while records from shallow waters dominate the global picture of recorded marine biodiversity, less than 10% of records are from abyssal plains, which constitute nearly 50% of the world's oceans by area (Webb et al. 2010). This under-representation is presumably higher for narrow-ranging species, as species with widespread distributions predominate in current catalogues of deep-sea diversity (Higgs and Attrill 2015). Although examinations of deep-sea areas have been steadily increasing, sampling of open- and deep-sea waters is expensive and logistically difficult, which unbalances sampling effort toward large-economy countries (Hughes et al. 2021).

Since differences in infrastructure and funding required to study open waters seems to reduce sample coverage in oceanic areas, database occurrence records from intertidal areas, the most easily accessible marine habitat, should be less affected by such limitations. That is, these records can potentially be more complete, less biased, and more evenly distributed across space. Intertidal ecosystems are renowned for an array of essential ecosystem services – including carbon sequestration, nursery, habitat provision, and shoreline protection (Johnston et al. 2002, Barbier et al. 2011, Donato et al. 2011), that mitigate climate change and support livelihoods. Intertidal ecosystems can also be used as a warning system, or bellwether, for climate change impacts

and range shifts (Gauzens et al. 2020, Mieszkowska et al. 2021, Thyrring et al. 2021) because they are vulnerable to sea-level rise, and intertidal species in low latitude trailing-edge populations usually live close to their upper thermal limits. Compared to subtidal organisms, intertidal species predominantly have inadequate capacity to acclimate to projected future temperature increases (Nguyen et al. 2011), making them highly responsive to small temperature fluctuations (Stillman 2003).

An unbiased and more complete inventory of intertidal biodiversity would be useful, not only to monitor climate change impacts, but also to produce reliable estimates of species diversity and distribution without the sampling constraints present in other marine habitats. The geographic variation in species richness does not seem to be uniformly distributed across all intertidal systems. Rocky shore communities, for example, seem to contradict the classical latitudinal diversity gradient (LDG), where richness peaks in the tropics and declines towards polar areas (Schoch et al. 2006, Griffiths and Waller 2016, Cruz-Motta et al. 2020, Thyrring and Peck 2021, Thyrring and Harley 2024). Conversely, there is evidence of a latitudinal biodiversity cline in tidal flats (Attrill et al. 2001, Vogt et al. 2019). If intertidal database records are indeed unbiased, these data could be used to explore marine diversity patterns and shed light on large-scale trends derived from subtidal records that can be easily interpreted as a by-product of data limitation (Menegotto and Rangel 2018). Yet, the extent of sampling biases and inventory completeness of intertidal records in online biodiversity databases remains largely unknown.

In this study, we evaluated the geographic distribution and latitudinal patterns in observed species richness, sampling effort, and inventory completeness of intertidal records available on OBIS, the largest marine biodiversity database. Since the intertidal zone is, by definition, subject to tidal variation, it is nearly impossible to identify its records using bathymetrical proxies. Therefore, to properly link marine records to this habitat, we used here, for the first time, a newly developed high-resolution tidal flat map covering the entire world from 60°S to 60°N (Murray et al. 2019). Following global tidal flats delimitation, we isolated 126 533 intertidal occurrence records consisting of 11 563 benthic species from an initial > 17 million records in the OBIS database. Our results show that despite greater accessibility and relative research facility compared to other marine habitats, the intertidal zone is not free from the same biases observed in the wider marine realm.

Material and methods

Database species-occurrence data and quality control

We retrieved over 17 million records of all taxonomic groups with benthic species from the OBIS database (Supporting information). All records were screened by applying a thorough data filtering (Menegotto and Rangel 2018). Briefly, we removed duplications, records without coordinate information, and records above species level (Supporting information). Scientific names were standardized using the World Register of Marine Species (WoRMS). We used WoRMS to select only species with a benthic adult life stage. To obtain intertidal records, we first selected only records within 1° from the coast (~ 110 km at the equator). This buffer was created using a land polygon derived from 10 m coastline (Natural Earth; https://www.naturalearthdata.com/). Then we used 30 m spatial-resolution tidal flat raster images to identify which occurrences were recorded on intertidal habitats (Murray et al. 2019). Because intertidal habitats are very dynamic and raster images are grouped in 3-year windows (between 1984 and 2016), occurrences were evaluated using maps corresponding to the year of sampling. Records older than 1984 (7.87%) were evaluated using maps from the first 3-year period (1984–1986). All periods were used when the sampling year was unknown (15.73% of the records). The entire process was conducted in R (www.r-project.org), using the packages 'raster' (Hijmans 2020), 'terra' (Hijmans 2023), and 'worrms' (Chamberlain 2019).

