Drivers of genetic diversity across the marine tree of life

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Why do some species have more genetic diversity than others? This question is one of the greatest remaining mysteries in evolutionary biology, and is particularly urgent in marine species, which are experiencing catastrophic anthropogenic impacts. We address this critical gap by estimating genetic diversity for 93 marine species sampled over 9,000 localities. For each species, we aggregate biotic traits and abiotic geographic data for their ranges. We show that diversity increases with range extent and planktonic dispersal. We hypothesize that these traits increase a species' ability to avoid or recover from bottlenecks, thereby maintaining diversity. Our findings provide insights into the factors interacting to shape genomic variation in the ocean, and offer a predictive framework for understanding marine biodiversity in the face of global change.

Introduction

Why does genetic diversity vary among species? This is a central question in population genetics (*1–4*), and may inform a species' adaptive potential, extinction risk, or conservation priority (*5–8*). Little is known about the factors that predict the observed variation in diversity across species (*9*). Indeed, for most species, we have no estimate of genetic diversity at all.

Understanding what drives variation in genetic diversity within and across species is particularly difficult and urgent in the study of marine biodiversity. Oceans are taxonomically diverse (*10*); how this diversity is generated and maintained in a dynamic, fluid environment, without obvious barriers to gene flow, continues to be a fundamental problem in evolutionary biology (*11–13*). This problem is compounded by the fact that the majority of the ocean is difficult to sample (*14*). Moreover, marine biota exhibit tremendous variation in range size and life history traits that govern connectivity across those ranges (*15*). These biological traits interact with oceanic processes (physical and chemical) to generate spatial patterns of genomic diversity, which in turn feedback to affect speciation and biogeography (*16–18*). There is a critical need to understand and generalize such diversity patterns because oceanic biodiversity is being rapidly affected by climate change (*19–23*) and other anthropogenic threats, including overfishing (*24*), pollution (*25*), disease (*26*), and habitat change.

Species-level genetic diversity is ultimately the outcome of the relative rates of alleles entering and leaving the species gene pool, and is thus controlled by population genetic and ecological processes that affect those rates (*9*), such as the mutation rate, population demography, and selection. Although selection, including linked and background selection, can affect patterns of genetic diversity across the genome (*27, 28*), evidence from both theoretical and empirical studies suggest that selection is unlikely to be the major determinant of genetic diversity across species (*4, 29*). And, while data on mutation rate are rare for most non-model organisms (*30*), previous work suggests that variation in mutation rate alone is also unlikely to explain patterns of genetic diversity across species (*3*).

Population genetic theory offers several hypotheses about the mechanisms by which different factors should increase or decrease genetic diversity within a species. First, the genetic diversity of a population is expected to increase with the census number of reproductive individuals (*31*). Second, for a continuously distributed species, the total amount of genetic diversity is expected to decrease with a species' dispersal ability and increase with its range extent (*32, 33*). Third, bottlenecks, whether local (i.e., confined to a local deme) or range-wide, are expected to decrease a species' genetic diversity (*34, 35*). Therefore, traits that impact a species' population size, structure, and demography, have the potential to drive patterns of genetic diversity across species.

Some specific traits that have been hypothesized to predict genetic diversity include dispersal traits, morphological characteristics, and life history traits (*15, 36, 37*), as well as abiotic factors such as habitat stability and range location (*38–41*). In addition, factors that emerge as a function of the interaction between biotic and abiotic traits, like range size and geographic complexity (*42*), can also influence both recent and historical population demography, and thereby

affect genetic diversity. Understanding why levels of genetic diversity vary within and across species has received considerable attention since the first molecular measurements of genetic variation were made (*43, 44*), but despite these clear theoretical predictions and hypothesized relationships, empirically testing these ideas has proven challenging.

Several factors have hindered empirical progress in understanding drivers of genetic diversity across species. First, quantifying genetic diversity remains difficult, particularly in species for which field sampling is laborious or costly. Estimates made from limited genetic information, such as mitochondrial DNA or microsatellites, might give noisy (*45*) or biased (*46*) estimates of diversity, but generating genomic datasets remains expensive. Second, even with genomic sequence data in hand, there are myriad bioinformatic pipelines and choices used to transform raw sequence data into assembled loci and called genotypes. Each bioinformatic decision point can have large impacts on downstream analyses (*47*). To make meaningful comparisons of genetic diversity, it is therefore vital that the methods used for analyzing sequencing data and subsequently estimating genetic diversity are standardized across species. Finally, in comparative population genetic studies, estimates of genetic diversity are implicitly treated as species-level traits, which requires correcting for phylogenetic non-independence (*48*). Implementing such a phylogenetic correction necessitates an accurate, time-calibrated phylogeny that includes all species under consideration. Our understanding of phylogenetic relationships across the tree of life continues to grow, but many species still lack a branch tip, constraining the scope of comparative population genetic analyses that can be conducted.

Heterogeneity in sampling effort across species, and specifically in the spatial pattern and extent of sampling, poses another hurdle to a comparative analysis of species-level genetic diversity. Because many (if not most) species exhibit a pattern of isolation by distance (*49, 50*) – as well as possible hierarchical or cryptic spatial structure – the geographic extent of sampling may often be a strong predictor of the estimated genetic diversity in a species. Even if sampling effort were standardized, variation in density, dispersal, and recent demography across species could result in biased estimates of a species' genetic diversity (*51*). These factors hinder our ability to accurately quantify genetic diversity within species and test hypotheses about its predictors across species.

In the context of global environmental change and the sixth mass extinction event currently occurring, as well as from a basic science perspective, the ability to determine the effect of different factors on genetic diversity is critical (*52, 53*). Here, we begin to address this by building a predictive framework using a novel, unified, spatially and phylogenetically explicit approach to test hypotheses about drivers of genetic diversity in the sea.

Results

We identified and downloaded all georeferenced, publicly available reduced-representation and whole-genome datasets of marine species present in the International Nucleotide Sequence Database Collaboration as of October 2020. A total of 93 sampled species covered a signif-

icant proportion of the phylogenetic diversity of the eukaryotic tree of life (Fig 1), including representatives from vascular plants, invertebrate animals — including cnidarians, crustaceans, and molluscs — and vertebrate animals, including cartilaginous fishes, mammals, birds, reptiles, and ray-finned fishes. We included as broad a phylogenetic diversity of species as we could in order to maximize the generality of our findings. Starting from raw sequence reads, we filtered, cleaned, and assembled each genetic dataset using multiple parameter combinations, then picked the best using an objective optimality criterion (see Methods). This resulted in a final dataset of 93 species (Figure 1a); each with a mean of: 101 individuals (range: $8-366$), 3.6 million raw sequence reads per individual (range: $0.4-30.1$ million), and 3.7 million aligned nucleotide base pairs (range: $5,800-22.3$ million). The mean number of unique sample localities per dataset was 18 (range: $2-121$). For each georeferenced genomic dataset, we calculated sea-wise distance between all collection locations and estimated pairwise homozygosity (i.e., the probability that a pair of alleles sampled at random from two individuals are the same).

Using these genetic and geographic distances, we then employed the parametric modeling approach introduced by Hancock *et. al* (*54*) to generate an estimate of species-level genetic diversity that is robust to heterogeneity in sampling area and intensity. Briefly, we fit an asymptotic curve to the observed Isolation by Distance (IBD) pattern of pairwise homozygosity (*49, 55*) in each species; the asymptote — a parameter estimated as part of the model-fitting procedure — captures the extrapolated genetic diversity contained within the entire species range, which we refer to as π. This estimate explicitly accommodates patterns of population structure in the genotyped data. Estimates of π varied greatly across species, spanning two orders of magnitude from 3.369×10^{-4} to 3.001×10^{-2}, with a mean of 5.224×10^{-3} (phylogenetically corrected mean: 5.335×10^{-3}) (Figure 1c and S3).

To test hypotheses about what predicts genetic diversity across marine species, we assembled a time-calibrated phylogeny and aggregated biotic trait data as well as abiotic factors for all 93 species in our dataset (Figure 1b). Genetic diversity is affected by species-level characteristics and mechanisms that emerge as the result of the interaction of biotic and abiotic processes, such as effective dispersal ability, reproductive census population size, and the frequency, magnitude, duration, and geography of bottlenecks. These characteristics and mechanisms are difficult to directly observe, so instead we collated biotic and abiotic traits that are hypothesized to affect them. The suite of biotic traits was comprised of body size, egg size, spawning, pelagic larval duration, philopatry, iteroparity, planktotrophy (larval feeding behavior), benthicity (degree of association with seafloor), and planktonicity. Abiotic predictors consisted of mean species' range latitude, the number of ecoregions within the species' range (ecological complexity), and overall range extent. Genetic diversity had significant phylogenetic structure (Pagel's λ=0.697, $p = 0.039$; Blomberg's K=0.098, $p = 0.016$) (*56–58*), although the strength of the correlation between phylogenetic relatedness and similarity in genetic diversity was strongest over the most recent timescales (Figure S4).

Range extent, number of ecoregions, and planktonicity had significant positive effects on species-level genetic diversity (Figure 2 and 3); species with planktonic life stages, as well as species with larger range extents or ranges that included more ecological regions, all had

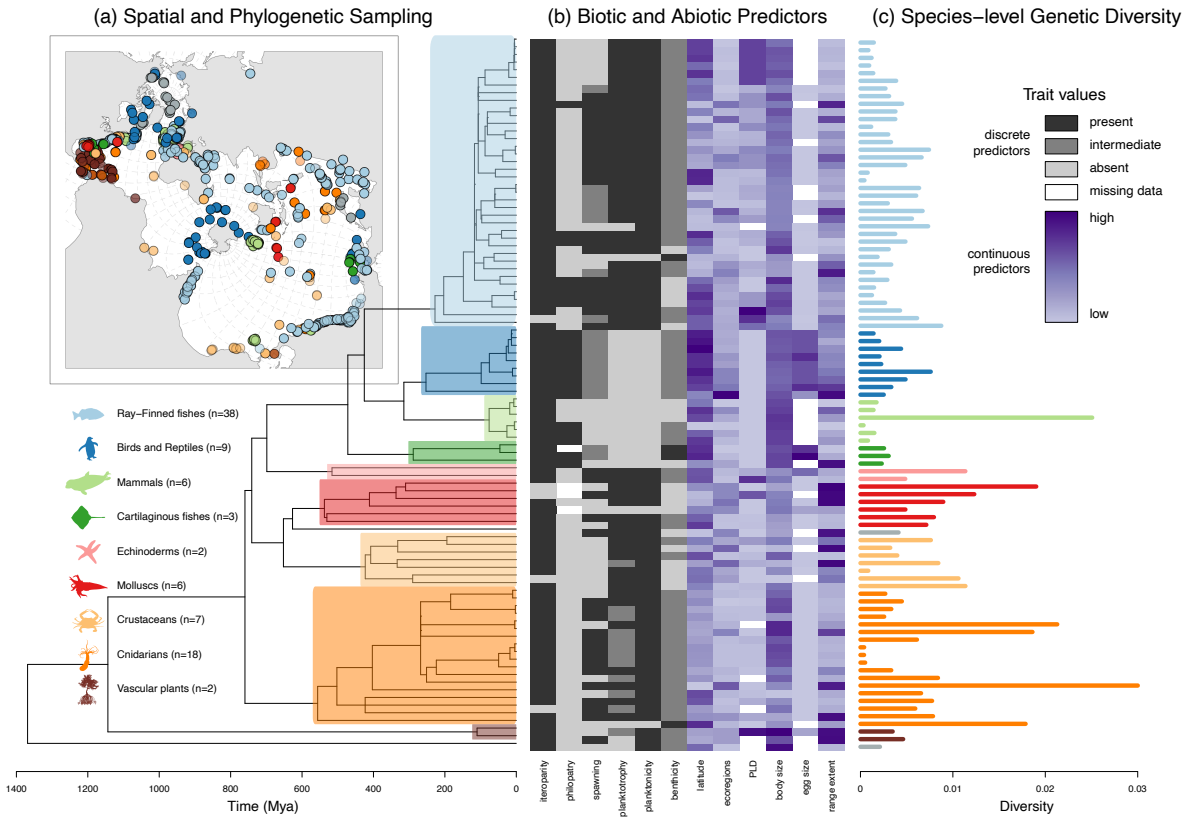

Figure 1: **Species-level genetic diversity varies by orders of magnitude in the world's oceans.** (a) Time-calibrated phylogeny of all species (N = 93) and map of all samples (N = 9,430) included in this study (b) Set of discrete (gray-scale) and continuous (blue-scale) biotic and abiotic predictors collated for each species. Colors represent the trait state or value for each species. (c) Species-level genetic diversity estimated using a spatially explicit model and genomic sequence data.

