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Marine Parasite Biogeography Mirrors Host Patterns Across Latitude, Area, and Diversity

Thomas C. Morris¹  | Mark John Costello^{1,2}  | Nicholas J. Matzke³

¹Institute for Marine Science, The University of Auckland, Auckland, New Zealand | ²Faculty of Biosciences and Aquaculture, Nord University, Bodo, Norway | ³School of Biological Sciences, The University of Auckland, Auckland, New Zealand

Correspondence: Thomas C. Morris (mrrthom@gmail.com)

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ABSTRACT

Parasites are integral components of biodiversity, yet they remain poorly represented in large-scale biogeographic theory. In this study, we test whether marine parasites follow three macroecological patterns established for free-living taxa, namely that parasite species richness: (1) scales positively with area (both host body size and geographic area) and (2) follows the latitude diversity gradient and (3) increases with host species richness. We assembled a spatially explicit dataset of parasites of cartilaginous fish, which were relatively well-sampled, and consisted of 7198 host–parasite associations involving 778 host species and 2093 parasite species. We found strong support for all predictions. Host traits (notably body size and range size) explained significant variation in parasite richness across host species. Parasite richness followed a bimodal latitudinal gradient, with richness peaks in both hemispheres—consistent with emerging patterns in marine biodiversity. Finally, parasite richness covaried with host species richness across space. These results provide robust, global-scale evidence that parasite distributions are shaped by the same large-scale processes as free-living organisms.

1 | Introduction

Biogeography is a top-down view of the distribution of organisms through geological time and aims to record and understand spatial variations across environments (Gaston and Blackburn 1999; Gaston 2000; Lomolino et al. 2017; Shade et al. 2018). One of the fundamental goals of biogeography is searching for drivers of spatial variation in biodiversity (Gaston and Blackburn 1999; Gaston 2000; Rohde 2002). This often requires substantial effort to compile species distribution data while taking into account data incompleteness and biases, a step also necessary to inform conservation strategies globally (Lucifora et al. 2011; Gormley et al. 2015). Large spatial biodiversity datasets, once compiled, may help to decipher general ecological patterns that span systems and time and are applied globally. One such general pattern is the latitudinal diversity gradient.

The latitudinal diversity gradient is one of the clearest and best documented geographic biodiversity patterns (Pianka 1966; Rohde 1978; Gaston 2000; Hillebrand 2004; Poulin and Leung 2011; Lomolino et al. 2017; Lin et al. 2021). Among marine parasites, an increase in diversity towards the equator has been shown for genera within Monogenea and Digenea (Rohde 1984, 2002). However, these results were not corrected for sampling bias, unlike more recent studies (Chaudhary, et al. 2017; Jorge and Poulin 2018). Although it seems likely that large-scale patterns in parasite richness should mirror those of their hosts, as parasites and their hosts are intimately linked, studies have revealed only weak and inconsistent evidence in favor of marine parasite latitudinal diversity gradients (Poulin and Morand 2004; Rasmussen and Randhawa 2018; Poulin and Jorge 2019).

A persistent challenge in global-scale biogeographic studies is the strong geographical bias in biodiversity data, with records

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overwhelmingly concentrated in the Northern Hemisphere and temperate regions of the Global North (Hughes et al. 2021). This bias is particularly prevalent in parasite research, where taxonomic expertise, institutional infrastructure, and research funding have historically been concentrated in Europe and North America (Poulin and Jorge 2019). As a result, marine parasite communities of the Global South—encompassing the Southern Hemisphere oceans adjacent to South America, sub-Saharan Africa, and Australasia—remain poorly documented relative to their northern counterparts (Poulin and Morand 2004). This under-representation means that global-scale conclusions drawn from existing datasets risk reflecting the Northern Hemisphere's sampling footprint rather than genuine biogeographic processes. Addressing this gap is therefore not only a matter of improving geographical coverage, but of ensuring that macroecological patterns reported at global scales are not artifacts of where researchers have historically worked.

Increased availability of parasite occurrence data has facilitated efforts to understand the spatial distribution of parasite diversity (Carlson et al. 2017; Dallas et al. 2018; Jorge and Poulin 2018; Poulin and Jorge 2019). Dallas et al. (2018) used one of the largest helminth databases (London Natural History Museum's host-parasite record) and found terrestrial helminths showed an increase in richness with a decrease in latitude, a strong positive relationship between host and parasite richness at a global scale, and that larger geographic areas supported higher parasite richness. However, as host mass increased, their data showed that this increase did not seem to influence parasite richness. This study was one of the first to explicitly assess macroecological theories at a global scale and show that global parasite diversity is linked to both environmental and host factors.

Each of these patterns has a theoretical basis established for free-living organisms that we predict should extend to parasites. The positive scaling of parasite richness with host body size follows from island biogeographical theory: when hosts are treated as islands for parasite colonization (Kuris, et al. 1980), larger hosts provide greater habitat area, more diverse microhabitats, and more resources, and should therefore support more parasite species (MacArthur and Wilson 1963). The scaling of parasite richness with host geographic range reflects the increased opportunity for parasite colonization as hosts encounter more diverse parasite communities across environmental gradients. Additionally, trophic position is expected to influence parasite richness: predatory hosts that consume infected prey are exposed to a greater richness of larval parasites over time than planktivorous species, resulting in higher colonization rates (Luque, et al. 2004). Finally, the positive scaling between host and parasite richness across space follows from the same consumer-resource relationship: regions with more host species provide more colonization opportunities and transmission pathways for parasites (Kamiya et al. 2014a).

Despite their diversity, parasites may constitute one-third to one-half of global biodiversity (Poulin 2014; Carlson et al. 2020), yet they remain underrepresented in biogeographic theory. Parasites influence ecosystem structure by modifying competitive and trophic interactions, increasing food web complexity, and altering energy flow (Lafferty et al. 2008). Understanding their biogeographic patterns is therefore essential not only for comprehending marine ecosystem function but also for predicting how marine systems will respond to environmental change.

Chondrichthyes (elasmobranchs and holocephalans) are found in all the world's oceans, latitudes, depths, and a wide range of marine habitats (Lin et al. 2021). These cartilaginous fish occupy the upper levels of the marine food chain and as a result, are host to many adult forms of marine parasites. There is a significant body of work describing, cataloging, and analyzing parasites of cartilaginous fish (Randhawa and Poulin 2010, 2019; Caira and Jensen 2014, 2017; Pollerspöck and Straube 2020). However, the vast majority of this work focused on cestodes of elasmobranchs (Randhawa and Poulin 2010, 2019; Caira and Jensen 2014) and did not take into account the many other taxa that infest the full range of cartilaginous fish.