Diversity estimates and sample coverage

We calculated the observed species richness, number of latitudinal gaps (i.e. the number of species with missing occurrence records in a latitudinal band within their distribution range; Menegotto and Rangel 2018), number of sampling events, and sample completeness for each 5° latitudinal band. Sampling events, as implemented in our study, include all sampling efforts on a single day at a single unique location (i.e. geographical coordinates). Using the R package 'iNEXT' (Hsieh et al. 2016), sample completeness was computed by sample coverage using the theoretical framework for incidence data, which quantifies the proportion of the total number of incidences belonging to detected species (Chao et al. 2020). To avoid unreliable estimates, sample coverage was computed only for spatial units with more than five sampling events and not composed uniquely by singletons (Kusumoto et al. 2020). We also mapped the spatial distribution of observed species richness, number of sampling events, sample coverage, and the spatial variation in species composition across coastlines by aggregating the intertidal records within 5° resolution grid cells (n=310). To map spatial variation in species composition (β-diversity), we calculated the Simpson pair-wise dissimilarity matrix (β_{sim}) among all neighbour cells in our gridded domain adopting a queen contiguity criterion (i.e. considering all neighbouring cells that share a border or a corner with a focal grid cell). β_{sim} is unaffected by difference in species richness, and is used to describe spatial turnover (Baselga 2010). The turnover associated to each cell was then quantified by averaging the dissimilarity values calculated between the respective cell and its up to eight neighbours, when any neighbouring cell containing intertidal records was available (Melo et al. 2009). Relationships between observed species richness, number of sampling events, sample coverage, and β-diversity were assessed using Pearson's correlation coefficients (r).

In an effort to mitigate the effects of sampling bias and estimate species richness accurately, we standardized the species richness of individual grid cells using the rarefaction and extrapolation technique based on sample coverage (Chao and Jost 2012, Chao et al. 2020). Due to the prevalence of low sample coverage across numerous grid cells (only 47% of the cells allowed estimations at a coverage level equal or superior to 0.75; Results), we implemented the estimations at four sample coverage levels: 0.25, 0.50, 0.75, and 0.90. The latitudinal variation in species richness across different sample coverage levels was assessed by averaging the estimated richness value of the grid cells over 5° latitudinal bands. To examine the modality of the estimated richness distribution, we employed the bimodality coefficient (BC), which indicates whether an empirical distribution leans towards unimodality (BC < 0.55) or bimodality (BC > 0.55; Pfister et al. 2013). Finally, we evaluated the influence of tidal flats' accessibility on sampling effort using the on-ground accessibility map developed by Weiss et al. (2018), which measures the travel time to city centres. Specifically, we standardized the tidal flat map to the same spatial resolution of the accessibility map (~ 1 km) to obtain the estimated travel time to each tidal flat pixel. Then, we tested whether the minimal travel time to access a tidal flat within a grid cell can predict its observed species richness, sampling events, and sample coverage through a linear regression model. Furthermore, we employed a logistic regression model to investigate whether the probability of a grid cell having sufficient data for calculating sample coverage is influenced by the accessibility of the tidal flats.

Results

The intertidal database records were dominated by three phyla: Mollusca (4643 species), Arthropoda (2553 species), and Annelida (1303 species), together constituting 73% of all identified species (Supporting information). From the 126 533 occurrence records, we demonstrate that the observed number of species peaks predominantly at mid-latitudes (Fig. 1a, BC = 0.66; Fig. 2a, BC = 0.72; darker colours indicate higher species richness), coinciding with high richness in Europe, North America, and Oceania, where estimates of hundreds of species within 5° grid cells are reported (Fig. 2a). In contrast, species richness drops between 20°S and 20°N (Fig. 1a). This tropical depression in intertidal species richness corresponds to a high frequency of latitudinal gaps in species range (Fig. 1a), which is consistent for different taxonomic groups (Supporting information), even after searching for the same species on subtidal records (Supporting information). Despite only 17.5% of the investigated species presenting any latitudinal gap through their latitudinal range, 78.6% of all quantified gaps occurred in tropical latitudes. Between 0° and 5°N, for example, we estimated five times more missing than recorded species and almost three times more latitudinal gaps than in latitudes outside the tropics (Supporting information).
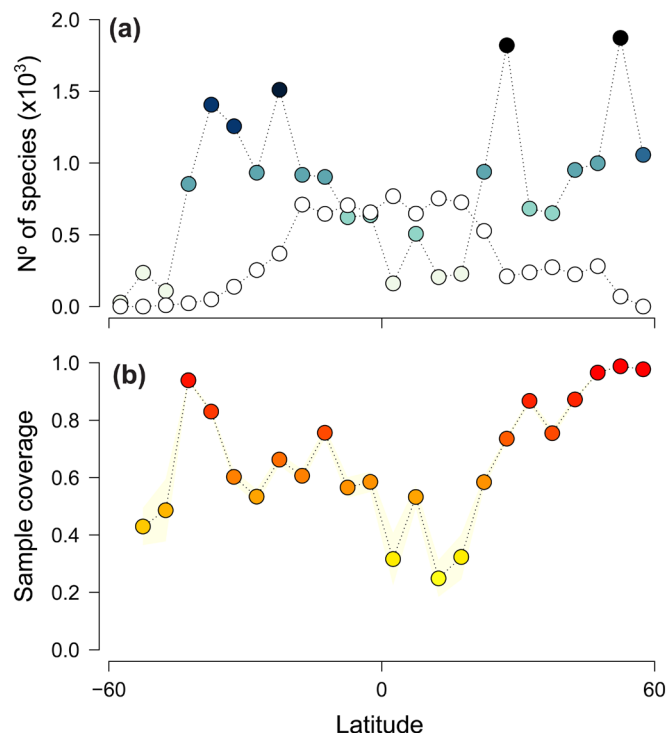