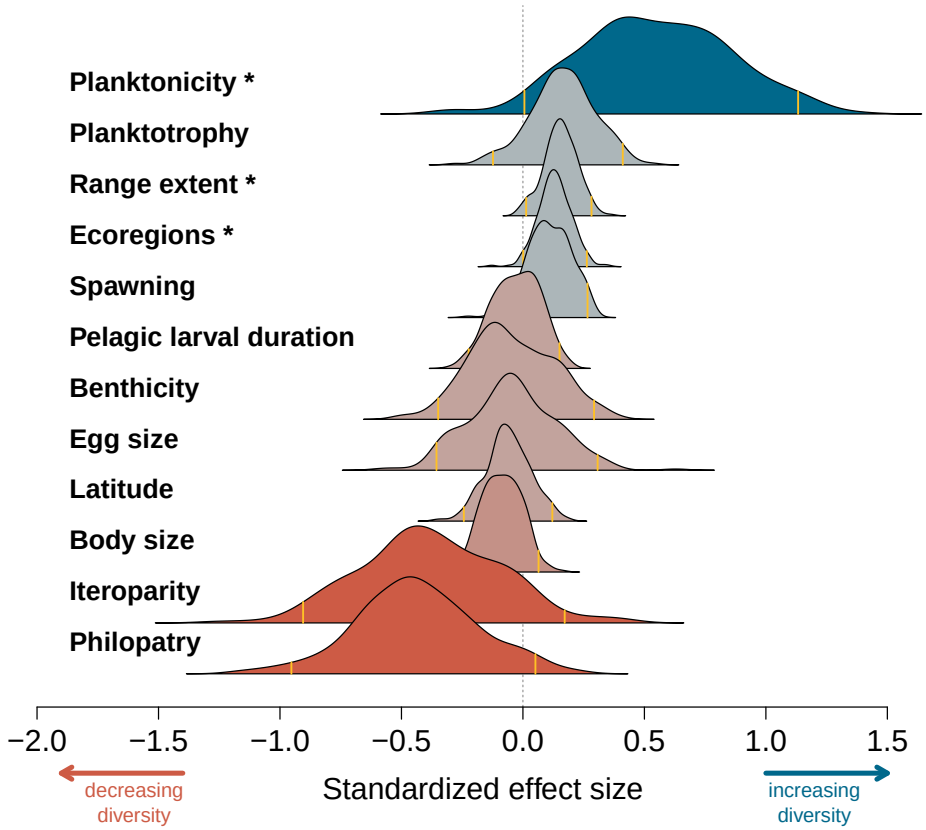

Figure 2: **The estimated effects of biotic and abiotic predictors on species' genetic diversity vary in their magnitude and direction**. Estimated effect sizes (presented via their marginal posterior distributions) are standardized by the standard deviation of their predictor and are ordered from top to bottom by mean effect on species-level genetic diversity. Significant predictors – those for which the 95% equal-tailed credible interval of the marginal distribution of effect sizes did not overlap zero (gray, vertical dashed line) - are denoted with an asterisk.

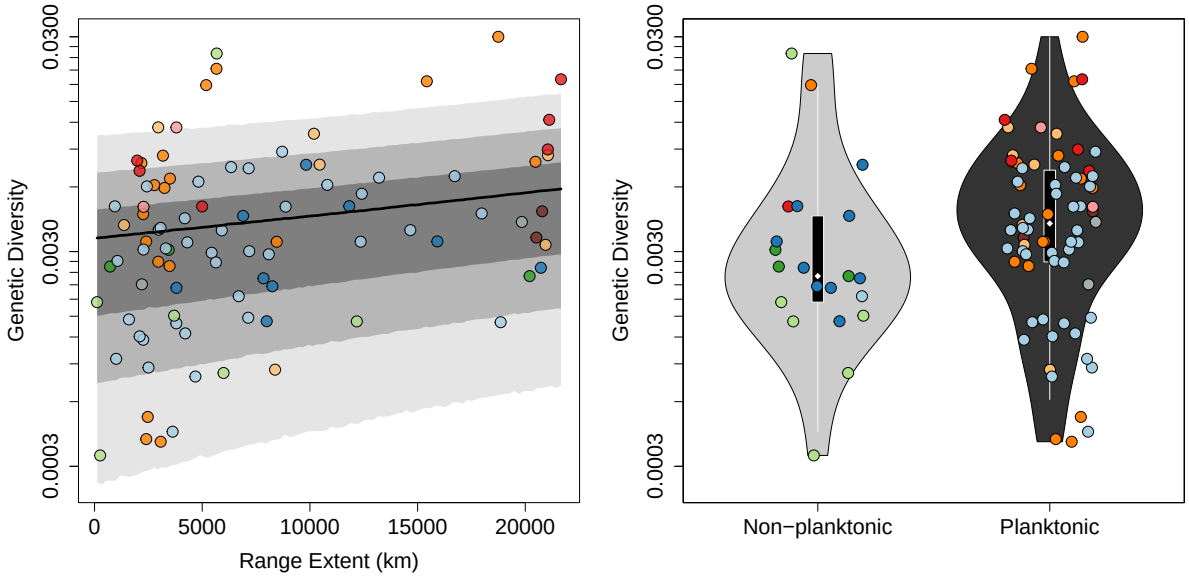

Figure 3: **Species-level genetic diversity is most significantly predicted by species range extent and the presence of a planktonic life stage.** (a) Species with larger range extents have higher genetic diversity. Shaded polygons represent 50%, 80%, and 95% model prediction credible intervals. (b) Species that have at least one planktonic life stage have higher genetic diversity than species that are never planktonic. Each point represents a unique species (N = 93) and is colored by taxonomic clade (as in Figure 1).

higher expected π. Range extent, defined as the greatest overwater distance between any pair of individuals of that species in the Global Biodiversity Information Facility (GBIF) – with filtering to ensure incidental range-edge observations did not inflate this value, had a mean effect of 0.53 (95% CI: 0.06–0.95). Number of ecoregions, defined as the number of ecoregion polygons from Spalding et al. (2007) (*59*) that contained filtered GBIF observation points for that species, had a mean effect of 0.007 (95% CI: -0.0002 – 0.011). Planktonicity, defined as whether the species was planktonic at any point in their life cycle, had a mean effect of 0.560 (95% CI: -0.055–1.17). Planktotrophy and external spawning had a strongly positive estimated effect on genetic diversity, and the effects of body size, iteroparity, and philopatry were strongly negative. However, these effects' credible intervals overlapped 0 and were not inferred to be significant (see Methods), so those results should be interpreted with caution. Range extent and number of ecoregions were highly correlated (Kendall's τ = 0.78; Figure S2), and subsequent analyses (see Methods) suggest that the inferred effect of ecoregions on genetic diversity is at least partially driven by the range extent. Planktonicity and range extent were very weakly correlated (Kendall's τ = -0.05; Figure S2), indicating that the significance levels of their effects are independent.

Discussion

Our analyses reveal enormous variation in the amount of genetic diversity harbored within marine species across the tree of life. Estimates of species-level genetic diversity varied over almost two orders of magnitude. Such variation offers immense opportunity to test hypotheses about what factors predict genetic diversity across species. We found strong phylogenetic signal in genetic diversity, suggesting that diversity may be reasonably predicted in species of known phylogenetic position but lacking population genomic sampling resources. We also found strong evidence that range extent and planktonicity were positively correlated with genetic diversity (Figure 3), in line with previous findings in terrestrial environments (*3*). Unexpectedly, we found that the estimated effects of all dispersal-related traits were in the opposite direction of what is expected from theory; we propose that these relationships reflect the effects of dispersal-related traits on species' capacity to avoid or recover from bottlenecks. Below, we relate the biotic and abiotic traits we collected and their estimated effects on genetic diversity back to the evolutionary mechanisms shaping variation in genetic diversity among species.

Based on population genetic theory, the genetic diversity of a species is expected to increase with its census size of reproductive individuals (*31*). In lieu of estimates of census size, which would be unreliable for the majority of taxa included in our study, we included two factors likely to be correlated with census population size: body size and range extent. Body size is expected to be negatively correlated with census size (*60*) and we find that body size has a negative effect on genetic diversity. Conversely, range extent is expected to be positively correlated with census population size (*61, 62*), and, consistent with predictions from theory, we find a positive effect of range extent on diversity (Figure 2). Although neither body size nor range extent is a perfect predictor of population census size, their mean estimated effect sizes are nonetheless consistent with the predicted effects of census size on diversity.

Range extent is expected to be correlated with census size, and thereby with species-wide genetic diversity, but it can also influence a species' genetic diversity via its impact on spatial population genetic processes. Range extent is expected to be positively correlated with genetic diversity (*32, 33*) because lineages separated by a larger distance must wait longer before coalescing, and the geographic distance between a pair of lineages can be larger in a larger area. Thus, larger ranges increase the expected time to most recent common ancestor of a sample and thereby also increase the amount of standing genetic diversity. Ecological complexity within a range is also expected to increase the overall amount of genetic diversity, as ecological heterogeneity may act as a direct barrier to dispersal or decrease effective migration due to selection against locally maladaptive alleles and linked variation (*63, 64*). However, because the total amount of ecological complexity contained within a range is inextricably linked to the range size (e.g., Figure S2), it is difficult to tease apart the relative contributions of range extent and ecological complexity to total genetic diversity.

Intriguingly, all four dispersal-related traits were estimated to have the opposite of their predicted effects on species-level genetic diversity. Dispersal homogenizes local genetic variation that has arisen due to drift, selection, and mutation; therefore, dispersal is expected to reduce the

overall amount of genetic differentiation in a spatially structured metapopulation (*65*). In lieu of direct estimates of the effective parent-offspring dispersal distance (*66*), we included biological traits related to effective dispersal: planktonicity, planktotrophy, spawning (internal vs. nesting vs. free-floating), and philopatry. Planktonicity, planktotrophy, and more dispersive spawning modes were positively correlated with diversity, while philopatry was negatively correlated. Planktonicity and planktotrophy were strongly correlated with each other (Kendall's τ = 0.76), and both were negatively correlated with philopatry (τ = -0.646 and -0.431 respectively; Figure S2), so it is possible that some of the signal in the estimated effects of these predictors are due to those correlations. Nonetheless, we see no evidence for the prediction, supported by theory, that an increase in dispersal leads to lower levels of genetic diversity within a species.

The associations of dispersal-related traits with a species' ability to recover quickly after a local bottleneck might explain why their estimated effects were the opposite of what is predicted via dispersal's direct effect on diversity. Population bottlenecks will reduce the genetic diversity of a species, to an extent that is determined by their longevity and severity, so species traits that reduce the prevalence or severity of bottlenecks, or that increase the rate of recovery after a bottleneck, are predicted to increase species-level genetic diversity. Predictors associated with higher dispersal (e.g., planktonicity, planktotrophy, dispersive spawning modes) might lead to faster recovery from local bottlenecks, as extirpated demes may be recolonized more quickly if there is greater connectivity among demes (*67, 68*). And, conversely, philopatry, which decreases the connectivity between demes, might lead to slower recovery from local bottlenecks and decreased genetic diversity (*69, 70*).

Other life history traits are also predicted to affect the capacity of a species to recover from a bottleneck, and thereby genetic diversity. In addition to being highly dispersive, species with higher fecundity are also expected to recover more quickly from bottlenecks and thus to harbor more genetic diversity. In their comparative population genomic analysis, Romiguier *et al.* (*3*) found strong support for this hypothesis, with more fecund species harboring more genetic diversity, as well as those species with smaller propagules. Likewise, the multiple reproductive events of iteroparous species may speed their recovery to local bottlenecks, especially bottlenecks resulting from a generation of failed reproduction. In line with these predictions, we found egg size (which is often inversely correlated with fecundity (*71, 72*)) to have a negative inferred effect on diversity and iteroparity a strong positive one.

Lastly, while dispersal and fecundity are expected to affect species' responses to bottlenecks, geographic position may influence how frequently species experience bottlenecks. Populations closer to the equator are hypothesized to experience greater abiotic stability (*73, 74*) and may therefore be subjected to fewer extreme climatic events and associated bottlenecks. In addition, due to their geological history, lower latitude regions have had more similar abiotic environments for longer (*75*). Both patterns have been proposed as explanations for the latitudinal gradient in species diversity (*76*) (but see (*77*)). These hypotheses also suggest predictions for *intra*-specific diversity: namely that genetic diversity should be higher in lower latitudes. Consistent with this prediction, we find that species with lower mean range latitudes have higher genetic diversity.

There are a number of important caveats to our results. First, the lack of information on variation in mutation rate across taxa precluded employing mutation rate as a predictor in our models. However, assuming mutation rate is phylogenetically correlated (*78, 79*), variation in genetic diversity across species due to variation in mutation rate will have been captured by the phylogenetic covariance structure of our regression analyses. Second, we focused on deep evolutionary time, yet the lability of many life history traits can be quite high even within families or genera (*80*). Therefore, we hope to see complementary comparative population genomic analyses that focus on more recent phylogenetic scales. Only a minute subset of marine diversity has been studied intensely enough to support such analyses (*81*), but this will change as large-scale datasets become increasingly available. Finally, though we have controlled for phylogenetic dependence on the associations studied, still greater insights could be gained from removing as much of the phylogenetic effect as possible (*82*).

Conclusions

No single factor explained the majority of variation in genetic diversity across taxa (as in, e.g., (*3*)). Instead, we found two factors that were significantly predictive of genetic diversity in the sea; species with larger range extents had higher genetic diversity, as did species with at least one planktonic life-stage. The effects of other predictors, though not significant, suggest that species traits that facilitate greater resilience to, or quicker recovery from, bottlenecks have higher diversity. Taken together, our work sheds light on the mystery of heterogeneity in genetic variation across species and suggests exciting future avenues of comparative genomic research. Predicting spatial patterns of diversity based on life history traits and spatial distribution represents a significant step forward in both fundamental research and applied conservation.