In this study, we show that marine parasites of cartilaginous fish and their hosts support three main biogeographic patterns: (1) strong scaling of species richness with habitat size (host body size and host geographic range), (2) the latitudinal diversity gradient, and (3) areas with high host diversity correspond to areas of high parasite diversity.

2 | Methods

2.1 | Host-Parasite Data

We gathered data on 7200 host-parasite associations spanning 556 cartilaginous fish host species and 2525 parasite species from three publicly available datasets, namely Shark Reference (<https://shark-references.com/>) (Pollerspöck and Straube 2020), World Register of Marine Species (WoRMS) (www.marinespecies.org) (Horton et al. 2019), and the Elasmobranch Host Specimen Database (www.elasmobranchs.tapewormdb.uconn.edu) (Caira and Jensen 2017). This dataset included extant marine species and duplicate records and synonyms were resolved.

Limiting the dataset to just parasites of cartilaginous fish may skew richness counts. Therefore, a host list was back-engineered from the parasite list above using the WoRMS database to develop a host list of potential hosts that go beyond cartilaginous fish. This increased the dataset by 758 noncartilaginous host species, resulting in a total of 1314 hosts and an increase to 8503 host-parasite interactions (detailed in Table 1).

This host-parasite species list was then used to download occurrence information for both parasites and their hosts from the Global Biodiversity Information Framework (GBIF: *The Global Biodiversity Information Facility* 2021) and the Ocean Biodiversity Information System (OBIS 2021). Only 1049 of the 2525 parasites had occurrence records (22,296) globally from these sources (see Supplementary Material). Records with missing data points, missing coordinates and duplicates were removed. To account for geographic outliers (e.g., erroneous coordinates, mislabeled specimens, or vagrant individuals), we removed records where the minimum distance to all other conspecific records exceeded 10°. This threshold identifies improbable isolated occurrences while retaining true range edge populations and has been used in similar marine biogeography studies (e.g., Chaudhary, et al. 2016).

Additionally, the high-resolution coastal layer from the Global Self-consistent, Hierarchical, High-resolution Geography Database (GSHHG) (Wessel and Smith 1996) was used to remove

TABLE 1 | Number of (a) parasite and (b) host species downloaded from Shark Reference (<https://shark-references.com/>) (Pollerspöck and Straube 2020), World Register of Marine Species (WoRMS) (www.marinespecies.org) (Horton et al. 2019), and the Elasmobranch Host Specimen Database (www.elasmobranchs.tapewormdb.uconn.edu) (Caira and Jensen 2017).

(a)			Number of parasite species		
<i>Parasitic taxa</i>	Habitat	Lifestyle	Raw dataset	Corrected dataset	
Arthropods					
Class Hexanauplia	ecto	direct	242	216	
Class Malacostraca	ecto	direct	53	45	
Class Ostracoda	ecto	direct	1	1	
Class Thecostraca	ecto	direct	1	1	
Helminths					
Phylum Acanthocephala	endo	indirect	7	6	
Phylum Annelida	ecto	direct	17	16	
Phylum Nematoda	endo	direct	111	96	
Phylum Platyhelminthes					
Class Cestoda	endo	indirect	1698	1362	
Class Monogenea	ecto	direct	299	265	
Class Trematoda	endo	indirect	59	52	
Minor groups					
Phylum Chordata	ecto/endo	direct	5	5	
Phylum Cnidaria	endo	indirect	32	28	
TOTAL PARASITES			2525	2093	
(b)			Number of host species		
	Raw Dataset	Corrected Dataset	GAMM Dataset		
Arthropods					
Class Insecta	1	—	—		
Class Malacostraca	18	16	—		
Chordata					
Class Actinopterygii	591	437	134		
Class Aves	67	1	—		
Class Elasmobranchii	540	279	209		
Class Holocephali	16	7	7		
Class Mammalia	65	26	12		
Class Petromyzonti	1	1	—		
Phylum Cnidaria	2	2	—		
Phylum Mollusca	12	11	—		
Phylum Echinodermata	1	1	—		
TOTAL HOSTS	1314	778	362		

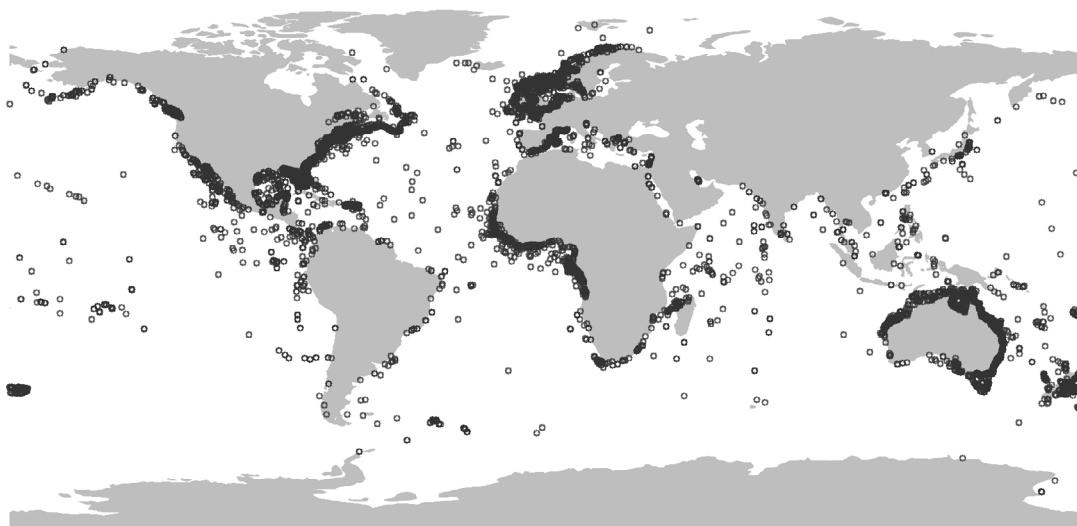
land-based occurrence points with a one kilometer buffer. This 1 km buffer accounts for minor georeferencing imprecision near coastlines and historical changes in shoreline databases, ensuring genuinely marine records are not inadvertently excluded due to slight coordinate inaccuracies. Cleaning the data in this way reduced the dataset to 392 species of parasite (with 11,474 records). With respect to hosts, we downloaded and cleaned the host data using the same methods as for parasites. This resulted in a dataset of 884 host species (with 4,827,342 host records) which was used to calculate host latitudinal range (Figure 1).

Datasets were updated in August of 2021 (All datasets can be accessed through <https://github.com/Moose37/MarineParasitePhD>).