Figure 1. Latitudinal variation in species richness, latitudinal gaps, and sample coverage for intertidal benthic species retrieved from the OBIS biodiversity database. (a) Number of observed species (filled circles) and number of species with a latitudinal gap (empty circles) at each 5° latitudinal band from 60°S to 60°N. (b) Sample coverage of the respective latitudinal bands. Dark (a) and hot (b) colours indicate high values.

The latitudinal distribution of sampling events showed a similar pattern to observed species richness, with peaks in the mid-latitudes (r = 0.81, n_{bands} = 24). However, the number of sampling events was disproportionally high in the Northern Hemisphere (Fig. 3a; darker colours indicate higher values), reaching up to 8228 sampling events between 50 and 55°N (Supporting information). Sampling effort was notably high around Europe, with only four grid cells accounting for 52% of all recorded sampling events (Fig. 2b; darker colours indicate a higher number of sampling events). Tropical latitudes, on the other hand, were poorly sampled despite their larger tidal flat area (Fig. 3a and b; Supporting information). At the equator, where latitudinal gaps peak, we found only 40 unique sampling events (Supporting information). The least sampled regions had the lowest species richness (r = 0.85, n_{cells} = 310) and the lowest sample coverage (r = 0.62, n_{cells} = 134; Fig. 2c; darker colours indicate higher sampling coverage). Not surprisingly, sample coverage was highest in the mid-latitudes, matching latitudinal bands of high sampling effort (r = 0.85, n_{bands} = 23; Fig. 1b).