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METHODS

Locating genomic datasets

We located and downloaded all georeferenced, publicly available, reduced-representation and whole-genome sequence datasets of marine species present in the International Nucleotide Sequence Database Collaboration (INSDC) as of October 2020. We included an additional 48

datasets for which we retrieved sampling coordinates external to INSDC (*53*). We retained datasets that had $\geq$10 georeferenced individuals and $\geq$2 sampled locations (Figure S1). We excluded samples from non-native ranges, freshwater/inland locales, captive or lab populations, quantitative genetic studies, ancient time, pooled genetic sequences, known species hybrids, and salmonids (due to philopatry to freshwater habitats).

Bioinformatic processing of genomic datasets

Starting from the raw sequence reads, we filtered, cleaned, and assembled each genomic dataset *de novo* using a standardized, custom pipeline and Stacks2 (*83*). Post-Stacks, we dropped low coverage individuals (mean number of genotyped and/or co-genotyped base pairs $<$30% of median for dataset) and low coverage loci (scored in $<$50% of remaining individuals). We then used the r80 method to pick the optimal *de novo* assembly for each dataset of nine different standardized Stacks2 parameter combinations tested (*84*); we used the optimal assembly for each dataset (unique species) to estimate species-level genetic diversity.

Estimating species-level genetic diversity

We estimated species-level genetic diversity for each of the 93 species in this study using a Bayesian parameterization of the Wright-Malécot isolation by distance model (IBD) (*54*). This approach allowed us to generate comparable estimates of genetic diversity across datasets that differed in sampling extent (number of individuals, absolute geographic area, and proportion of species' range). We used pairwise homozygosity between sequenced individuals and pairwise sea-wise distances (the distance in kilometers between sampling locations traveling via water and avoiding land) as model inputs. We ran five independent chains of the Wright-Malécot IBD model per dataset and reported results from the chain with the highest mean log posterior probability (5,000 iterations/chain, 2500 iteration burn-in, chains thinned to every 500 iterations). In all downstream analyses, we used an estimate of π (post burn-in mean of the marginal distribution from the best chain) as our species-level estimate of genetic diversity. This parameter is best understood as long-term diversity; it describes the expectation of the maximum genetic divergence between any pair of samples in a species, regardless of where they are sampled in the species range. This quantity is related to the long-term effective population size, and is determined by the species mutation rate, dispersal rate, and the geometry of its range (*33*).

Collecting biotic, abiotic, and phylogenetic predictors

We collected a suite of biotic traits, abiotic traits, and phylogenetic divergence times for all species in the study to test the extent to which they predict species-level genetic diversity. We selected biotic traits hypothesized to influence levels of genetic diversity via their associations with population size and/or dispersal, specifically: iteroparity (whether individuals can mate multiple times before death, or once); philopatry (habitual return to birthplace to mate);

spawning mode (i.e., internal vs. nesting vs. free-floating, which relate to the degree of parent-progeny dispersal); benthicity (degree to which the adult species is associated with the ocean floor); planktonicity (whether the species has a planktonic stage); planktotrophy (larval feeding behavior, which is related to early-life dispersal and r- vs K-selection); pelagic larval duration (PLD - time spent drifting in the plankton); egg size; and body size.

We tested abiotic predictors related to the size and ecological complexity of each species' range, which may influence species-level genetic diversity via associations with population size and levels of genetic divergence. Specifically, we quantified: range extent (maximum linear extent of range); mean range latitude (absolute value of mean latitude of range); and the number of unique ecoregions present within each species' range (Marine Ecoregions of the World (*85*)). We used species occurrence records from the Global Biodiversity Information Facility (GBIF) (*86*) as input for estimating these three abiotic predictors. Finally, we used the January 2022 beta release of TimeTree 5 (*87*) to obtain estimates of the pairwise divergence times between all 93 species in the study. For the 26 species that were not present in TimeTree, we assigned them randomly to a tip within the clade representing the lowest/shallowest taxonomic level possible or formed a polytomy.

Modeling effects of predictors on genetic diversity

We tested for an effect of phylogenetic relatedness on similarity in π using Blomberg's K (*57*) and Pagel's λ (*56*), implemented with the function *phylosig* in the R package *phytools* 2.0 (*58*). We tested for a correlation between phylogenetic relatedness and similarity in π using the R package *phylosignal* 1.3.1 (*88*). We tested hypotheses about the effects of biotic and abiotic predictors on π, using a custom Bayesian phylogenetic multiple regression model with beta-distributed errors (*89*) implemented in Rstan (*90*). To reduce model complexity, avoid issues with multicollinearity, and increase the interpretability of estimated coefficients, we estimated the effect of each biotic and abiotic factor on π one at a time, in each case incorporating a phylogenetic variance-covariance structure (*91*) as well as four technical "nuisance" predictors: (1) number of individuals in the species' dataset; (2) the mean raw read count; (3) the mean read length; and (4) the mean locus depth. By including these nuisance predictors in each analysis and jointly estimating their effects with those of the biotic and abiotic factors in which we are interested, we ensured that technical artifacts are not having a significant impact on the results of this study.

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48 of the genomic datasets included in this study. We are grateful to Bruce Martin for writing code to assist with phylogentic analyses and the Spilhaus map projection. Ricardo Lemos also provided code for implementing the Spilhaus projection. Pat Bills, Yaniv Brandvain, Doc Edge, Steve Goldstein, Morgan Kelly, Katie Lotterhos, Misha Matz, Marjorie Weber, Will Wetzel, Ben Winger, Max Witynski, and members of the Bradburd lab all provided helpful feedback and scientific discussion. Computational work was performed using computational resources and services provided by the Institute for Cyber-Enabled Research at Michigan State University. **Funding**: R. H. T. was supported in part by NSF-OCE 1764316 and the U.S. Department of Agriculture, Forest Service. This research was also supported by the National Institute of General Medical Sciences of the National Institutes of Health (R35GM137919, awarded to G.S.B.). The content of this publication is solely the responsibility of the authors and should not be construed to represent official views of the NSF, NIH, USDOC, NOAA, USDA, or any other government body. **Author contributions**: All authors contributed to conceptualization and writing. R.H.T. and R.S.B. designed the bioinformatics workflow and processed the genomic datasets. E.D.C., C.R., and J.P.W. amassed and curated biotic trait data. J.M.P. and R.H.T. calculated abiotic predictors. G.S.B. conceived of population genetic analyses. R.H.T and G.S.B provided supervision and leadership. We hold the time we had to work with and learn from E. D. Crandall fondly and with gratitude; more about his life and career can be read at https://rcn-ecs.github.io/.

Supplementary Materials for

Drivers of genetic diversity across the marine tree of life

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The PDF file includes:

Supplementary Methods
Supplementary Appendices S1 to S6
Figs. S1 to S5

Supplementary Methods

Locating genomic datasets

We searched the International Nucleotide Sequence Database Collaboration (INSDC) to locate publicly available genomic-level sequence data for marine organisms. We accessed the INSDC from the United States National Center for Biotechnology Information (NCBI) data center using R (*92*) and the *rentrez* R package (v1.2.3, (*93*)). We used the entrez_search function to locate entries in INSDC and entrez_summary and/or entrez_fetch to download the associated metadata. We first identified all non-human, non-viral, non-metagenomic, and non-bacterial datasets (BioProjects) that were focused on DNA sequencing and had publicly available sequence data. Next, we downloaded all metadata for the individuals in each of these datasets from the Sequence Read Archive (SRA) and BioSample databases. We retained sequences with library strategies: WGS, WCS, WGA, RAD-Seq, or OTHER. We then queried the remaining organism names (assigned in the BioSample database) in the World Register of Marine Species (*94*) to identify marine organisms. We used the *worms* R package (v0.2.2, (*95*)) with no fuzzy name matching to execute this query.

We then filtered the remaining potentially marine genomic datasets to those that included at least 10 unique individuals (BioSamples) and 2 unique collection locations (based on the geospatial coordinates provided in the BioSamples database). Finally, we manually dropped samples (or datasets) from non-native ranges, captive or lab populations, quantitative genetic studies, ancient time, and pooled genetic sequences. We also dropped known species hybrids, salmonids (due to philopatry to freshwater habitats), and freshwater/inland samples. In cases where there were multiple genomic datasets for a species, we retained the dataset with the broadest geographic sampling extent (as our goal was to estimate species-level genetic diversity). We manually recovered latitude/longitude from associated scientific publications for 48 datasets that met all of our filtering criteria but lacked spatial coordinates in INSDC (*53*); we dropped those where latitude/longitude were unrecoverable. We performed this search strategy on October 28, 2019 and again on October 19, 2020. See Appendix S1 for the exact search strategy and Appendix S2 for the citations of all 93 genomic datasets used in this study.

Bioinformatic processing of genomic datasets

We started with the raw reads published in the SRA for each relevant dataset, then cleaned, filtered, and assembled them into loci using a standardized bioinformatic pipeline. Applying the same bioinformatic steps to all datasets allowed us to make meaningful comparisons across datasets. Furthermore, many studies associated with the publication of these datasets only published diversity metrics (and/or derived files) for polymorphic loci. As a result, we could not calculate absolute measures of diversity without re-assembling the reads to obtain the number of both polymorphic and nonpolymorphic base pairs sequenced (*96*). The following steps were all performed on the Michigan State Institute for Cyber-Enabled Research High Performance Computing Cluster (https://icer.msu.edu/).

We downloaded raw reads from the SRA using the fasterq-dump function in the SRA Toolkit v2.10.7 (*97*). We treated all paired-end datasets as single-end datasets, retaining all forward reads (regardless of whether they had a reverse pair) and discarding all reverse reads (SRA Tools fasterq-

dump –split-files option). Next, we used the Stacks2 process_radtags module v2.54 (*83*) to remove reads with uncalled bases and/or where the mean Phred score in a sliding window 15% of the read length dropped below 15. After removing low quality reads, we used cutadapt v2.1 (*98*) to search for and remove adapter sequences (e.g. the Illumina common adapter) from the 3' end of reads. See Appendix S3 for the complete list of next-generation sequence adapters that we searched for. Datasets with adapters were easy to identify by the presence of adapter hits in >25% of the reads (compared to ∼5% of reads in clean datasets). About a fifth of the datasets (20 of 93) contained adapters. We confirmed that no adapter sequences remained in cleaned, trimmed reads by running a final adapter search. Lastly, we trimmed all reads to a standardized length within each dataset; *de novo* loci assembly is more robust when all raw reads are a uniform length within each dataset (*83*). For datasets with variable length reads, we selected a uniform read length for each dataset by visually assessing the distribution of read lengths for the dataset and choosing a length that retained long reads in a majority of samples.

We assembled each dataset *de novo* using Stacks2 v2.54 (*83*). For each dataset, we identified a set of optimal assembly parameters following guidelines from (*84*) and (*83*). We used a custom parallel workflow to assemble each dataset with 9 different parameter combinations of *M* (ustacks) and *n* (cstacks): $\{M = 3, n = 2\}$, $\{M = 3, n = 3\}$, $\{M = 3, n = 4\}$, $\{M = 6, n = 5\}$, $\{M = 6, n = 6\}$, $\{M = 6, n = 7\}$, $\{M = 9, n = 8\}$, $\{M = 9, n = 9\}$, and $\{M = 9, n = 10\}$. These are the parameters that most strongly influence assembly behavior (*83*). The *M* parameter controls the number of mismatches allowed between reads within individuals and *n* controls the number of mismatches allowed between loci among individuals. We used default values for all other parameters.

For each assembled dataset and parameter combination, we dropped individuals with a mean number of genotyped and/or co-genotyped base pairs <30% of the median for the dataset (including nonpolymorphic and polymorphic sites). These individuals with few final assembled loci also commonly had few raw reads (suggesting they were poorly sequenced, rather than poorly assembled). We then dropped any loci that were scored in less than 50% of the remaining individuals. We performed this filtering after the populations module using the populations.samples.fa and populations.snps.vcf Stacks output files and custom R scripts. Finally, we selected the assembly parameter combination (of the nine standardized combinations tested) that yielded the highest number of polymorphic loci scored in at least 80% of individuals for each dataset (r80 method, (*84*)). The r80 method has been demonstrated to identify the set of assembly parameters that yield the maximum number of conservatively plausible polymorphic loci for a genomic dataset.

Estimating species-level genetic diversity

Estimates of species-level genetic diversity can be heavily influenced by the number of individuals sampled, where in the species' range those samples are located, and what proportion of the species' range is sampled. Such biases result from spatial genetic structure (i.e., correlations between genetic ancestry and geographic location) within a species' range (*99–101*). To generate unbiased estimates of diversity from datasets with heterogeneous sampling, we used the Bayesian parameterization of the Wright-Malécot model of isolation by distance (IBD) (*49, 55*) implemented in (*54*) for each of the 93 species in our study. Briefly, this method implements the theoretical model of isolation by distance introduced by Wright (*49*) and Malécot (*55*) to describe the decay of genetic relatedness between individuals as an asymptotic function of the geographic

distance separating them. The asymptote – a parameter estimated by the model-fitting procedure – captures the mean maximum genetic divergence between individuals of a species, regardless of their geographic separation (*54*). In Hancock *et al.*, the estimate of the value of this asymptote is designated as collecting phase π, or π_c, in reference to the collecting phase of the spatial coalescent (*33*); for simplicity, we refer to it as π throughout this manuscript. Our estimate of species-level genetic diversity is informative about long-term inbreeding N_e and relatively insensitive to recent demography (*54*). Because this approach explicitly models the rate of isolation-by-distance, our estimates of species-level diversity are robust to both the number of samples and their spatial distribution (and comparable across studies with heterogeneous sampling schemes).