2.2 | Sampling Effort

Hosts which have been thoroughly sampled for parasites appear to have more parasites than those which have been less well sampled (Walther et al. 1995), and this is certainly the case for these

(a) Parasites



(b) Hosts

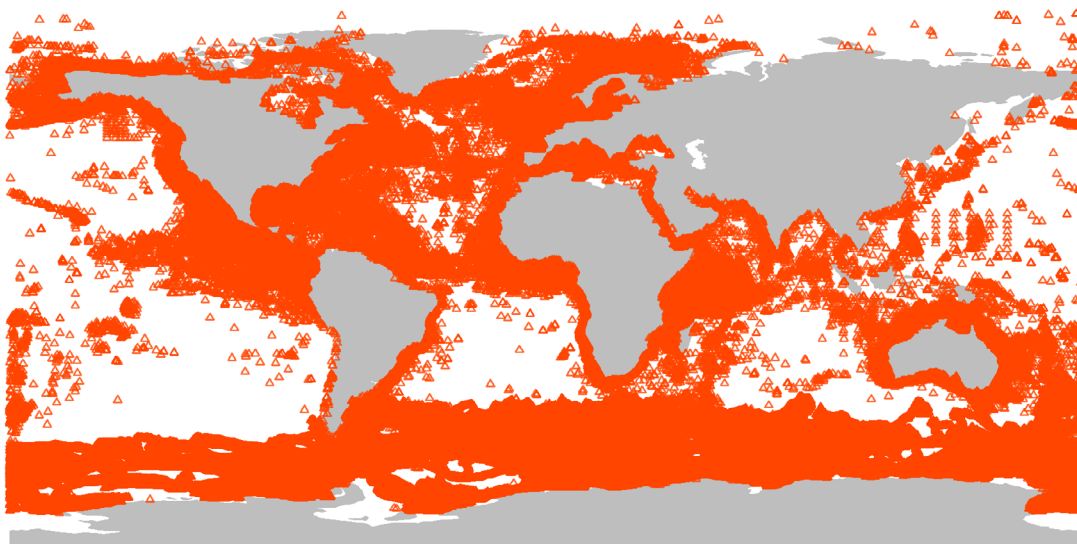


FIGURE 1 | Occurrence records for (a) parasites of cartilaginous fish ($n = 11\,474$) and their (b) hosts ($n = 4\,827\,342$).

data, which show a strong positive correlation between sampling effort and parasite richness ($r(480) = 0.91$, $p < 0.001$). Sampling effort is measured here as the number of published records per host species in the Shark Reference database. This sampling bias operates at two scales relevant to this study. At the species level, cartilaginous fish that have received more research attention accumulate more recorded parasite species, irrespective of their true parasite richness. At the geographic level, parasite biodiversity data aggregated from open-access repositories such as GBIF and OBIS are strongly concentrated in the Northern Hemisphere, reflecting the historical distribution of taxonomic expertise and museum collections in Europe and North America (Hughes et al. 2021). Of the 11,474 parasite occurrence records used in the latitudinal analyses, 67.2% originated from north of the equator, as did 59.2% of the 4,827,342 host occurrence records. Left unaddressed, this hemispheric imbalance risks producing latitudinal

diversity patterns that reflect where researchers have historically worked rather than genuine biogeographic processes.

To address these issues, we applied complementary standardization approaches at both scales. To correct for uneven sampling at the species level, we focused analyses on well-sampled cartilaginous fish, defined as species with at least five different recorded parasites plus evidence for saturation in their parasite species accumulation curves (SAC; see Appendix SA1 for outcome of SAC per host species). These curves were created using the *specaccum* function in the R package *vegan* (Oksanen et al. 2012). We collected citation counts from the Shark Reference database (<https://shark-references.com/>) (Pollerspöck and Straube 2020), which contains the most complete bibliography of recent and fossil cartilaginous fish parasites available. For each host species, a paper from Shark Reference was randomly sampled (without

replacement) and cumulative parasite richness calculated; this process was repeated until all papers had been sampled, then iterated 1,000 times per host to obtain rarefied accumulation curves. To correct for geographic sampling bias at the latitudinal scale, see “latitudinal diversity gradient” section below.

Because the bibliography from Shark Reference database was used to conduct the parasite SAC’s, this limited the original data to only cartilaginous fish hosts. Therefore, any hosts from the overall dataset that matched parasite species were added to the corrected dataset. Therefore, the reduction to only well sampled parasites and their cartilaginous and noncartilaginous hosts reduced the analysis pool to 778 hosts, 2093 parasite species, and 7198 host-parasite associations.

2.3 | Host Trait Scaling

By treating each host species as a habitat, parasite species richness was calculated for each host from the corrected dataset (accounting for sampling effort). Host adult maximum length (mm), maximum weight (g) and latitudinal range were obtained from FishBase collated through its R package interface *rfishbase* (Boettiger, et al. 2012). Host latitudinal range was the degrees latitude between the northern and southernmost occurrence records.

To test if parasite species richness scales to host variables, a Generalized Additive Mixed Model (GAMM) was fitted using the *mgcv* package in R (Wood 2017). Richness values (corrected for sampling effort) were used as the response variable, with host length (continuous), weight (continuous), and latitudinal range (continuous) (see Supplementary Material for definitions of all variables). To incorporate the dependency of parasites to infest hosts of similar phylogeny (Tedesco et al. 2020), host order was used as a random effect. As richness is highly skewed discrete data, a log link function with a negative binomial distribution was used to predict the effects of host variables.

Since host maximum weight and length were highly co-varied ($r(194) = 0.64$, $p < 0.001$), only maximum adult length was used in model predictions. Model assumptions were verified by using a quantile–quantile plot and histogram of the model residuals as well as plotting residuals versus fitted values. Concurrency (non-parametric collinearity) was assessed to test if smooth terms in the model could be approximated by one or more of the other terms in the model. All GAMs were built with the package “*mgcv*” (Wood 2011, 2017) using REstricted Maximum Likelihood (REML) approach, for reasons outlined in Wood (2011, 2017). `Select = TRUE` was used to add an extra penalty to each term so that each term could be penalized to zero in model comparisons.

In addition to host body size and latitudinal range, we included host depth range and habitat in the GAMM as covariates to account for ecological variation that could influence parasite richness independently of size and spatial extent. Host species that occupy a broader vertical range or occur across several habitats (habitat descriptions in appendix SA2) are likely to encounter a wider array of parasite transmission environments, intermediate hosts, or infection routes. These traits may

confound or inflate the apparent effects of body size or range. Including depth range and habitat controls for these potentially confounding ecological factors, allowing a more conservative test of whether host size and range alone drive parasite richness patterns.