Most mapped tidal flats (65%) are located within 3 hours of a city centre via surface transport (78.6% < 6 hours; 88.7% < 12 hours; 94.2% < 24 hours), with 90% of all sampling events occurring at these sites. Although grid cells with the closest tidal flat located more than 3 hours away are mainly
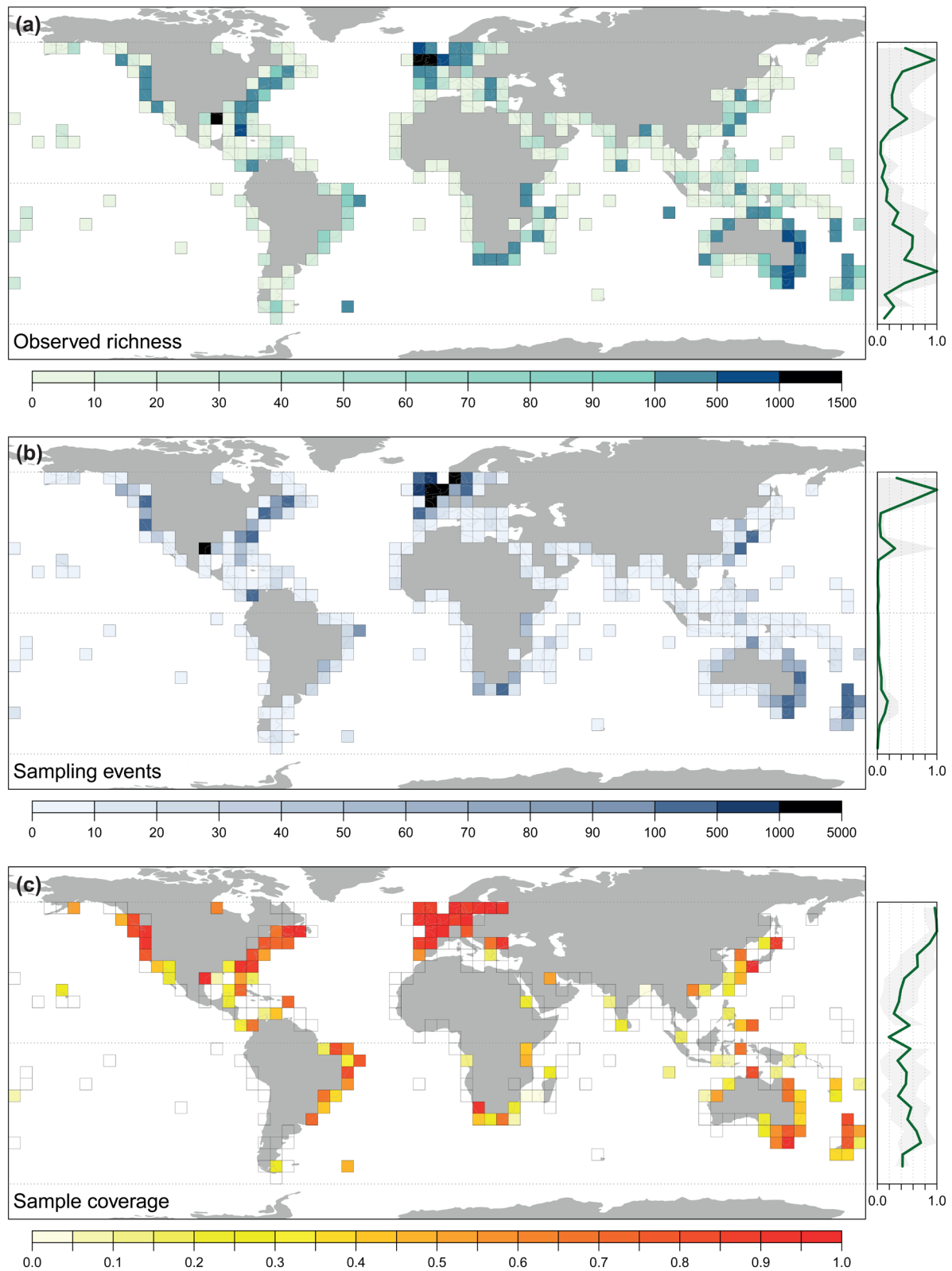
Figure 2. Global distribution maps of intertidal records retrieved from the OBIS biodiversity database. Maps showing the number of observed species (a), the total number of sampling events (b), and the estimated sample coverage (c) within each 5° resolution grid cell (empty grid cells, n = 176, indicate that it was not possible to estimate sample coverage). The subplot on the right presents the average values per latitudinal band (± standard deviation), standardized by the maximum observed value to range between 0 and 1. Note the paucity of sample coverage along the African Atlantic, South American Pacific, and Indo-Pacific coasts.
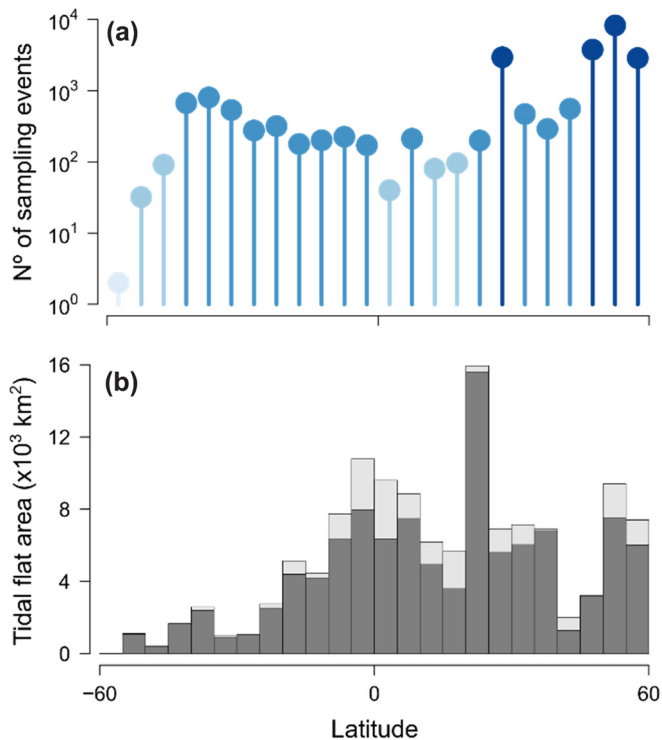
Figure 3. (a) Latitudinal variation in total number of unique sampling events for intertidal benthic species, as retrieved from the OBIS biodiversity database. Dark colours indicate high values. (b) Total tidal flat area across latitude (year 2014–2016). Dark grey colour represents the tidal flat area when considering only those grid cells with any record of intertidal benthic species, as displayed in Fig. 2. The percentage representation of the same estimate is shown in the Supporting information.

present in the tropics and Southern Hemisphere (Supporting information), 79% of all grid cells are highly accessible (i.e. < 3 hours of travel time). The increasing distance of the closest intertidal site to a city centre has a slightly negative effect on species richness ($r^2 = 0.02$, $n_{cells} = 229$; Fig. 4a) and the number of sampling events ($r^2 = 0.04$, $n_{cells} = 229$; Fig. 4b), which affects to some degree the probability of the grid cell having enough data to conduct completeness estimation (pseudo-$r^2 = 0.03$; Fig. 4d). However, for the grid cells with data available, accessibility does not seem to explain the differences in sample coverage ($r^2 < 0.01$, $n_{cells} = 130$; Fig. 4c).

To test whether variation in sample coverage shaped the observed richness pattern, we standardized species richness across grid cells using fixed levels of sample coverage (Supporting information). Estimations at low sample coverage (≤ 0.50) resulted in an asymmetrical distribution, peaking at mid-latitudes in the Southern Hemisphere. However, these latitudinal bands also showed the highest variability among grid cells (Fig. 5a and b). Estimations at high sample coverage (≥ 0.75) increased the bimodality coefficient and the tropical dip (Fig. 5c and d), but this was associated with a notable decrease in the number of cells with enough data to be included, especially in the tropics (Fig. 5e and f). Similar patterns were evident using a species accumulation curve, which indicated that tropical species richness is further from its asymptote than in temperate latitudes (Supporting information).