To calculate species-level genetic diversity, the Hancock et al. (*54*) model implementation requires as inputs – a matrix of pairwise homozygosity (identity-by-state) and a corresponding matrix of pairwise geographic distances between genotyped individuals. We calculated pairwise homozygosity as 1-D_{XY} using custom R scripts following (*54*); these scripts accounted for missing genotypes by defining the denominator for D_{XY} as the total number of base pairs co-genotyped for each pair of individuals (within a dataset). We calculated pairwise geographic distance as the distance between each pair of individuals traveling via the sea (avoiding crossing land). We used the National Oceanic and Atmospheric Administration ETOPO1 global bathymetric data with a resolution of 4 arc-minutes (*102*) and the *trans.mat* and *lc.dist* marmap functions of the *marmap* R package v1.0.6 (*103*) to calculate these sea-wise distances. For individuals that fell on land (e.g., near coastlines), we used the *dist2isobath* marmap function with isobath = 0 to relocate each “land point" to the closest point in water. We calculated each sea-wise distance using two resistance matrices (one with longitudes from -180 to 180, the other with longitudes from 0 to 360) and retained the shorter distance.

For each species dataset, we then ran five independent chains of the model in (*54*) for 5,000 iterations each. We discarded the first 2,500 chains as burn-in and sampled the remaining chain ever 500th iteration to reduce autocorrelation. We discarded chains that mixed poorly and identified the single best chain for each species as that with the highest mean log posterior probability. We used the mean of the marginal distribution of π from the best chain for each dataset as our estimate of species-level genetic diversity in downstream analyses.

Collecting biotic, abiotic, and phylogenetic predictors

Biotic predictors We focused on nine biotic traits related to reproduction and dispersal: philopatry, iteroparity, spawning, egg size, benthicity, planktonicity, planktotrophy, pelagic larval duration [PLD], and body size. We selected these traits because they have demonstrated associations with intraspecific spatial genetic diversity and divergence or are expected to be correlated with genetic diversity via their associations with population size and/or dispersal. We defined each discrete trait (i.e., all but PLD, egg size, and body size, which are continuous) as "present", "intermediate", or "absent" for each species (Figure 1).

Specifically, we defined iteroparity as “present" for species that can breed multiple times per lifetime, and “absent" for species that can only breed once. We defined philopatry as “present" for species where individuals return to their natal breeding area to reproduce and “absent" for species that do not perform such migrations. We defined three categories for spawning to capture variation in how far embryos disperse from parents. Embryos can be internally fertilized and remain attached to the parent (“absent"), laid in nests or other benthically attached structures that are often

(but not always) dissociated from the parents ("intermediate"), or free-floating, typically the product of broadcast spawning ("present"). Note this is a distinct life history facet from the presence or absence of planktonic larvae (see below). We defined the trait benthicity to characterize the degree to which species have a relationship with the ocean floor (or other fixed location). Benthicity was "present" for species that maintain a strong connection to the bottom throughout their lifetime (e.g., hydrozoans and anemonefishes that lack planktonic larvae), "absent" for species that are never associated with the bottom (e.g., dolphins that give birth at sea to swimming young), and "intermediate" for species that have both benthic and pelagic life stages (e.g., fish with planktonic larvae and benthic adults). We used planktonicity to distinguish species that have at least one planktonic – floating or drifting – life stage ("present") from those that are never planktonic ("absent").

Planktotrophy is a predictor of the amount of time larvae spend drifting in the water column feeding, which is related to the level of provisioning provided by the egg as well as the capacity for external feeding. We coded planktotrophy as "absent" for species that lack a (planktonic) larval stage and instead develop directly from embryo into young that resemble miniature adults. We coded planktotrophy as "intermediate" for species that produce planktonic larvae that feed on yolk from well-provisioned eggs to facilitate metamorphosis into juveniles (i.e., lecithotrophic larvae); as these larvae are planktonic, they drift in the water column while developing, but develop relatively quickly given the well-provisioned eggs. Lastly, we coded planktotrophy as "present" for species that produce planktonic larvae that must feed on particulates in the water column to fuel metamorphosis into juveniles given they derive from minimally-provisioned eggs (i.e., planktotrophic species); development usually takes longer than planktonic larvae derived from well-provisioned eggs (*104*). We defined pelagic larval duration (PLD) as the mean (or midpoint) number of days that marine larvae spend in the plankton. Finally, we defined egg size as the largest dimension of the egg at hatching (or progeny at birth) and body size as the largest dimension of an adult individual. Extended trait definitions are available in Appendix S4.

When possible, we used trait values reported in FishLifeBase (*105*), SeaLifeBase (*106*), and large compilations (e.g., (*107*) for reef fishes). For most values, however, we performed Boolean searches in Web of Science or Google Scholar (e.g., <species name> AND egg size). We were able to obtain trait values for $> 90\%$ of the species in our study for all traits except egg size (72% coverage across species; Figure S6). All species had values for $> 77\%$ of the nine biotic traits (Figure S7). Full citations for all biotic trait values are listed in Appendix S5.

Abiotic predictors We used three abiotic predictors to characterize the geographic extent and amount of ecological complexity encompassed by each species' range – range extent, mean range latitude, and the number of ecoregions encompassed within the species' range. We estimated these three quantities for each species using species occurrence records from the Global Biodiversity Information Facility (GBIF) (*86*). We first downloaded all GBIF presence records for each species that were not fossils, not managed, and did not have identified geospatial issues using the occ_download() function of the *rgbif* R package (v3.5.0, (*108*)) on September 8, 2021 (see Appendix S6 for exact search parameters and full citations for all downloaded GBIF data). We then visually examined maps of the occurrence records returned for each species and manually removed spatial outliers (that were unlikely to be correctly identified records) and observations within non-native ranges. We used a combination of literature, expert opinion, and published range maps to

decide which additional GBIF occurrence records, if any, to manually drop for each species.

We defined the range extent as the longest axis of the species' range "as the fish swims", that is, traveling via the sea and avoiding crossing land. For each species, we calculated all pairwise "sea-wise distances" between the final, cleaned GBIF occurrence records using the same approach that we employed for the genotyped individuals (see *Estimating species-level genetic diversity*). We then used the value at the 97.5^{th} percentile of the resulting pairwise "sea-wise distance" distance matrix (between species occurrence records) as the final range extent; using the 97.5^{th} percentile minimized the influence of any one individual occurrence record, especially those near the range edges. For computational efficiency, we thinned occurrence datasets that had more than 15,000 points using a raster proportional to the spatial extent of the dataset before generating the pairwise "sea-wise distance" distance matrix.

We defined mean range latitude as the absolute value of the mean latitude of all the final, cleaned GBIF occurrence records for each species. We used original locations in this calculation, (rather than relocating "land points" to the nearest ocean), but mean latitudes were highly correlated between the two approaches (Pearson's $R = 0.98$). We did not include the genetic sample locations in the range extent or distance from equator calculations because they were nested within the spatial extent of, and often duplicated in, the GBIF occurrence records.

Finally, we characterized the amount of ecological complexity contained within each species' range by calculating the total number of unique Marine Ecoregions of the World (MEOW) ecoregions that at least one GBIF occurrence record or genetic sample fell within (*59, 85*). We refer to this predictor as "number of ecoregions". MEOW ecoregions are biogeographic units, developed in large part to facilitate conservation priority setting and planning, whose boundaries reflect synethetic discontinuities in taxonomic assemblages, dominant habitats, ocean currents and temperature, and geomorphological features (*59*). MEOW ecoregions classify coastal and shelf systems, where the majority of (known) marine species diversity resides (*59*). Note, the number of ecoregions was highly correlated with the spatially coarser MEOW realms and provinces as well as the Costello et al. (*109*) (Pearson's R all > 0.87).

Phylogenetic relationships We derived estimates of the pairwise divergence times between all species in the study using the January 2022 beta release of TimeTree 5 (*87*). We first identified species that were present in TimeTree (67/93 species in study). When a focal species was not in TimeTree but other closely related species were (more closely related than any other species in our study, based on published taxonomy), we assigned the focal species randomly to a tip within the clade representing the lowest/shallowest taxonomic level possible (15 species assigned to a representative tip in their genus, 1 species assigned at level of family). This approach is sensible because any tip within the focal clade will give the same divergence time to species outside of the clade, however, it assumes that the oldest species defining the focal clade is present in TimeTree. Divergence times for focal species in clades where this assumption is not met will be upwardly biased. Ten focal species were missing from TimeTree and shared a clade with other species in this study (meaning we could not assign them to a random tip within the clade). For 3 of these 10 species, we were able to identify the most closely related species present in TimeTree (using published literature) and use this tip. For the remaining 7 species absent from TimeTree, we added a tip to the tree that formed a polytomy with the lowest taxonomic level of classification present in TimeTree.

Modeling effects of predictors on genetic diversity

To test hypotheses about the effects of biotic and abiotic predictors on π, we used a custom Bayesian phylogenetic multiple regression model with Beta-distributed errors (*89*) implemented in Rstan v2.32.3 (*90*). Specifically, we used the mean/precision parameterization of the Beta distribution shown below:

$$\pi \sim \text{Beta}(a, b) \tag{1}$$

$$a = \mu \times \phi \tag{2}$$

$$b = (1 - \mu) \times \phi \tag{3}$$

$$\mu_i = \frac{1}{1 + \exp(-\theta_i)} \tag{4}$$

$$\vec{\theta} \sim \mathcal{N}\left(\gamma + \sum_M \beta_m \vec{X}_m \ , \ \alpha\Psi\right) \tag{5}$$

where a and b are the shape parameters of the Beta distribution, and μ and ϕ function as the mean and precision. The mean of the Beta distribution, μ, is given by the inverse-logit transformed parameter θ, which is modeled as a draw from a multivariate normal distribution. The mean of that multivariate normal distribution is given by the expression $\gamma + \sum_M \beta_m \vec{X}_m$, where γ is a global mean of θ, M is the number of predictor variables, $\vec{X}_m$ is the vector of predictor variable values for the mth predictor, and β_m is the effect size of the mth predictor. The covariance of the multivariate normal distribution on θ is given by $\alpha\Psi$, where Ψ is a phylogenetic correlation matrix (i.e. a phylogenetic variance-covariance matrix scaled so that all values fall between 0 and 1), and α is the estimated Brownian rate parameter (i.e. the macroevolutionary heritability) (*91*). We generated the phylogenetic variance-covariance matrix from our ultrametric phylogeny using the R package *ape* v5.0 (*110*).

The priors on our parameters were: $\alpha \sim \mathcal{N}(0, 10)$, $\phi \sim \text{Exp}(\mathbb{V}[\pi], 10)$, $\gamma \sim \mathcal{N}(\log(\mathbb{E}[\pi]/(1 - \mathbb{E}[\pi])), 10)$, and $\beta \sim \mathcal{N}(0, 10)$, where $\mathbb{V}[\pi]$ and $\mathbb{E}[\pi]$ denote the empirical variance and mean, respectively, of observed π across species. Each model contained one focal predictor of interest, the phylogenetic variance-covariance matrix, and four nuisance predictors (number of individuals in the species dataset; the mean raw read count; the mean read length; and the mean locus depth).

For each model, we included all species that were scored for the focal trait of interest (excluding species with missing data or for which the trait was not applicable). We ran each MCMC chain for 20,000 iterations, discarding the first half of the iterations as burn-in and thinning the remaining samples by retaining every 40th iteration. We assessed model convergence by examining parameter trace plots, marginal distributions, and joint marginal distributions. For each predictor discussed in the text, we report the 95% equal-tailed credible interval from the thinned, burned-in marginal distribution.

We assessed the significance of each parameter by determining whether the 95% equal-tailed credible interval contained the value 0; if it did, the parameter was deemed not significant. To compare effect sizes between predictors, we standardized them by multiplying the estimated effect size by the standard deviation of the predictor. In order to evaluate model adequacy (i.e., the ability of our model to describe the data), we used posterior predictive sampling (*111*). For each model

run, we randomly sampled 500 MCMC iterations, with replacement, from the burned-in, thinned, posterior distribution. For each sampled iteration, we recorded the estimated parameter values for the shape parameters of the Beta distribution used to model our response variable a and b. We then simulated draws from a Beta distribution parameterized by a_i and b_i for sampled iteration i. Those posterior predicted values of π were compared to the observed value of π for each species to determine whether the model as a whole was effectively capturing patterns in the data, as well as to determine whether diversity for specific species was well or poorly predicted by our model (Figure S5).

Because range extent and number of ecoregions were both significant predictors of genetic diversity (Figure 2), but were also highly correlated (Fig S2), we ran an additional analysis to try to get closer to ascertaining causality. Number of ecoregions is necessarily correlated with range extent, so we were concerned that the significance of ecoregions was being driven by its correlation with range extant. To test whether this suspicion was correct, we analyzed diversity as a function of number of ecoregions *per* unit range extent. The mean estimated effect size of this hybrid predictor was -0.003, with a 95% equal-tailed posterior credible interval of -0.0072 – 0.0003 which was not significantly different from zero. As a result, we cannot conclusively rule out the possibility that the effect of ecoregions on diversity is entirely being driven by the correlation of ecoregions with range extent, and we thus drop ecoregions from further investigation.