2.4 | Latitudinal Diversity Gradient

To analyze species richness distribution of marine parasites and their hosts, we used hexagons of size 209,904 km² (494.96 ± 29.8 km between centroids of cells) to define a regional scale, and 5° latitudinal bands to analyze global distributional gradients.

A rarefaction method known as Hurlbert’s index (Hurlbert 1971), which calculates the expected number of species that can be found in a random subsample of a community, was used to standardize results. Therefore, the use of Hurlbert’s index ameliorates the bias introduced by the uneven number of species across samples and geographies. In the present case, Hurlbert’s index calculated the number of species expected in ten samples (ES10) per hexagon for parasites and 10 samples per hexagon for their hosts (ES10) (Figure 2). The calculations were done using the *vegan* package (Oksanen et al. 2012) in R.

To test for the latitudinal diversity gradient, total number of species per hexagon averaged across each 5° latitudinal band was the measure of average local species richness, which corresponds to

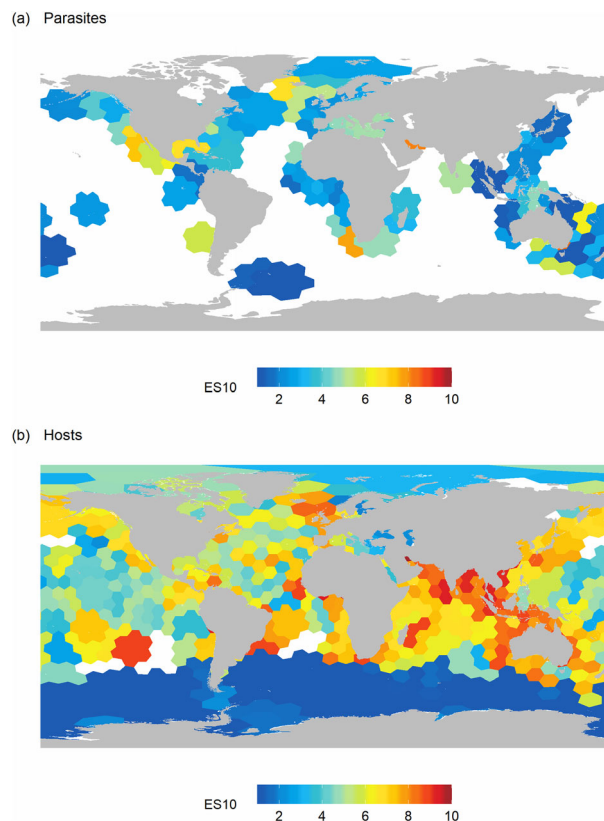


FIGURE 2 | Standardized species richness per ~210 000 km² hexagons for (a) parasites of cartilaginous fish ($n = 277$) and their (b) hosts ($n = 2605$).

alpha richness. For gamma richness, we used the total number of species per 5° latitudinal band. Generalized additive modeling (GAM) was used to explore the species richness gradient with latitude. In addition to standardizing using Hurlbert's index, the raw counts of species were standardized by using sampling effort as an offset variable in the GAM, rather than as a predictor. Using an offset compensates for the need to rarefy species richness and the number of species can be modeled given the total number of samples while promoting the use of the whole dataset. Sample size was considered as the number of records per hexagon.

The GAM plots report uncorrected values for species richness. However, the GAMs were then plotted on top of these data, with sample efforts standardized to the mean sampling effort for hosts (average sample size = 7,484.7: total sample size = 263,820) and parasites (average sample size = 33.3: total sample size = 799). This allowed determination of how sampling effort influenced the raw data, and explains why the models do not always seem to fit the points in the plots as well as the statistics suggest they should.

Model validation residuals did not show a particular pattern or bias, therefore the GAMM model was deemed to be valid and useful. Also, the model did not show levels of concavity that impacted the model's predictions. Therefore, the model terms were useful in explaining the response variable.

2.5 | Parasite Diversity Scales with Host Diversity

To test whether parasite diversity scaled with host diversity, the ES10 values were calculated for each hexagonal cell for both parasites and hosts. This allowed comparison of areas of equal size, and use of values that were already standardized for sampling effort. These values were plotted directly, and a GAM was used to test for significance. However, the hexagonal ES10 values were highly skewed and residuals deviated from the normality assumption (see Appendix S6), so these were excluded. We then tested across latitudinal averages, testing standardized species richness in ~210,000 km² hexagons averaged across 5° latitudinal bands. This aggregation removed the skew from the richness data, better conforming to model assumptions.

All analyses were conducted in R version 4.1.0 (R Core Team 2019). Code to reproduce all analyses and figures is provided at <https://github.com/Moose37/MarineParasitePhD>.

TABLE 2 | GAMM results for parasite species richness.

Predictor variable	χ^2	edf	p-value	Effect direction
Host length (full model)	41.07	2.03	0.004	Positive
Host length (excluding planktivores)	49.35	1.49	<0.001	Positive
Host latitudinal range	183.30	2.62	<0.001	Positive
Host habitat	13.95	6 ^a	0.03	Significant
Host order (random effect)	454.50	23.40	<0.001	Significant

^adf for habitat (categorical variables, n = 7).

Note: Model fit - REML = 1124.7, n = 334, deviance explained = 72%.

3 | Results

Occurrence records were unevenly distributed across hemispheres for both parasites and their hosts (Figure 1). Of the 11,474 parasite occurrence records, 67.2% (n = 7,710) originated from the Northern Hemisphere and 32.8% (n = 3,764) from the Southern Hemisphere. Host records showed a less pronounced but still marked imbalance, with 59.2% (n = 2,857,531 of 4,827,342) from the Northern Hemisphere. Within the Southern Hemisphere, parasite records were strongly concentrated in Australian and New Zealand waters, which alone accounted for 25.5% of all global parasite records (n = 2,928). The remainder of the Southern Hemisphere outside Australia and New Zealand contributed only 836 parasite records (7.3% of the global total), spanning 69 species. Key Global South regions were especially poorly represented: the east coast of Africa contributed 80 records across 11 species (0.7%), South America south of the equator 98 records across 28 species (0.9%), the Agulhas Bank off southern Africa 95 records across 27 species (0.8%), and the Coral Triangle 55 records across 7 species (0.5%).

Despite this recording imbalance, more parasite species had occurrence records in the Southern Hemisphere (244 species; 59.8% of all species) than in the Northern Hemisphere (223 species; 54.7%). Northern Hemisphere parasite species averaged 34.6 occurrence records per species compared to 15.4 records per species in the Southern Hemisphere (a 2.2-fold difference). This pattern indicates that Southern Hemisphere parasites are systematically under-recorded per species rather than genuinely absent, and that the true extent of parasite diversity in the Global South is likely underestimated by the available data.