In addition to species richness, our analysis of global trends in tidal flat β-diversity also revealed a generally high dissimilarity among neighbour grid cells containing intertidal records (Fig. 6). Yet the lowest dissimilarity among cells was observed in cells with a high number of sampling events ($r = -0.64$, $n_{cells} = 293$) and sample coverage ($r = -0.63$, $n_{cells} = 130$), which include North America, Europe, southeast Australia, and New Zealand (Fig. 6).

Discussion

The general perception of a classical latitudinal decline in biodiversity towards the poles has been challenged by discoveries showing an equatorial depression in the distribution of marine species (Keith et al. 2014, Chaudhary et al. 2016, Pamungkas et al. 2021), a pattern that has been suggested to intensify due to detrimental warming in the tropics (Chaudhary et al. 2021). However, evidence indicates that missing occurrence records caused by poor sampling efforts in tropical and remote open seas could also create an artefactual dip in tropical marine biodiversity (Menegotto and Rangel 2018). Owing to the inherent difficulties in reaching open-ocean and deep-sea areas, we analysed different measures of biodiversity and sample effort in the intertidal zone, the most accessible marine habitat, to explore whether this system has less sampling bias and could, therefore, be used to describe more accurately large-scale patterns in marine biodiversity. In agreement with previous works, we found that the distribution of observed species richness derived from the OBIS database exhibits pronounced peaks at mid-latitudes and a dip in the tropics. However, this tropical depression in species richness is (still) associated with a marked peak of latitudinal gaps in species distribution and reduced levels of sample coverage, similar to patterns described for the wider marine realm (Menegotto and Rangel 2018). These results reveal that, even for accessible and well-studied intertidal shorelines, database records are not free from sampling biases and their associated phenomena.

The globally uneven distribution of sampling efforts in the marine realm is widely known (Webb et al. 2010, Menegotto and Rangel 2018, Hughes et al. 2021). Evidence for similar problems in the intertidal zone might not be surprising considering the long history of ecological work in mid-latitudinal regions. In the early 19th century, Jean Victor Audouin and Henri Milne-Edwards studied vertical zonation on the French coast (Audouin and Edwards 1833), inspiring scientists across Europe to use the shoreline for studying distribution patterns and biodiversity (Forbes 1858, Børgesen and Jónsson 1905, Lewis 1964, Stephenson and Stephenson 1972). In North America, early seminal works on rocky shores generated leaps forward in our understanding of species interactions and the processes controlling community and food web structure (Paine 1966, Connell 1972). In addition to
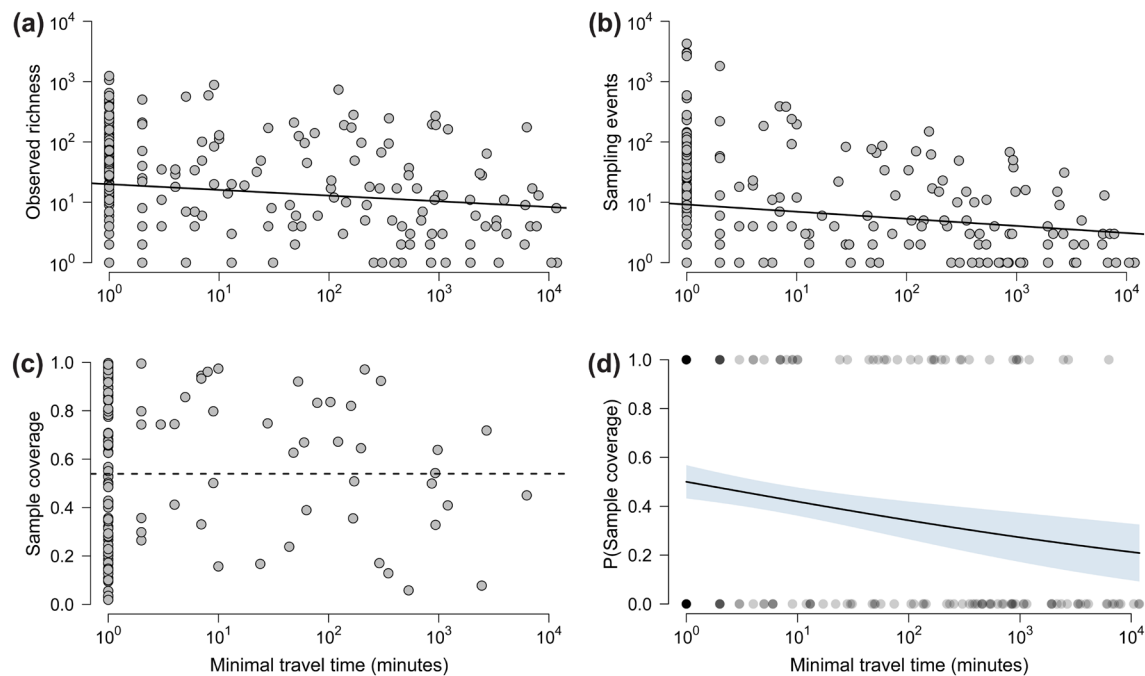
Figure 4. Effect of accessibility variation on tidal flat records. Plots show the effects of accessibility of tidal flats, as measured by the minimal travel time to reach a tidal flat from urban centres, on the observed species richness (a), sampling effort (b), and sample coverage (c). Solid and dashed lines indicate significant and non-significant relationships, respectively ($\alpha = 0.05$). Plot (d) shows the logistic regression between accessibility to city centres and the probability of grid cells having enough data to calculate the sample coverage. Shadow indicates the 95% confidence interval.