Table 1: Biotic and abiotic predictors of species-level genetic diversity included in analysis. “Trait values" describes the range of possible values species could have for each predictor. “Significant" describes whether the effect size of the predictor was inferred to be significantly different from zero. The final column gives the mean (unstandardized) effect size of the predictor, as well as the lower and upper bounds of the 95% equal-tailed credible interval of the marginal distribution of the effect size.

Predictor	**Trait values**	**Significant**	**Mean effect (95% CI)**
Benthicity	absent/intermediate/present	no	-4.401e-02 (-3.683e-01 – 2.881e-01)
Body size	continuous	no	-5.366e-02 (-1.588e-01 – 4.708e-02)
Ecoregions	integer	yes	7.627e-03 (-1.954e-04 – 1.154e-02)
Egg size	continuous	no	4.396e-04 (-1.228e-02 – 9.218e-03)
Iteroparity	absent/present	no	-3.795e-01 (-9.386e-01 – 2.721e-01)
Latitude	continuous	no	-1.066e-03 (-1.302e-02 – 6.846e-03)
Pelagic larval duration	continuous	no	1.314e-03 (-4.466e-03 – 3.453e-03)
Philopatry	absent/present	no	-4.665e-01 (-9.773e-01 – 4.253e-02)
Planktonicity	absent/present	yes	5.625e-01 (-5.532e-02 – 1.169e+00)
Planktotrophy	absent/intermediate/present	no	1.650e-01 (-9.903e-02 – 4.216e-01)
Spawning	absent/intermediate/present	no	1.071e-01 (-7.655e-02 – 2.765e-01)
Range extent	continuous	yes	5.291e-01 (5.943e-02 – 9.515e-01)

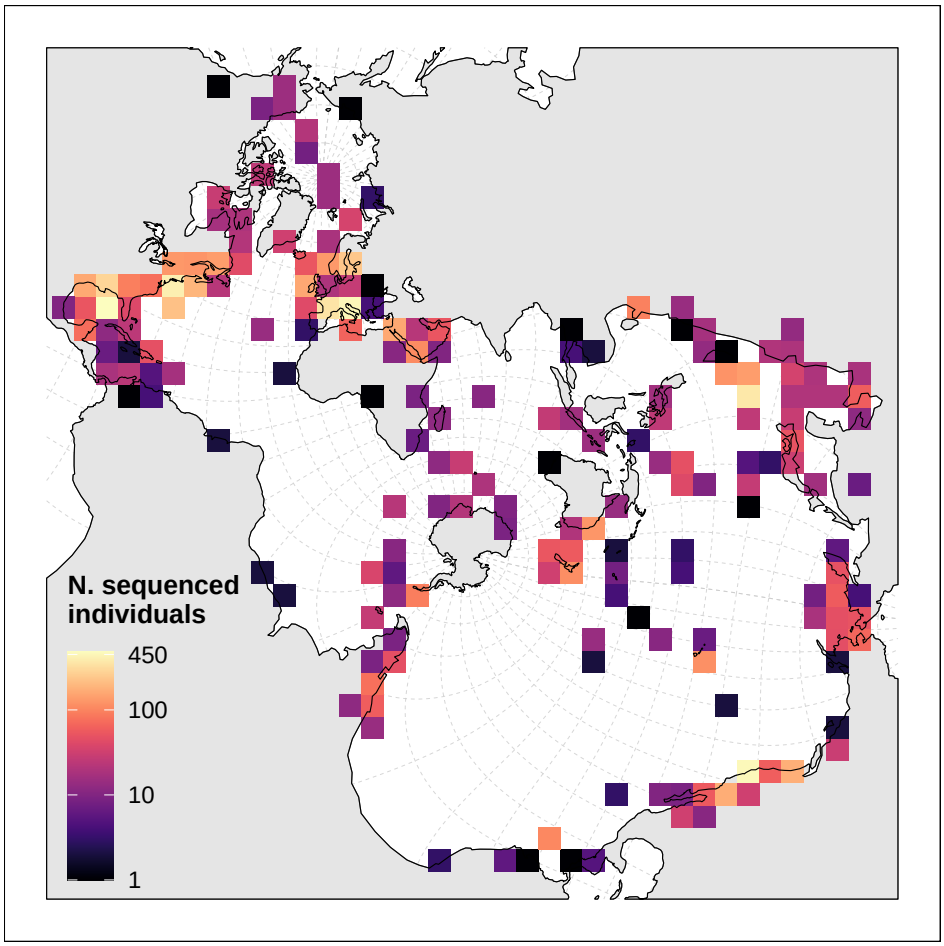

Figure S1: Spatial distribution and sampling intensity of sequenced individual marine organisms included in this study (N = 9,430 total). Colors represent the number of sequenced individuals within each grid square.

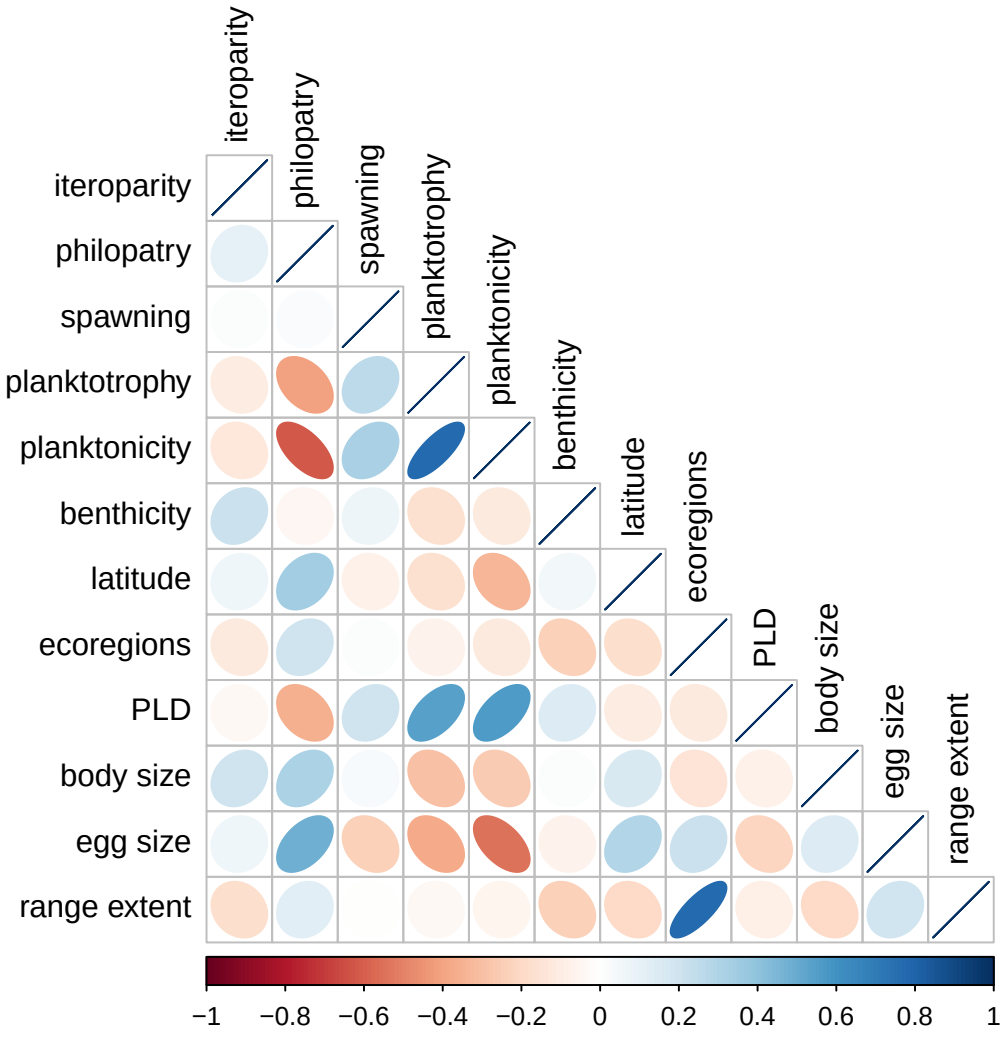

Figure S2: Kendall rank correlations (using pairwise complete observations) between all biotic and abiotic predictors analyzed. Blue and red colors indicate positive and negative correlations, respectively, and color intensity is proportional to the absolute value of the correlation.

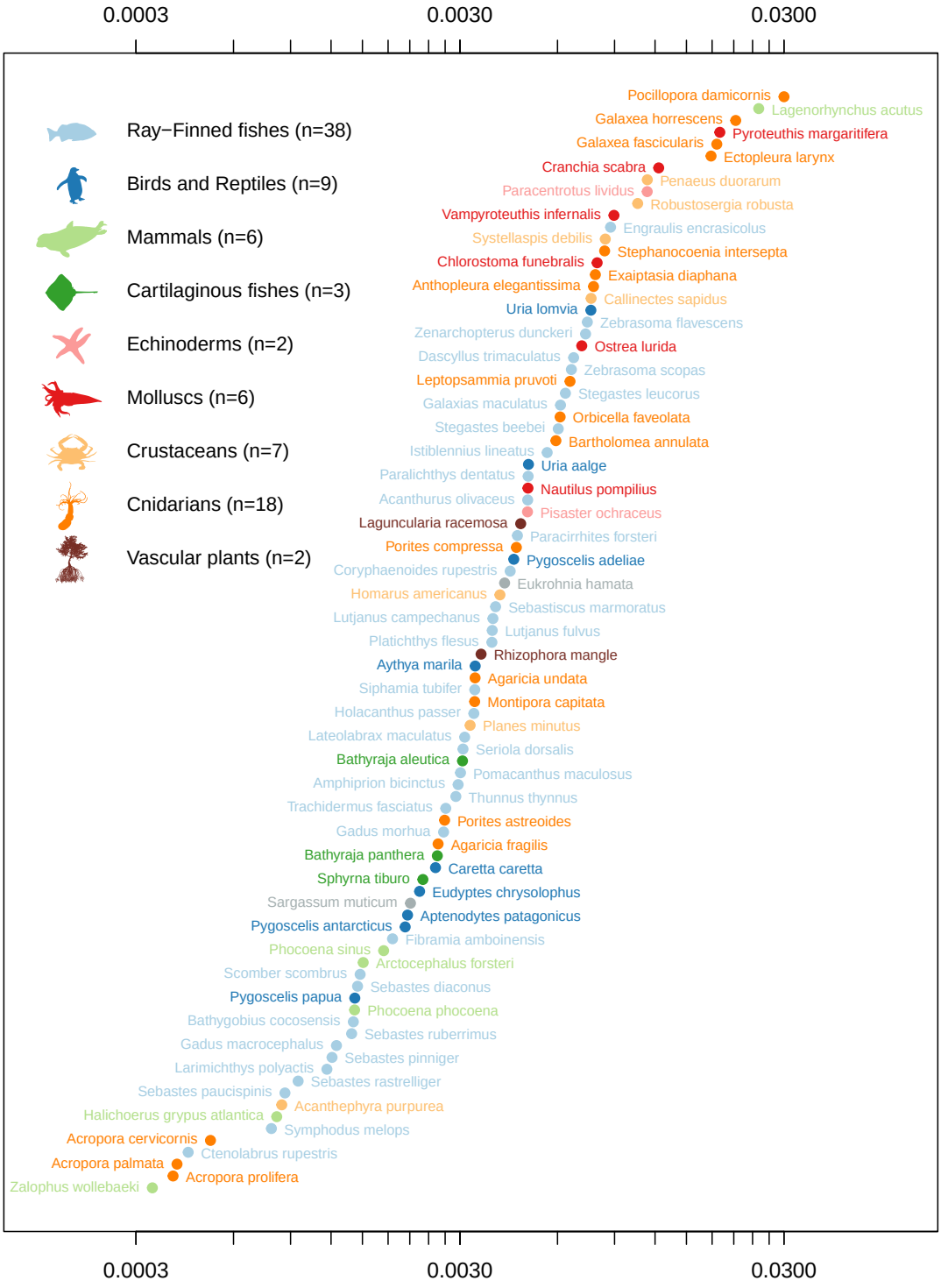

Figure S3: Species-level genetic diversity estimated for each species included in analysis. Species diversity estimates are colored by broad taxonomic group and sorted by value.