3.1 | Host Trait Scaling

The GAMM explained 72% of deviance in parasite species richness (Table 2; Appendix SA3). Host length significantly predicted parasite richness, with larger hosts supporting more parasite species (Figure 3a, Figure 4a). This pattern held even when excluding the two exceptionally large planktivorous species, the whale and basking sharks, *Cetorhinus maximus* at 1520 cm and *Rhincodon typus* at 1700 cm, which harbored fewer parasites than predicted by their body size (Figure 4a, red line; Appendix SA3). Among the remaining species, host length ranged from 25 cm to 960 cm.

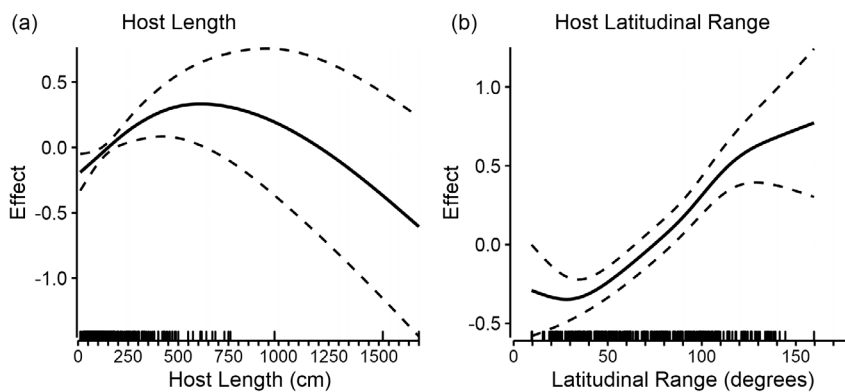


FIGURE 3 | Additive effect of (a) host length and (b) host latitudinal range on parasite species richness. Solid lines indicate GAMM fit, dotted lines represent 95% confidence intervals with tick marks along the lower axis representing individual observations.

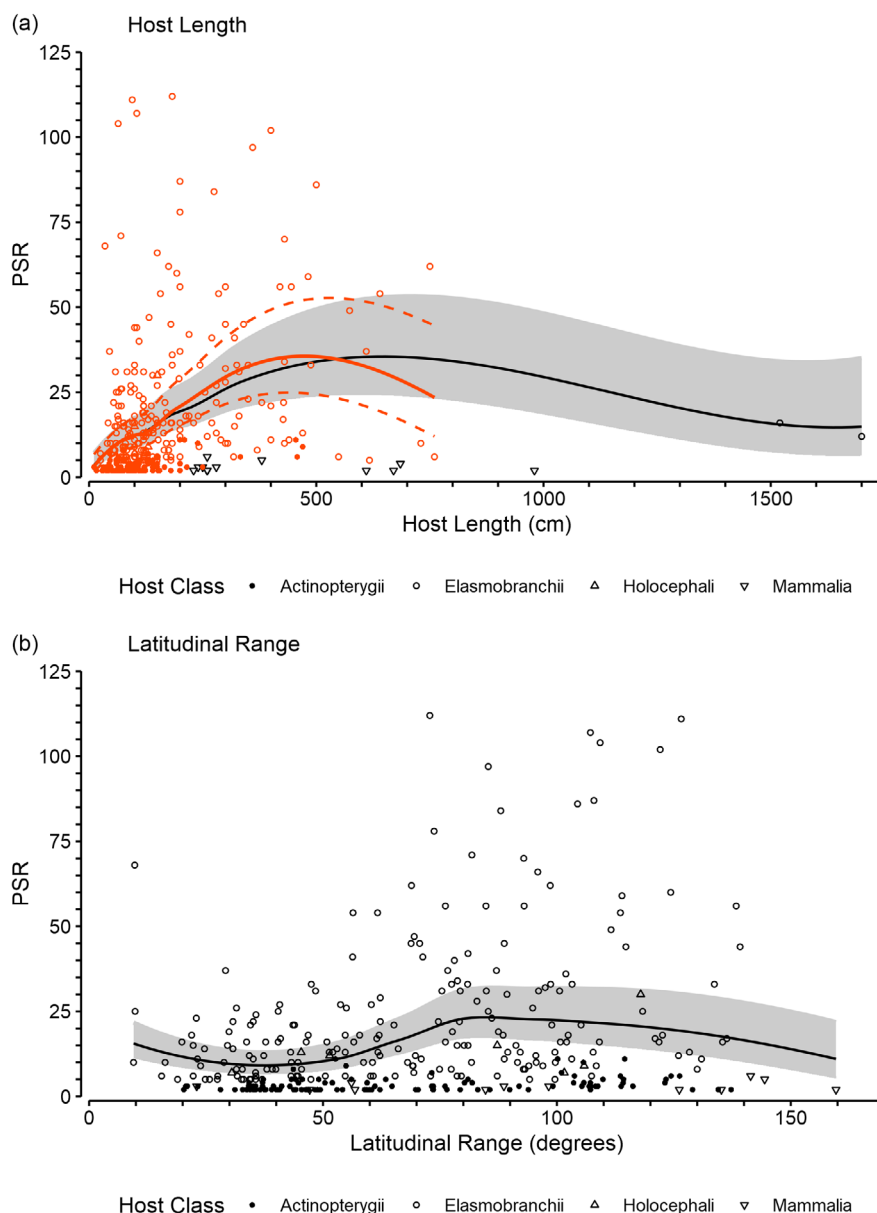


FIGURE 4 | Parasite species richness as a function of (a) host length and (b) host latitudinal range for parasites of cartilaginous fish, with host taxonomy included as a random variable (see Table 2 for model statistics; full model output in Appendix SA3). Point shapes indicate host class. Black trend line shows full GAMM model with 95% confidence interval in gray. Red line in (a) shows model excluding the two planktivorous species whale shark (*Rhincodon typus*) and basking shark (*Cetorhinus maximus*, indicated by black points above 1500 cm), which harbored fewer parasites than predicted by their body size.

Host latitudinal range also significantly predicted parasite richness. Hosts with wider latitudinal ranges supported more parasite species (Figure 3b, Figure 4b), with ranges varying from 9.6° to 159.7° (mean = 69.8°). Host taxonomy contributed significantly to model fit (Table 2), indicating that phylogenetic relatedness correlates with parasite richness patterns beyond the effects of body size and geographic range. Additionally, habitat also contributed significantly to model fit (Table 2, Appendix SA3).