the long history of research on intertidal shorelines in Europe and North America, a higher sampling intensity on temperate rocky shores and sandy beaches would also be expected simply by the global distribution of these marine ecosystems, as their area is reduced in tropical latitudes (Luijendijk et al. 2018, Fenberg and Rivadeneira 2019). Tidal flat area, on the other hand, increases in the tropics, rendering differences in sampling effort not justified by area limitation. We were unable to extract intertidal biodiversity data from shorelines above 60 degrees because higher latitude intertidal areas have not yet been mapped (Murray et al. 2019). Although pioneering polar scientists started exploring Arctic shorelines almost a century ago, high latitude shorelines have overall been poorly sampled as they were unreachable and believed sparsely colonised due to detrimental ice scour and extreme sub-zero temperatures (Thorson 1936, Madsen 1940, Ellis 1955). However, thriving communities are present on polar shorelines (Węsławski et al. 2010, Griffiths and Waller 2016, Sejr et al. 2021, Thyrring and Peck 2021, Thyrring et al. 2021), and future studies should investigate how well-represented the polar intertidal communities are in biodiversity databases.

The poor sampling effort in tropical regions, coupled with the correlation between observed species richness and the number of sampling events shown here, indicate that the spatial bias in data availability challenges our capacity to describe global patterns of intertidal biodiversity based solely on database records. Indeed, the database-derived richness pattern seems to contradict results from previous intertidal

biodiversity studies on mud and sandy tidal flats (Attrill et al. 2001, Barboza and Defeo 2015, Thyrring and Harley 2024). Standardizing database species richness by sample coverage also resulted in contrasting latitudinal patterns, depending on the cut-off level used. Including only cells with a high sample coverage increased the bimodal distribution. However, this selection resulted in the exclusion of many cells because species-rich regions require a high sampling effort to achieve high levels of sample coverage (Chao and Jost 2012). Meanwhile, species-poor grid cells have a strong chance of achieving high coverage and being retained in the analysis, so using high coverage cut-off levels may underestimate species richness in some latitudinal bands (for example, latitude −27.5 in Fig. 4a and c).