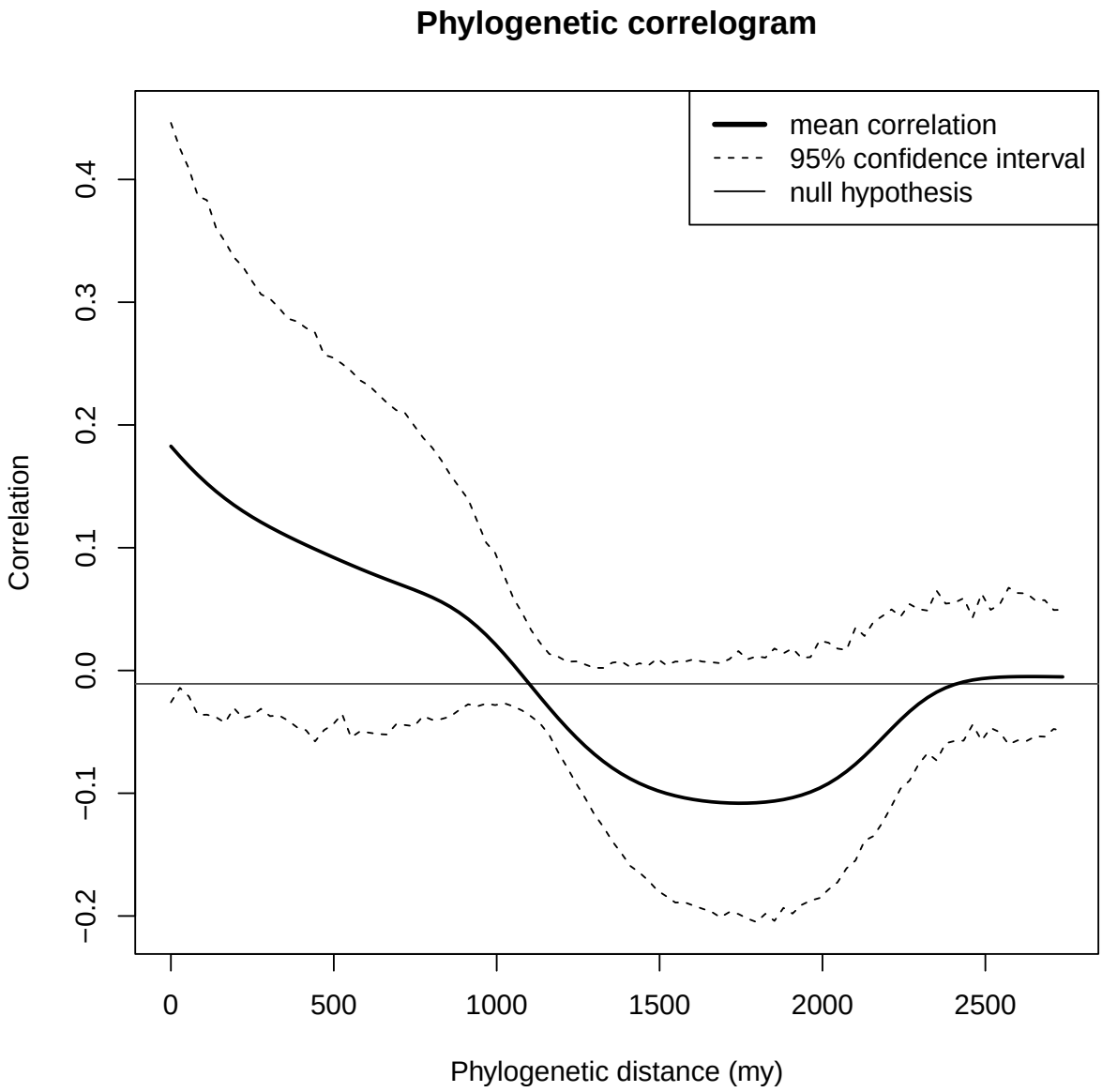

Figure S4: Phylogenetic correlogram showing the estimated correlation between phylogenetic relatedness and species-level genetic diversity at different temporal depths.

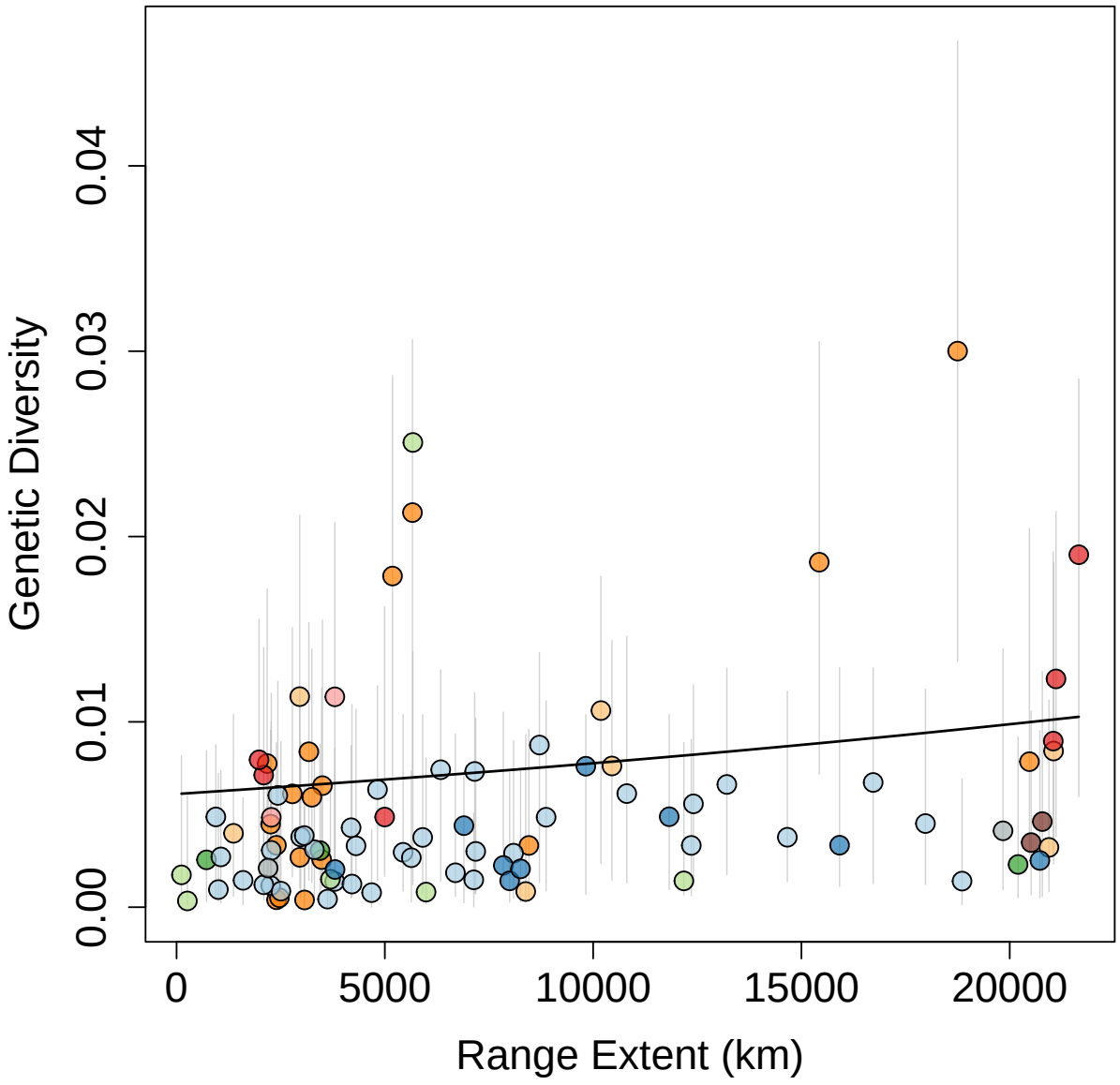

Figure S5: Relationship between range extent and species-level genetic diversity. Points are colored by broad taxonomic group as in Figure 1. Vertical gray lines show the 95% equal-tailed quantile of the posterior predictive distribution of estimates for diversity for each species.

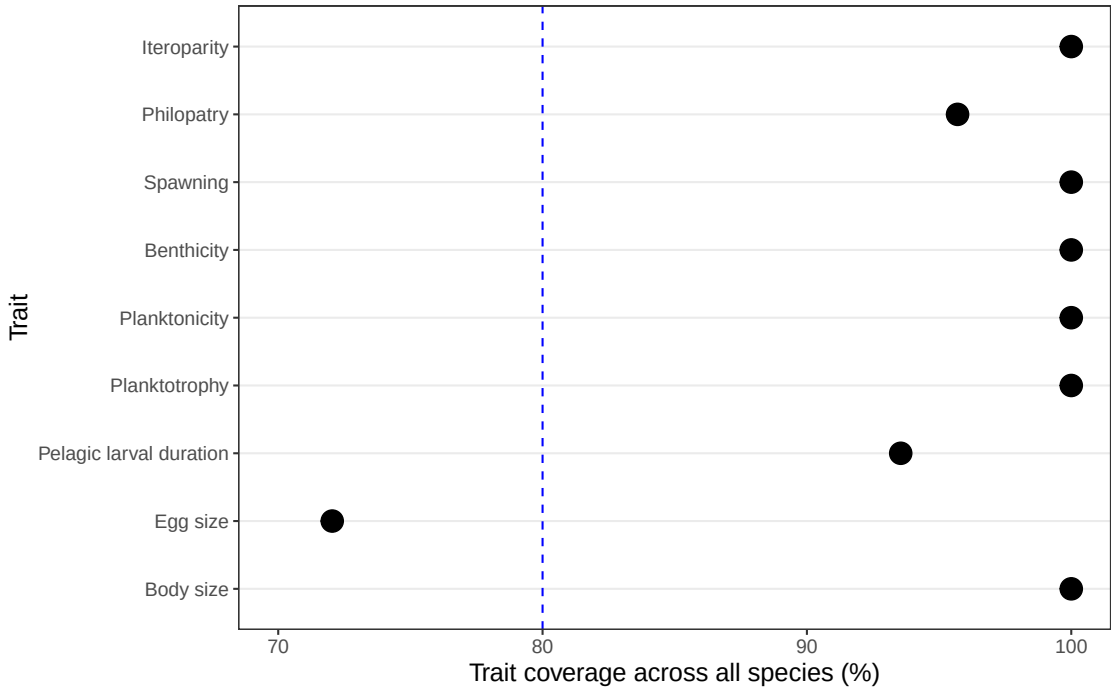

Figure S6: Trait coverage for each of the nine biotic traits included in this study; coverage calculated as a percentage across all 93 species in the study. Note the x-axis starts at 70% (rather than 0). The vertical blue dashed line denotes 80%, a commonly accepted conservative threshold for trait coverage. (Note the three abiotic predictors were available for all datasets in this study.)

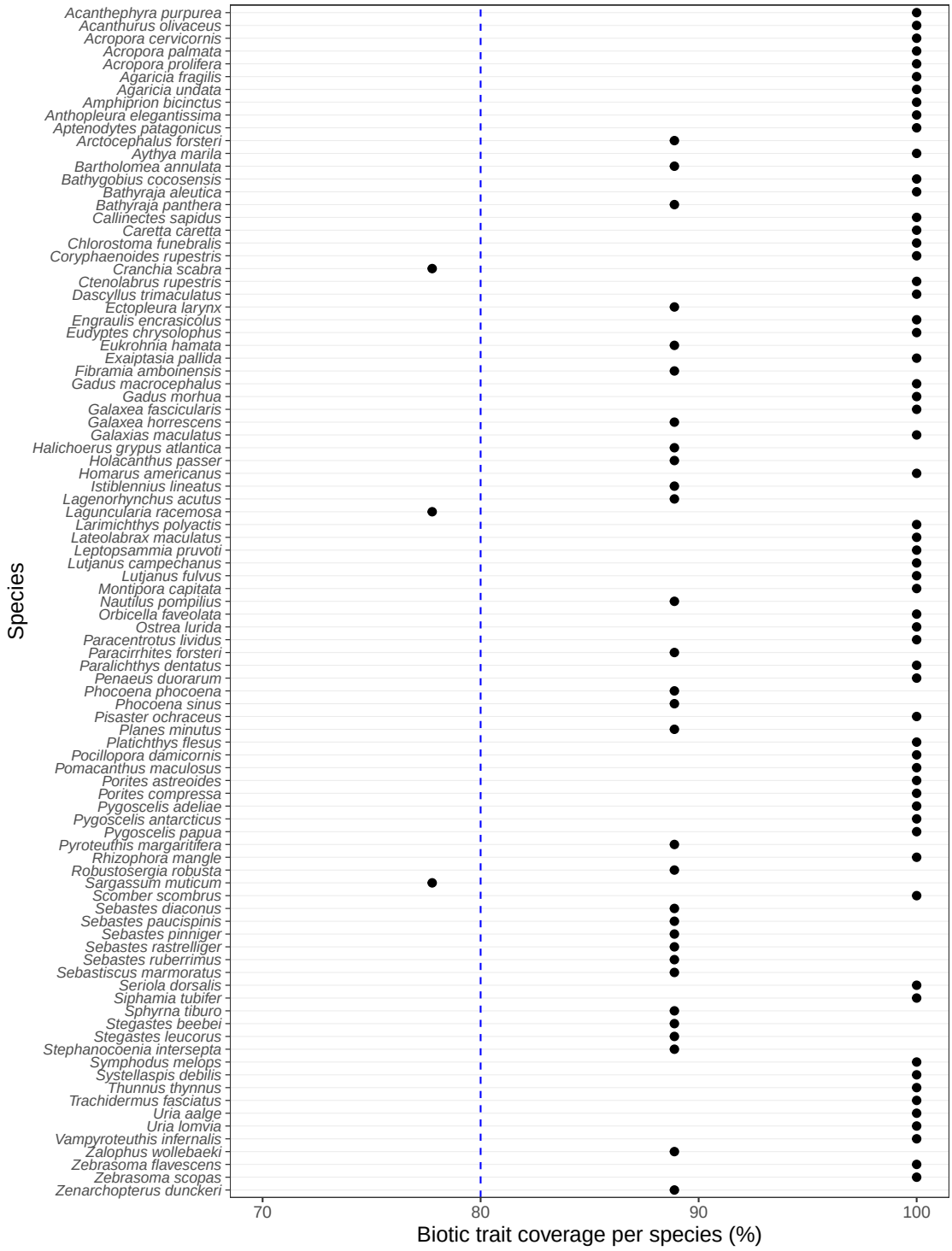

Figure S7: Biotic trait coverage for each species in the study (N = 93) as a percentage. There are nine biotic traits total. Note the x-axis starts at 70% (rather than 0). Species are ordered alphabetically by Latin name. The vertical blue dashed line denotes 80%, a commonly accepted conservative threshold for trait coverage.