3.2 | Latitudinal Diversity Gradient

Both host and parasite species richness correlated strongly with sampling effort (hosts: $R = 0.36$, $p < 0.001$; parasites: $R = 0.56$, $p < 0.001$). Therefore, Hurlbert's index was used to standardize richness estimates for sampling effort, following methods established for marine biodiversity studies (Chaudhary, et al. 2016, 2017). Parasite species richness exhibited a significant bimodal distribution with latitude (Table 3, Figure 5; Appendix SA5).

Both gamma and alpha richness showed peaks at approximately 38°S and 25°N, with the lowest richness occurring just south of the equator at 10°S. Host richness also displayed a bimodal pattern, with a prominent peak at 30°S and smaller peaks at 10°N and 40°N. The distributions of parasite and host richness differed significantly from one another ($F(1) = 203.4$, $p < 0.001$ for alpha diversity; $F(1) = 3055$, $p < 0.001$ for gamma richness) (Appendix SA5).

3.3 | Parasite-Host Richness Scaling

We tested for scaling between host and parasite richness by using ES10 standardized species richness in ~210,000 km² hexagons averaged across 5° latitudinal bands. We analyzed this trend using a GAM and showed a strong positive relationship between parasite and host richness ($F(2.6) = 3.2$, $p < 0.001$; deviance explained = 55.2%; Figure 6). We also attempted to model the relationship between host and parasite standardized richness using individual hexagons directly, as there were 95 hexagons that overlapped with parasite and host information. However, the data distribution did not conform to model assumptions (Appendix SA6).

4 | Discussion

4.1 | Host Body Size

A strong positive association between parasite richness and host body size emerged independent of host taxonomy and sampling

effort (Table 2, Figure 4a). This pattern aligns with island biogeographic theory, which predicts that larger habitat patches (here, host body size) support greater species diversity due to increased resources and niche space (MacArthur and Wilson 1963). When hosts are conceptualized as islands for parasite colonization (Kuris, et al. 1980), larger hosts provide more resources and microhabitats for parasites to exploit. This relationship has been documented across multiple parasite taxa and host systems (Randhawa and Poulin 2010; Kamiya et al. 2014a).

The two exceptionally large planktivorous species in our dataset—whale shark and basking shark—deviated from this pattern, harboring fewer parasites than predicted. This deviation likely reflects their unique feeding ecology. As low trophic level filter feeders targeting zooplankton, these species have reduced exposure to parasite transmission pathways available to predatory species. In theory, over time, predatory fish should be exposed to a greater richness of larval parasites through consumption of infected prey than planktivorous species. This increased interaction translates to higher colonization rates by parasites within predatory fish, as documented for teleost fish in Brazil (Luque, et al. 2004). The model excluding these two planktivorous species yielded similar statistical results (Table 2, Figure 4a red line), confirming the robustness of the body size effect across the remaining 332 predatory species. This suggested that while body size was a primary driver of parasite richness in cartilaginous fish, trophic position and diet may modulate this relationship. It is also worth noting that both whale sharks and basking sharks are rarely available for dissection, and low research effort on these species may contribute to their apparently depauperate parasite communities (Poulin and Jorge 2019).

Host habitat also contributed significantly to parasite richness, with hosts in structurally complex or ecologically diverse habitats (reef-associated, benthopelagic, demersal, pelagic-oceanic) supporting more parasites than those in simpler pelagic environments. This likely reflects differential exposure to intermediate hosts and parasite transmission stages across habitat types. This finding supports previous work showing habitat influences on parasite richness in elasmobranchs (Randhawa and Poulin 2010).

4.2 | Host Geographic Range

Host latitudinal range also significantly predicted parasite richness (Table 2, Figure 4b), consistent with findings for terrestrial parasites (Kamiya et al. 2014b; Dallas et al. 2018). Hosts with broader geographic ranges encounter more diverse parasite

TABLE 3 | GAM results for latitudinal diversity gradients.

Analysis type	Taxonomic group	F-statistic, edf	p-value	REML	n	Deviance explained
ES10 (alpha diversity)	Parasites	15.32 (6.7)	<0.001	72.18	64	95.7%
ES10 (alpha diversity)	Hosts	241.3 (7.82)	<0.001	153.25	68	98.3%
Gamma diversity	Parasites	7.80 (6.55)	<0.001	303.69	68	99.3%
Gamma diversity	Hosts	294.9 (8.42)	<0.001	303.69	68	99.3%