Different studies have indicated that inventory completeness is positively influenced by accessibility (Ballesteros-Mejia et al. 2013, Herrera-R et al. 2023). According to our estimates, most of the analysed grid cells have easily accessible intertidal sites with less than 3 hours of travel time from a city centre, so that 90% of the intertidal records in OBIS originated from these regions. Yet, our estimations revealed a low sample coverage at tropical latitudes. Assuming that accessibility to intertidal sites might not represent a major barrier to data collection, the under-representation of tropical regions in global biodiversity databases may be driven by factors like less effort in data mobilization. Indeed, differences in accessibility had minimal effect on sampling effort and sample coverage, suggesting that if intertidal data are being collected in these regions, they are not being made
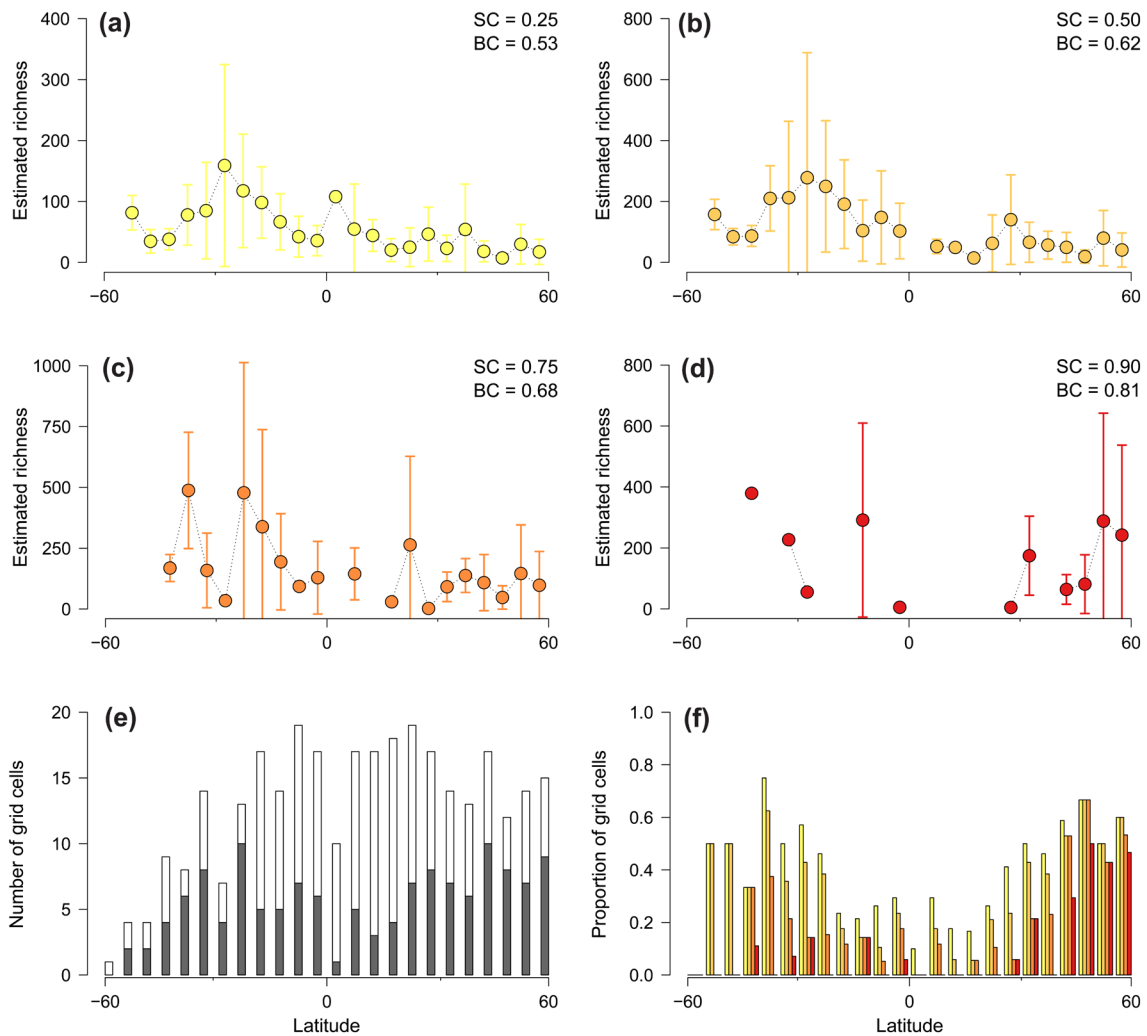
Figure 5. (a–d) Latitudinal variation in estimated species richness for intertidal benthic species retrieved from the OBIS biodiversity database after standardizing the number of species at the 5° grid cell across four levels of sample coverage (SC). Circles and arrows represent mean and standard deviation, respectively. (e) Latitudinal distribution of the number of grid cells with intertidal records, highlighting the fraction of cells with sufficient data to calculate sample coverage (grey). (f) Proportion of grid cells used to calculate the respective sample coverage (yellow = 0.25, dark yellow = 0.50, orange = 0.75, red = 0.90) shown in panels a–d.

adequately available in global databases. An alternative explanation is that, despite accessibility, most regions may not have the experts required to work with the multi-taxa intertidal biota. Collectors are known to restrict most of their sampling activities to areas close to their home institutions (Meyer et al. 2015, Moura et al. 2018), which may result in most intertidal regions not being sampled regardless of their on-ground accessibility. Therefore, providing incentives for sampling expeditions to less explored but accessible areas, and supporting the training of taxonomists across the global south, as well as facilitating the exchange of experts among institutions to encourage researchers to venture beyond their primary research facility, could enhance sampling efforts and the level of sample coverage in this habitat.