Appendix S1: Search strategy used to locate relevant genomic datasets in the INSDC

This appendix details the search strategy that we used to locate relevant genomic datasets in the International Nucleotide Sequence Database Collaboration (INSDC). Note that we accessed the INSDC from the North American portal – the National Center for Biotechnology Information (NCBI). We list the general types of filters that we applied, in the order we applied them, and the number (and type) of records remaining after each filtering step in our pipeline. We also detail the exact NCBI variable names and values that we used in our search and filtering pipeline to locate genomic datasets. NCBI uses BioProjects to denote a study or dataset, BioSamples to refer to individual organisms sampled, and SRA sequence records to refer to the genetic sequence data derived from a BioSample.

After the final filtering step listed below – passing species names to the World Register of Marine Species – we identified and dropped BioProjects (datasets) with fewer than 10 BioSamples (individuals) and 2 collection locations using R. We then curated the remaining potential datasets by hand. We dropped known species hybrids, salmonids, freshwater/inland samples, samples from locations not part of the native species' range, and samples from ancient time. We also dropped studies that were focused on specific organelles (e.g., chloroplast) and quantitative genetic studies. Final sequence samples were included if they had collection latitude and longitude, the raw FASTA file downloaded without errors, the FASTA sequence files were at the level of sampled individual (not pooled sequencing), and were not outliers with respect to read count.

Overview of filters applied and number of records retained after each filtering step:

⇒ 184,155 total BioProjects in INSDC on 10/19/2020

Search BioProject database for all BioProjects that are:
Non-human, non-viral, non-metagenomic, and non-bacterial
⇒ 32162 BioProjects returned

Remove BioProjects related to:
Gene expression, RefSeq, targeted loci, metagenomic, metabarcoding, exome, microbial
⇒ 19,495 BioProjects retained

Download metadata from the Sequence Read Archive (SRA) for all sequence records in each of the above BioProjects.
⇒ 948,446 SRA sequence records returned

Retain SRA records with library strategies:
WGS, WCS, WGA, RAD-Seq, OTHER
(removing: AMPLICON, ATAC-seq, Bisulfite-Seq, ChIA-PET, ChIP-Seq, CLONE, CLONEEND, CTS, DNase-Hypersensitivity, EST, FAIRE-seq, Hi-C, FINISHING, FL-cDNA, MBD, MeDIP, miRNA-Seq, MNase-Seq, MRE-Seq, ncRNA-Seq, POOLCLONE, RIP-Seq, RNA-Seq, SELEX, Synthetic-Long-Read, Targeted-Capture, TetheredChromatinConformationCapture, Tn-Seq, WXS)
⇒ 523,537 SRA sequence records retained

Merge retained SRA records to the BioProject records using PRJ BioProject accession numbers.
Remove BioProjects that did not return any SRA records matching the above specified library

strategies.

⇒ 7,314 BioProjects retained

Use the NCBI common tree online tool to view all taxonomic IDs assigned to the current list of sequence records. Remove sequences with a taxonomic identification of:

Synthetic, metagenome, unidentified, bacteria, environmental, viral

Download metadata from the BioSample database associated with each of the above sequence records.

⇒ 505,932 SRA sequences from
⇒ 432,400 BioSamples from
⇒ 6,755 BioProjects retained representing
⇒ 18,556 purported species

Retain records with species names present in the World Register of Marine Species (WoRMS).

⇒ 114,865 SRA sequences from
⇒ 100,118 BioSamples from
⇒ 1,336 BioProjects retained representing
⇒ 1,738 purported species

Exact variables and terms used to locate and filter INSDC datasets:

The exact search terms and filters that we used to identify the INSDC datasets analyzed in this publication follow. We use "!=" below to denote "does not equal". Bold headers refer to the NCBI databases, quoted terms denote variables/fields of metadata defined by NCBI within said database, and text beneath quoted terms denotes controlled vocabulary values of the specified variable.

Initial BioProject search:

```
"scope multiisolate"[Filter] OR "scope multispecies"[Filter] OR
"scope other"[Filter] NOT "org human"[Filter] NOT "org archaea"[Filter]
NOT "org viruses"[Filter] NOT "org bacteria"[Filter] NOT "metagenome"[Filter]
NOT "targeted locus loci"[Filter] NOT "clone ends"[Filter]
NOT "metagenomic assembly"[Filter] NOT "transcriptome gene expression"[Filter]
NOT "proteome"[Filter] NOT "epigenomics"[Filter] NOT "exome"[Filter]
NOT "bioproject protein"[Filter] NOT "bioproject gds"[Filter]
NOT "phenotype genotype"[Filter] NOT "metagenome"[All Fields] NOT "map"[Filter]
```

BioProject filters:

```
"project_data_type" !=

RefSeq Transcriptome or Gene expression
Targeted loci cultured
RefSeq Genome
RefSeq Genome sequencing and assembly
RefSeq Other
RefSeq Targeted Locus (Loci)
```

```
"project_target_material" !=
```

```
Phenotype
Proteome
Purified Chromosome
Reagent
Transcriptome
Targeted loci environmental
```

```
"project_target_capture" !=

Clone Ends
Exome
```

```
"organism_name" does not contain:

metagenome
```

```
"project_title" does not contain:

metagenome, Metagenome, Metagenomic, metagenomic, metabarcoding
transcriptome, Transcriptome, Transcriptomic
RNA
16S, 16s, 18S, 18s
CRISPR
gene expression, Gene Expression, Gene expression"
viral
microbiome, Microbiome, microbial, microbiota
bacteria, Bacteria
methylation
Plasmodium falciparum
```

SRA filters:

```
"library_strat" =
RAD-Seq
WCS
WGA
WGS
OTHER
```

```
"scientific_name" !=
metagenome, Metagenome
```

The below taxonomic IDs represent synthetic DNA, environmental DNA, metagenomic DNA, and bacterial DNA that we identified using the NCBI phylogenetic common tree online tool.

```
"taxid" !=
```

```
2293429
1440148
32630
1427524
81077
32644
496923
77133
669196
2282120
668369
727
2590021
28448
272943
2021969
527802
477819
562
227
83333
316407
703612
224308
1229511
1126252
1126251
```

Taxonomy filters:

```
"division" !=
Environmental samples
Bacteria
Viruses
```

BioSample filters:

```
"organism" =
# species returned by
worms::wormsbynames(match = FALSE, marine_only = TRUE)
```

We filtered remaining records to retain BioProjects with at least 10 BioSample IDs and at least two unique georeferenced sampling locations per species/BioProject combination (dataset). Finally, we manually dropped samples (or entire datasets) that were located in non-native areas of the species' ranges, were sampled from captive or lab individuals, and those derived from quantitative genetic studies, ancient time, or pooled genetic sequences. We also dropped known species hybrids, salmonids, and samples collected from freshwater or inland locations.

Appendix S2: Citations for genomic datasets

This appendix contains citations for the scientific papers associated with the genetic sequence data utilized in this study. The BioProject accession number where the genetic data are archived in the National Center for Biotechnology Information (NCBI) is also included with each citation. Note some papers include multiple BioProjects and some genomic datasets (BioProjects) have multiple paper citations.

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Appendix S3: List of sequencing adapters used in sequence read cleaning

Below is a list of all adapter sequences that we searched for on the 3' end of all raw sequence reads downloaded from the International Nucleotide Sequence Database Collaboration. Lines that start with > denote adapter names and the directly succeeding line contains the adapter sequence.

We generated the below list from:
https://github.com/stephenturner/adapters/blob/master/adapters_combined_152_unique.fasta;
FastQC (https://github.com/s-andrews/FastQC/blob/master/Configuration/contaminant_list.txt);
and BBMap (https://github.com/BioInfoTools/BBMap/blob/master/resources/adapters.fa);
all accessed on April 9, 2020.

We removed duplicate adapters among the above sources and merged adapters with highly similar sequences using IUPAC base pair ambiguity (names of merged adapters begin with "MERGED"). Using the program cutadapt, we searched each FASTQ sequence file in our study for each of the below sequences. Datasets that contained adapters were easy to distinguish from those that did not; datasets with adapters returned hits in >25% of the reads per individual compared to <5% of reads per individual in clean datasets. When present, we removed identified adapter sequences from all reads in the dataset. We then performed a final adapter search to ensure no adapters remained in raw reads (i.e., all sequences below returned hits in $\sim$ 5% or fewer of the sequence reads per individual across the dataset).

```
>Adapter1 / aka PhiX_read1_adapter aka the Illumina common adapter
AGATCGGAAGAGCGGTTCAGCAGGAATGCCGAGACCGATCTCGTATGCCGTCTTCTGCTTG
>MERGED-Primers_and_dimers-GROUP
AATGATACGGCGACCACCGAGATCTACACTCTTTCCCTACACGACGCTCTTCCGATCTMRWKMDRMRGMSVSSWYMVVVRBBHWY
VCBVWBWCCSWWCWCGWMKSYCKTCYKMTSYTTG
>MERGED-PCR_Primer1_rc-PhiX_read2_adapter
AGATCGGAAGAGCGTCGTGTAGGGAAAGAGTGTAGATCTCGGTGGTCGCCGTATCATTAAAAAA
>MERGED-Reverse_adapter-1-Reverse_adapter-2
MKRTCKSWWRWRCACACGTCTGAACTCCAGTCACATCACGATCTCGTATGCCGTCTTCTGCTTG
>MERGED-TruSeq_Adapter_Index-GROUP1
GATCGGAAGAGCACACGTCTGAACTCCAGTCACVNBNVNNNATCTCGTATGCCGTCTTCTGCTTG
>MERGED-TruSeq_Adapter_Index-GROUP2
GATCGGAAGAGCACACGTCTGAACTCCAGTCACNNNNNNNTCTCGTATGCCGTCTTCTGCTTG
>MERGED-TruSeq3_IndexedAdapter / PE2_rc-Bisulfite_R1
AGATCGGAAGAGCACACGTCTGAACTCCAGTCAC
>MERGED-ABI_Solid3_Adapter_B-ABI_Solid3_5p_AMP_Primer
CCACTACGCCTCCGCTTTCCTCTCTATGGGCAGTCGGTGAT
>MERGED-Illumina_DpnII_and_NlaIII_Adapters-GROUP
ACAGGTTCAGAGTTCTACAGTCCGACATG
>MERGED-I7_Primer_Nextera_XT-GROUP
CCGAGCCCACGAGACNNNNNNNNATCTCGTATGCCGTCTTCTGCTTG
>MERGED-Clontech_SMARTer_II_A_Oligonucleotide-Clontech_SMART_CDS_Primer_II_A
AAGCAGTGGTATCAACGCAGAGTACT
>MERGED-ABI_Solid3_Adapter_A-ABI_Solid3_3p_AMP_Primer
CTGCCCCGGGTTCCTCATTCTCTCAGCAGCATG
>MERGED-I5_Primer_Nextera_XT-GROUP
GACGCTGCCGACGANNNNNNNNGTGTAGATCTCGGTGGTCGCCGTATCATT
>MERGED-Bisulfite_R2-PE1_rc / TruSeq3_UniversalAdapter
AGATCGGAAGAGCGTCGTGTAGGGAAAGAGTGTA
>MERGED-Nextera_Transposase-GROUP
CTGTCTCTTATACACATCTSHSRBBSSVSDVGVVAGGC
>MERGED-Illumina_PCR_Primer_Index-GROUP
CAAGCAGAAGACGGCATACGAGATNNNNNNGTGACTGGAGTTC
```

```
>PrefixPE_1 / PE1
TACACTCTTTCCCTACACGACGCTCTTCCGATCT
>TruSeq2_PE_r
AGATCGGAAGAGCGGTTCAGCAGGAATGCCGAG
>I5_Adapter_Nextera
CTGATGGCGCGAGGGAGGCGTGTAGATCTCGGTGGTCGCCGTATCATT
>I7_Adapter_Nextera_No_Barcode
CTGAGCGGGCTGGCAAGGCAGACCGATCTCGTATGCCGTCTTCTGCTTG
>Nextera_LMP_Read1_External_Adapter / Illumina Multiplexing Index Sequencing Primer
GATCGGAAGAGCACACGTCTGAACTCCAGTCAC
>Nextera_LMP_Read2_External_Adapter
GATCGGAAGAGCGTCGTGTAGGGAAAGAGTGT
>Stop_Oligo_STP_8
CCACGGGAACGTGGTGGAATTC
>TruSeq2_SE
AGATCGGAAGAGCTCGTATGCCGTCTTCTGCTTG
>PrefixNX_1 / >PrefixNX/2
AGATGTGTATAAGAGACAG
>Illumina_Single_End_Adapter_1
GATCGGAAGAGCTCGTATGCCGTCTTCTGCTTG
>Illumina_Single_End_Adapter_2 / Illumina Single End PCR Primer 2 /
>Illumina DpnII expression Adapter 2
CAAGCAGAAGACGGCATACGAGCTCTTCCGATCT
>Illumina_Single_End_Sequencing_Primer / Illumina Paired End Adapter 1 /
>Illumina Paried End Sequencing Primer 1 / Illumina Multiplexing Adapter 2 /
>Illumina Multiplexing Read1 Sequencing Primer
ACACTCTTTCCCTACACGACGCTCTTCCGATCT
>Illumina_Paired_End_Adapter_2
GATCGGAAGAGCGGTTCAGCAGGAATGCCGAG
>Illumina_Paired_End_PCR_Primer_2 / PrefixPE/2 / PCR_Primer2
CAAGCAGAAGACGGCATACGAGATCGGTCTCGGCATTCCTGCTGAACCGCTCTTCCGATCT
>Illumina_Paired_End_Sequencing_Primer_2
CGGTCTCGGCATTCCTGCTGAACCGCTCTTCCGATCT
>Illumina_DpnII_expression_Adapter_2 / Illumina DpnII expression PCR Primer 1 /
>Illumina NlaIII expression Adapter 2 / Illumina NlaIII expression PCR Primer 1 /
>Illumina Small RNA RT Primer / Illumina DpnII Gex Adapter 2 /
>Illumina DpnII Gex PCR Primer 1 / Illumina NlaIII Gex Adapter 2.01 /
>Illumina NlaIII Gex PCR Primer 1 / Illumina Small RNA PCR Primer 1
CAAGCAGAAGACGGCATACGA
>Illumina_DpnII_expression_PCR_Primer_2 /
>Illumina NlaIII expression PCR Primer 2 / Illumina DpnII Gex PCR Primer 2 /
>Illumina NlaIII Gex PCR Primer 2
AATGATACGGCGACCACCGACAGGTTCAGAGTTCTACAGTCCGA
>Illumina_DpnII_expression_Sequencing_Primer / Illumina DpnII Gex Sequencing Primer
CGACAGGTTCAGAGTTCTACAGTCCGACGATC
>Illumina_NlaIII_expression_Sequencing_Primer / Illumina NlaIII Gex Sequencing Primer
CCGACAGGTTCAGAGTTCTACAGTCCGACATG
>Illumina_Multiplexing_Adapter_1
GATCGGAAGAGCACACGTCT
>Illumina_Multiplexing_PCR_Primer_2_01 / Illumina Multiplexing Read2 Sequencing Primer
GTGACTGGAGTTCAGACGTGTGCTCTTCCGATCT
>Illumina_DpnII_Gex_Adapter_1
GATCGTCGGACTGTAGAACTCTGAAC
>Illumina_DpnII_Gex_Adapter_2_01 / Illumina NlaIII Gex Adapter 2.02
TCGTATGCCGTCTTCTGCTTG
>Illumina_NlaIII_Gex_Adapter_1_01
TCGGACTGTAGAACTCTGAAC
>ABI_Dynabead_EcoP_Oligo
CTGATCTAGAGGTACCGGATCCCAGCAGT
>ABI_Solid3_EF1_alpha_Sense_Primer
CATGTGTGTTGAGAGCTTC
>ABI_Solid3_EF1_alpha_Antisense_Primer
GAAAACCAAAGTGGTCCAC
>ABI_Solid3_GAPDH_Forward_Primer
TTAGCACCCCTGGCCAAGG
>ABI_Solid3_GAPDH_Reverse_Primer
CTTACTCCTTGGAGGCCATG
>Clontech_Universal_Primer_Mix_Short
```

```
CTAATACGACTCACTATAGGGC
>Clontech_Universal_Primer_Mix_Long
CTAATACGACTCACTATAGGGCAAGCAGTGGTATCAACGCAGAGT
>FlowCell2
TTTTTTTTTTCAAGCAGAAGACGGCATACGA
>FlowCell1
TTTTTTTTTTAATGATACGGCGACCACCGAGATCTACAC
>Trans1
TCGTCGGCAGCGTCAGATGTGTATAAGAGACAG
>Trans2
GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAG
```