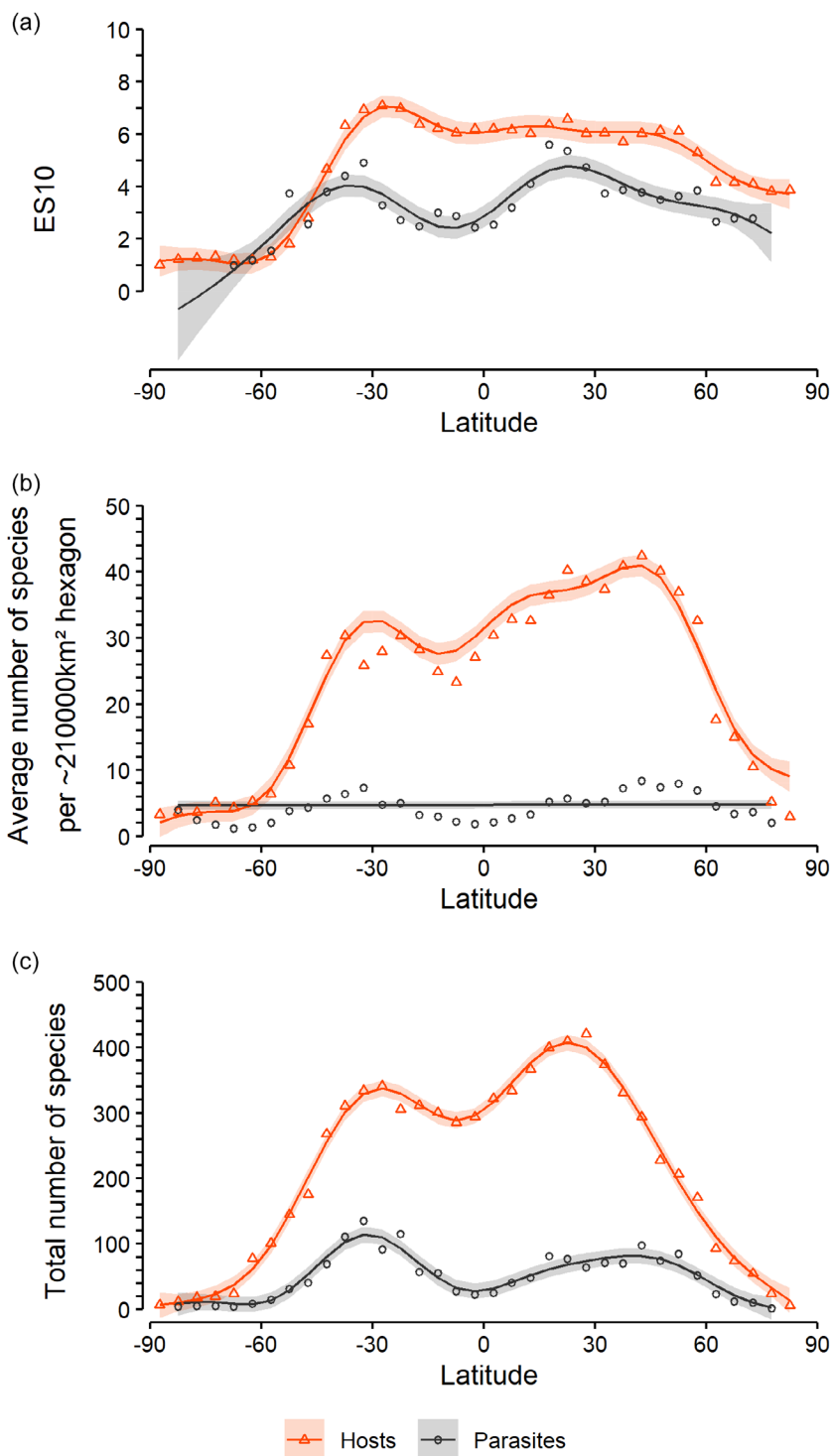


FIGURE 5 | Latitudinal gradient of parasite species richness represented by (a) ES10 standardization per ~210 000 km² hexagonal cell averaged per 5° latitudinal band, (b) number of species per ~210 000 km² hexagonal cell averaged per 5° latitudinal band (alpha richness), and (c) total number of species per 5° latitudinal band (gamma richness). Lines indicate generalized additive models (GAMs; Table 3 for statistics, Appendix SA5 for full model output) with 95% confidence intervals. Parasites of cartilaginous fish shown in black, their hosts in red. Models in (b,c) include an offset to standardize for sampling effort (see Methods for details).

communities across environmental gradients, providing more opportunities for parasite colonization. This pattern supports the general ecological principle that geographic range correlates positively with species richness in consumer-resource systems (Kamiya et al. 2014b; Dallas et al. 2018).

4.3 | Parasite Host Range and Biogeographic Implications

Our dataset revealed that more than half (54.6%; 1142 of 2093 species) of the parasite species infecting cartilaginous fish also

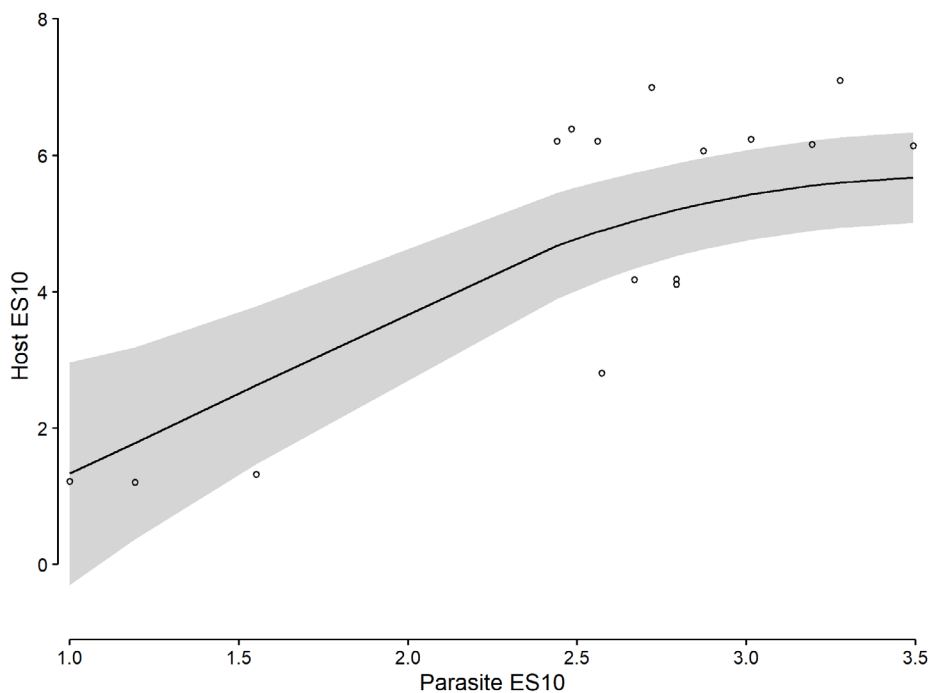


FIGURE 6 | Host richness as a function of parasite richness using Hurlbert's (1971) "Expected Species" (ES10) standardization in ~210 000 km² hexagons averaged across 5° latitudinal bands. Black line is generalized additive model with 95% confidence interval (Appendix SA6).

had records from other vertebrate taxa, particularly teleost fishes. This pattern, however, requires careful interpretation in the context of parasite life history. Many endohelminth groups (incl.: cestodes, trematodes and acanthocephalans) have complex, multihost life cycles in which cartilaginous fish serve as definitive hosts while teleosts and invertebrates function as intermediate or paratenic hosts (Marcogliese 2002; Rohde 2005). In such systems, the same species will necessarily appear across taxonomically disparate hosts at different life stages, and host specificity is more appropriately assessed at each life stage separately rather than across the entire life cycle. The dataset used here does not distinguish between records of adult parasites in definitive hosts and larval stages in intermediate hosts, and so the 54.6% figure likely reflects the prevalence of complex life cycles in this parasite assemblage rather than a generalized absence of host specificity. Previous work on parasites of cartilaginous fish has shown that while host range at the species level may appear broad, the hosts utilized tend to be taxonomically clustered at the order to class level (Poulin 2011; Wells, et al. 2019), consistent with the significant effect of host taxonomy in our models (Table 2). This is an important limitation of the present dataset and resolving it will require life-stage-resolved host-parasite data, which remain rare in open-access repositories for marine systems.