The above-mentioned limitations of databases have major implications not only for the description of diversity patterns but also for studies of climate change and geographic range shifts (Wisz et al. 2015). Recent studies have revealed a rapid compositional change in marine communities in response to climate change (Blowes et al. 2019, Burrows et al. 2019), and major changes are projected in a warmer future as species redistribute poleward into sensitive high-latitude ecosystems (Molinos et al. 2016). For instance, in the Antarctic, small experimental temperature increases have resulted in dramatic changes in marine communities because polar marine ectotherms have poor acclimation capacities (Ashton et al. 2017, Clark et al. 2019). In Arctic waters, compositional changes have already occurred (Fossheim et al. 2015), increasing biomass and biodiversity (Węsławski et al. 2010), whilst the changing conditions negatively impact the endemic fauna (Węsławski et al. 2008, Descamps et al. 2017). Standardized quantitative methods are thus increasingly necessary for monitoring marine biodiversity over large spatial scales, as current biases in occurrence records from global biodiversity databases
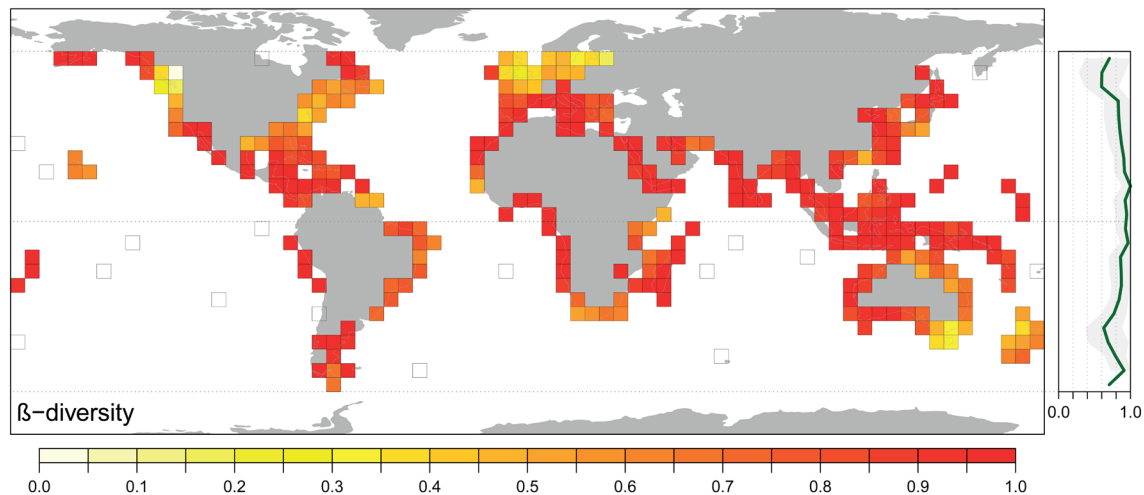
Figure 6. Dissimilarity of intertidal species composition (β-diversity) retrieved from the OBIS biodiversity database across grid cells of 5° resolution. Mapped dissimilarity is calculated by averaging the Simpson pair-wise dissimilarity matrix (β_{sim}) estimated between a focal cell and all its respective adjacent cells containing intertidal records. Empty grid cells (n = 17) indicate that it was not possible to estimate the surrounding dissimilarity. The subplot on the right presents the average values per latitudinal band (± standard deviation), standardized by the maximum observed value to range between 0 and 1.

make them less efficient for, and in some cases incapable of, directly tracking species redistribution (Edgar et al. 2016). Specifically, spatial biases may produce artefactual variation in patterns of species composition, increasing species dissimilarity in less covered areas (Chollett and Robertson 2020). Our results support these findings, revealing an unexpected and generalized high dissimilarity among neighbour grid cells at a 5° resolution associated with low sampling effort and inventory incompleteness, making it almost impossible to distinguish range shifts from previously unrecorded occurrences. This is worrying because alterations to intertidal shore biodiversity have the potential to be used as an early warning system for climate change impacts (Wethey and Woodin 2008). Fortunately, several large-scale standardized monitoring programs have emerged recently, including some programs focused on the intertidal zone (Bernardino et al. 2016, Muelbert et al. 2019, Obst et al. 2020, Montes et al. 2021, Gilbane et al. 2022). While such programs are challenging to maintain and require stable funding (Livore et al. 2021), these initiatives are crucial to advancing our understanding of the impacts of sea level rise and climate change on marine biodiversity.

In conclusion, biodiversity databases provide unique platforms that underpin current efforts to understand large-scale biogeography and biodiversity patterns. However, our study demonstrates that even for intertidal shorelines, the most easily accessible and inexpensive marine ecosystem to survey, notable gaps still exist. Considering the relative ease of sampling tidal flats, we speculate that this data shortage may occur due to an uneven distribution of taxonomic specialists to identify the diverse organisms that compose benthic communities, which will naturally result in occurrence gaps across the globe in most, if not all, marine environments. Reduced data availability may also indicate a poor data sharing or mobilization culture, at least regarding well-studied taxa.

By highlighting these coverage gaps, we hope to encourage initiatives that promote more and better-distributed research efforts to collect and mobilise occurrence information as well as long-term network monitoring programs in the marine realm. Indeed, intertidal ecosystems can offer a starting point to increase the data availability for under-represented regions, and reduce the current substantial uncertainty in the distribution of data-limited species, steps that are essential in order to understand the impacts of climate change at regional and global scales.

Author contributions

Jakob Thyrring: Conceptualization (equal); Writing – original draft (lead); Writing – review and editing (equal). **Lloyd S. Peck**: Conceptualization (supporting); Writing – review

and editing (equal). **Mikael K. Sejr**: Conceptualization (supporting); Writing – review and editing (equal). **Jan Marcin Węsławski**: Conceptualization (supporting); Writing – review and editing (equal). **Christopher D. G. Harley**: Conceptualization (supporting); Writing – review and editing (equal). **André Menegotto**: Conceptualization (equal); Formal analysis (lead); Methodology (lead); Visualization (lead); Writing – original draft (supporting); Writing – review and editing (equal).

Transparent peer review

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Data availability statement

All occurrence records used in this study are freely available from the Ocean Biogeographic Information System (OBIS; www.iobis.org), and a complete reference list of the data providers can be found in Supporting information. The code needed to replicate the findings of this study is available from the Zenodo Digital Repository: https://doi.org/10.5281/zenodo.13128761 (Thyrring et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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