Appendix S4: Extended definitions and coding of biotic traits

This appendix contains detailed explanations of how we defined the nine biotic traits included in this study. Headers indicate the variable name used in the paper followed parenthetically by the variable name used in archived data files and scripts. Bullet points denote possible values for discrete traits; values after the colon specify the short-hand coding (capital letters) used to record trait data, numerical values represent the dummy numerical values that characters were transformed into for modeling, and bracketed text specifies how discrete traits are shown in Figure 1. See *Supplemental Methods – Collecting biotic, abiotic, and phylogenetic predictors* for a description of how trait values were obtained.

Iteroparity ("Generational_Structure")

This variable captures variability in the number of times an individual can breed in its lifetime. Iteroparous species can breed more than once in their lifetime, whereas semelparous species only breed once.

- Iteroparous: I = 1 [present]
- Semelparous: S = 0 [absent]

Philopatry ("ReturnToSpawningGround")

We defined philopatry as the intentional movement of reproductively mature individuals back to an established spawning or breeding area to reproduce. Species where evidence indicated such migration were coded as TRUE and species lacking such evidence were coded as FALSE. For species that could plausibly have such migratory life histories (i.e., *Bathyraja panthera* and *Pyroteuthis margaritifera*, with large bodied and strong swimming adults with poorly described life histories with related species known to be philopatric), we scored this trait as unknown.

- Philopatric: TRUE = 1 [present]
- Not philopatric: FALSE = 0 [absent]
- Unknown trait state: NA [missing data]

Spawning ("Spawning_mode")

Marine taxa have a wide array of reproductive strategies with respect to fertilization and subsequent embryonic development and parental care. Our primary focus here was on capturing variation in how far embryos disperse from parents. For animals, eggs or developing young can be internally fertilized and then retained in a parents' body or on a parent's body in specialized brooding structures (pouches, chambers, sacs). Alternatively, animals can lay eggs in nests or other benthically attached structures; parents often (but not always) then disassociate from the laid eggs. Finally, many fishes and invertebrates release free floating embryos, typically preceded by broadcast spawning of gametes. We coded all mammals as "I" and all birds as "N"; fishes and invertebrates had a diverse mix of values. For plants and algae, we applied similar logic as for animals and scored species that retain young on the parent as "I".

- Embryos internally fertilized and attached to parents: I = 0 [absent]
- Embryos in a nest or otherwise benthically attached: N = 1 [intermediate]
- Embryos free floating: F = 2 [present]

Benthicity ("isBenthic")

This variable attempts to capture the diversity of relationships between organisms and a fixed location (e.g., for birds this can be nesting sites on land). We considered organisms to be "never" benthic if their entire life cycle was dissociated from any bottom surface (e.g., anchovy that have planktonic larvae and pelagic swimming adults or dolphins that give birth at sea to swimming young). "Sometimes" benthic organisms have a mixture of life stages that are benthic and pelagic, for example many fishes and invertebrates with planktonic larvae and benthic adult stages. "Always" benthic organisms live their entire life with a strong connection to the bottom (such as hydrozoans and anemonefishes that lack planktonic larvae).

- Always: A = 2 [present]
- Sometimes: S = 1 [intermediate]
- Never: N = 0 [absent]

Planktonicity ("isPlanktonic_atanypoint")

We defined planktonicity to capture whether or not species were planktonic – floating or drifting and not able to actively swim against ocean currents – at any point in their lifetime. This variable attempts to distinguish species that have at least one planktonic life stage (larval, adult, or both) from species that entirely lack a planktonic stage. For example, all mammals, birds and elasmobranchs were coded as FALSE.

- Species is planktonic at any point in their lifecycle: TRUE = 1 [present]
- Species is not planktonic at any point in their lifecycle: FALSE = 0 [absent]

Planktotrophy ("Larval_feeding")

Many marine species, especially invertebrates, have a larval stage that differs in morphology from their adult forms. One common way to classify differences in larval life history is based on larval feeding mode, which in turn influences dispersal (as well as development time and survival probabilities). We defined three categories of larval feeding for this trait: species that do not have planktonic larvae, species with non-feeding planktonic larvae, and species with feeding planktonic larvae. Species that do not have planktonic larvae produce progeny that develop directly into young that resemble miniature adults; these young do not spend time drifting or floating in the water column. Species with non-feeding planktonic larvae, often called lecithotrophic, produce energy-rich eggs that facilitate development from larvae into juveniles without the need to feed; as these larvae are planktonic, they drift in the water column while developing, but development is relatively quick given the well-provisioned eggs. Finally, feeding (or planktotrophic) planktonic

larvae derive from eggs that provide only enough energy to produce a larvae; these larvae must then spend time drifting in the water column feeding on particulate food to fuel development into juveniles, which usually takes longer than in (well-provisioned) non-feeding planktonic larvae. All fish with planktonic larvae are feeding (coded "P"). For corals, we coded species that do not have zooxanthellae in their larvae and rely fully on maternal provisioning as "L", and coded corals with larvae that eat at some point and/or are autotrophic (contain zooxanthellae that can photosynthesize and provide nutrition “on the go”) as "P".

- No planktonic larvae: N = 0 [absent]
- Non-feeding (lecithotrophic) planktonic larvae: L = 1 [intermediate]
- Feeding (planktotrophic) planktonic larvae: P = 2 [present]

Pelagic larval duration ("PLD_point2")

A continuous variable representing the mean or midpoint of the estimates available for each species for the length of time (in days) that marine larvae spend in the plankton. We assigned this variable a value of 0 for species that have live birth or brood their young that become benthic adults (isBenthic=Always) and for species who are never benthic (isBenthic=Never); thus pelagic larval duration and benthicity are not conflated in our analyses.

Egg size ("Fecundity_EggSize")

A continuous variable in millimeters, representing the largest dimension of the egg or juvenile at birth or hatching (the propagule size, in the sense of (*3*)).

Body size ("BodySize")

A continuous variable in centimeters, representing the largest dimension of an average organism of each species at its full-grown adult size. As corals and seagrasses are colonial, the meaning of body size is unclear. While we acknowledge that genet size (the collective size of a genotype that might include many discrete ramets or colonies) would be most appropriate in terms of scaling to likely reproductive output, genet sizes are largely unknown and therefore we used ramet or colony size. In some instances only colony area was provided, so we assumed a circular shape to derive the diameter.

Appendix S5: Citations for biotic trait data

This appendix contains the citations for all of the biotic trait values used in this study. The citation numbers in this document correspond to the numbers in the columns labeled: "**<trait_name>_citation**" in the data file: "**/data/biotic/final_biotic_traits_for_suppmat-with-citation-numbers.csv**" in the Dryad archive for this study. Note that the trait Benthicity ("isBenthic") does not have a corresponding citation column (in "final_biotic_traits_for_suppmat-with-citation-numbers.csv") because these values reflect common knowledge within our author group. Other individual trait values that have "NA" in the corresponding citation column also reflect common knowledge within our author group.

We obtained as many trait values as possible from public trait databases (e.g., FishLifeBase (*105*) and SeaLifeBase (*106*)). For species/trait combinations not present in centralized databases (which were the majority), we performed Boolean searches in Web of Science or Google Scholar (e.g., <species name> AND egg size).

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Appendix S6: Search parameters and citations for Global Biodiversity Information Facility species occurrence records

This appendix contains the search parameters and citations for the resulting occurrence records that we downloaded from the Global Biodiversity Information Facility (GBIF) for each species included in this study. The search parameters section denotes the exact search and filtering terms that we passed to the `occ_download` function (rgbif R package V3.5.0, Chamberlain and Boettiger 2017) to retrieve species occurrence records from GBIF for each species in this study. The citations capture the specific snapshots of GBIF data used in this study; the DOIs are specific to the exact search parameters that we used and the date that we executed the query.

Search and filtering parameters used to retrieve GBIF records:

```
library(rgbif)

OurSearchRequest <- occ_download(type='and',
                                 pred('taxonKey',taxonKey),
                                 pred("hasGeospatialIssue", FALSE),
                                 pred("hasCoordinate", TRUE),
                                 pred_not(
                                   pred("basisOfRecord", "FOSSIL_SPECIMEN")
                                 ),
                                 pred_or(
                                   pred_not(pred("establishmentMeans","MANAGED")),
                                   pred_not(pred_notnull("establishmentMeans"))
                                 ),
                                 pred_or(
                                   pred("occurrenceStatus","PRESENT"),
                                   pred_not(pred_notnull("occurrenceStatus"))
                                 ),
                                 format='SIMPLE_CSV',
                                 user=user,pwd=password,email=email)
```

Citations

1. GBIF.org. GBIF occurrence download for species: *Acanthephyra purpurea*. *The Global Biodiversity Information Facility*, 08 September 2021. doi:10.15468/DL.TFGCY5.

2. GBIF.org. GBIF occurrence download for species: *Acanthurus olivaceus*. *The Global Biodiversity Information Facility*, 08 September 2021. doi:10.15468/DL.UVAHKV.

3. GBIF.org. GBIF occurrence download for species: *Acropora cervicornis*. *The Global Biodiversity Information Facility*, 08 September 2021. doi:10.15468/DL.36NY9X.

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