Notwithstanding this caveat, the prevalence of multihost life cycles in this assemblage has direct biogeographic relevance. Parasites with indirect life cycles that incorporate teleosts as intermediate hosts can access a far greater diversity of transmission pathways than those reliant on cartilaginous fish alone, potentially facilitating broader geographic distributions. This may partially explain the positive relationship between host geographic range and parasite richness observed here (Figure 4b, Table 2) hosts with wider distributions encounter more diverse

assemblages of both definitive and intermediate host species across their range. As climate change drives poleward range shifts in marine species (Chaudhary et al. 2021; Gordó-Vilaseca et al. 2023), changes in the geographic overlap between cartilaginous fish, their teleost intermediate hosts and invertebrate first intermediate hosts will alter transmission opportunities in ways that are difficult to predict without life-stage-resolved data. Incorporating life history information into future global host-parasite databases is therefore a clear priority for improving our understanding of how parasite communities will respond to environmental change.

4.4 | Latitudinal Diversity Gradient

These results support a bimodal latitudinal diversity gradient (LDG) in marine parasites and their hosts, independent of sampling effort (Table 3, Figure 5). This pattern appears typical for marine organisms at present (Chaudhary, et al. 2016, 2017; Yasuhara et al. 2020; Chaudhary et al. 2021; Lin et al. 2021; Pamungkas, et al. 2021). Evidence that the marine LDG was flatter during the last glacial maximum (Yasuhara et al. 2020) and has been becoming more bimodal in line with ocean warming over the last century (Chaudhary et al. 2021) indicates that temperature is a primary driver of this gradient.

Previous research has yielded mixed results regarding marine parasite latitudinal gradients (Randhawa and Poulin 2010; Poulin and Leung 2011; Kamiya et al. 2014b; Poulin 2014; Rohde 2016). In general, this lack of consensus has been attributed to uneven sampling across regions (Poulin 2014; Dallas et al. 2018) and to previous analyses not accounting for sampling effort. However, these studies included fewer species and distribution records than the present analysis. By using

Hurlbert's index and a GAMM to standardize results for sampling effort, we demonstrate that marine parasite diversity, both as alpha and gamma richness, follows general trends within the marine realm.

In terms of biogeography, marine parasites appear to follow the same patterns of species richness in relation to latitudinal gradients, geographic range, and habitat size as their hosts. As latitude is a proxy for changes in temperature and solar radiation (Chaudhary, et al. 2017), these results demonstrate that parasite and host distributions are influenced by similar environmental variables. As projected for caligid copepod sea lice (Mackintosh, et al. 2025), parasites of cartilaginous fish are thus likely to contract their range near the equator and expand toward high latitudes under continued ocean warming.

4.5 | Geographic Sampling Bias and the Global South

These results should be interpreted in the context of a well-documented Northern Hemisphere bias in global biodiversity data (Hughes et al. 2021). Parasite occurrence records were heavily concentrated in temperate Northern Hemisphere coastlines, and within the Southern Hemisphere, coverage was dominated almost entirely by Australian and New Zealand waters, leaving key Global South regions—the east coast of Africa, tropical South America, the Agulhas Bank, and the Coral Triangle—severely under-represented (Figure 1). This pattern is consistent with the known concentration of parasitological research effort in the Global North (Poulin and Jorge 2019). Critically, however, more parasite species had Southern Hemisphere records than Northern Hemisphere records yet averaged less than half the occurrence records per species. Southern Hemisphere parasites are therefore present in the data but under-recorded, and the recovery of a comparable richness peak at ~35°–38°S after standardization—further supported by predicted hotspots in the Agulhas Bank, the Patagonian shelf and coastal Australasia—suggests this signal is real.

Together, these results indicate that when sampling bias is accounted for, the Global South harbors marine parasite diversity comparable to that of the Northern Hemisphere. Increasing survey effort in under-sampled regions, particularly through collaboration with research institutions in East Africa, tropical South America, and the Indo-Pacific, is therefore a clear priority. Until occurrence data from these regions become available, global-scale conclusions about marine parasite biogeography, including those presented here, should be interpreted with the recognition that they rest on a sampling footprint heavily weighted toward the Northern Hemisphere.

4.6 | Parasite-Host Diversity Scaling

The strong association between host and parasite richness observed when richness estimates were standardized and averaged across 5° latitudinal bands (Figure 6) supports the concept of hosts as habitat patches for parasites to colonize (Kuris, et al. 1980). If hosts represent habitat, then an increase in habitat diversity within a region should scale positively with parasite species richness in that region, as predicted by island biogeographic theory (MacArthur and Wilson

1963). Although parasites did not show a statistically significant bimodal distribution at the hexagon scale, this is probably due to parasites having only 0.24% as many records as their hosts. This gradient was heavily influenced by sampling effort, spatial scale, and the grain size used (Wood and Johnson 2016). Therefore, increasing parasite sample size would strengthen the validity of this trend and allow for testing at finer regional scales.

5 | Conclusion

These results provide robust, global-scale evidence that parasites of cartilaginous fish follow the same three macroecological patterns established for free-living taxa: parasite richness scales positively with host body size and geographic range, follows a bimodal latitudinal diversity gradient, and covaries with host species richness across space. Taken together, this supports the view that parasite distributions are shaped by the same large-scale environmental and ecological processes that structure free-living biodiversity and that parasites should be incorporated into broader macroecological frameworks rather than treated as an exception to general biodiversity theory. The key limitations of the current dataset: sparse parasite occurrence records relative to hosts, the absence of life-stage information for parasites with complex life cycles, and the strong concentration of records in the Northern Hemisphere mean that the patterns reported here are likely conservative estimates of the true strength and extent of these relationships. Addressing these gaps, particularly through expanded survey effort in the Global South and the development of life-stage-resolved host-parasite databases, will be essential for testing whether the patterns observed here generalize across the full diversity of marine parasite systems.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in GitHub at <https://github.com/Moose37/MarineParasitePhD>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix A1:** Cartilaginous hosts reported in this study with number of parasites (no. parasite), the number of indexed papers (samp.effort) in Shark Reference database and the slope value of their species accumulation curve (SAC, see methods for details). Slope values equal to one indicate a SAC that shows no evidence for saturation in the curve and have been highlighted in red. **Appendix A2:** (a) continuous variables and (b) categorical variables used in the GAMM as downloaded from online sources (Fishbase, OBIS and GBIF). **Appendix A3:** GAMM model statistics (a) with outliers and (b) without outliers. **Appendix A4:** Additive effect of (a) host length, (b) host latitudinal range on parasite species richness (PSR) for model excluding mammals and cartilaginous species above 1500cm in length. Solid lines indicate GAMM fit, dotted lines represent 95% confidence intervals with tick marks along the lower axis representing a single observation. **Appendix A5:** GAM statistics for Latitudinal gradient. **Appendix A6:** GAM statistics for parasite richness scales with host richness.