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Global patterns and drivers of genetic diversity among marine habitat-forming species

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Abstract

Aim: Intraspecific genetic diversity is one of the pillars of biodiversity, supporting the resilience and evolutionary potential of populations. Yet, our knowledge regarding the patterns of genetic diversity at macroecological scales, so-called macrogenetic patterns, remains scarce, particularly in marine species. Marine habitat-forming (MHF) species are key species in some of the most diverse but also most impacted marine ecosystems, such as coral reefs and marine forests. We characterize the patterns and drivers of genetic diversity in MHF species and provide a macrogenetic baseline, which can be used for conservation planning and for future genetic monitoring programmes.

Location: Global.

Time period: Contemporary.

Major taxa studied: Bryozoans, hexacorals, hydrozoans, octocorals, seagrasses, seaweeds, sponges.

Methods: We analysed a database including genetic diversity estimates based on microsatellites in more than 9,000 georeferenced populations from 140 species, which belong to seven animal and plant taxa. Focusing on expected heterozygosity, we used generalized additive models to test the effect of latitude, taxon, and conservation status. We tested the correlation between the species richness and the genetic diversity.

Results: We reveal a significant but complex biogeographic pattern characterized by a bimodal latitudinal trend influenced by taxonomy. We also report a positive species genetic diversity correlation at the scale of the ecoregions. The difference in genetic diversity between protected and unprotected areas was not significant.

Main conclusions: The contrasting results between MHF animals and plants suggest that the latitudinal genetic diversity patterns observed in MHF species are idiosyncratic, as reported in terrestrial species. Our results support the existence of shared drivers between genetic and species diversities, which remain to be formally identified. Concerning, these macrogenetic patterns are not aligned from the existing network of marine protected areas. Providing the first macrogenetic baseline in MHF

species, this study echoes the call regarding the need to consider genetic diversity in biodiversity assessments and management.

KEYWORDS
bimodal gradient, latitudinal genetic diversity pattern, macrogenetics, marine benthic ecosystems, marine habitat-forming species, marine protected areas, species genetic diversity correlation

1 | INTRODUCTION

Intraspecific genetic diversity, hereafter genetic diversity, is one of the pillars of biodiversity (Lavergne et al., 2010). Genetic diversity has been recognized as one of the three levels of biological diversity that deserve particular attention in conservation biology (Stock, 1992). The need to focus conservation efforts on protecting genetic diversity has been recently strengthened based on research revealing the complex interactions linking the genetic diversity of ecological key species to higher levels of biological diversity, from species to community and ecosystem (see Raffard et al., 2019). Yet, genetic diversity remains only poorly considered in biodiversity assessments [e.g., International Union for Conservation of Nature (IUCN), Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services] and management (Hoban et al., 2020, 2021; Schmidt, Hoban, et al., 2022). For instance, protected areas are usually implemented based on species occurrence (Cook et al., 2021) missing other facets of diversity (e.g., Mouillot et al., 2016).

To date, our knowledge regarding the intraspecific patterns of genetic diversity and structure, as well as the underlying processes, is mostly built on a case-by-case basis. Taking advantage of the large number of population genetics datasets available, 'macrogenetics' recently emerged with the objective to identify general and repeated features in the genetic patterns in many species and across large spatial scales (Blanchet et al., 2017). In this way, life-history traits (e.g., longevity; Azizan & Paradis, 2021) and biogeographic factors (e.g., core versus periphery of species distribution ranges) were identified as important drivers underlying macroscale genetic patterns in terrestrial plants and animals (De Kort et al., 2021). The impact of latitude was shown to vary among taxa (Lawrence & Fraser, 2020; Millette et al., 2020; Miraldo et al., 2016), contrasting with the prevalence of the latitudinal gradient in terrestrial species richness (Gaston, 2000). Moreover, echoing the contrasted links between genetic diversity in one particular species and diversity of the associated community at regional scale (e.g., Vellend & Geber, 2005), a positive species–genetic diversity correlation (SGDC) was reported by some macrogenetic studies (e.g., Manel et al., 2020; Theodoridis et al., 2020) but not by others (e.g., Lawrence & Fraser, 2020).

Yet, these studies were mostly focused on terrestrial species, excluding marine species in spite of the strong contrasts existing between the two environments (but see Manel et al., 2020). Terrestrial and marine habitats are characterized by different environmental parameters and selective pressures, different spatial patterns of species richness [a latitudinal gradient in terrestrial species

(Gaston, 2000) versus a bimodal distribution peaking close to tropical latitudes in marine species (Chaudhary et al., 2016)] and diverse phylogenetic compositions and life-history strategies (e.g., higher reproduction frequency in marine compared to terrestrial species; see Capdevila et al., 2020; Grosberg et al., 2012). Accordingly, a thorough understanding of the global pattern of genetic diversity requires the implementation of macrogenetics in marine species.

Marine habitat-forming (MHF) species, including reef-building corals, sponges, gorgonians, seagrasses and kelps among others, provide three-dimensional structures increasing overall habitat complexity, with direct benefits for associated species (e.g., provision of habitats, food; Bruno & Bertness, 2001). These species dominate highly diverse benthic habitats (e.g., tropical coral reefs, kelp forests and Mediterranean coralligenous assemblages), which provide essential ecosystem services for nature and society and are considered as key components of nature-based solutions to mitigate the impact of global change (Solan et al., 2020). In line with the accelerating decline of marine diversity (Lotze et al., 2019), MHF species and associated communities are under strong pressures as exemplified by recurrent bleaching events of corals inhabiting tropical reefs (Hughes et al., 2018) or mass mortality events of gorgonians inhabiting temperate coralligenous communities (Garrabou et al., 2021). In this context, a macrogenetics baseline in MHF species is timely to support the prioritization of conservation efforts. From a spatial perspective, this baseline should help in the identification of shared hotspots of genetic diversity while, from a temporal perspective, it will provide a reference point from which to monitor potential genetic erosion in MHF species.

Here, we compile a genetic diversity estimate (expected heterozygosity; H_e) obtained from microsatellites for more than 9,300 georeferenced populations belonging to 140 animal and plant species from seven different taxa (bryozoans, hexacorals, hydrozoans, octocorals, seagrasses, seaweeds and sponges). Since we focus on a functional rather than a phylogenetic group of species, we assume the species to show different evolutionary histories and, accordingly, we expect a complex spatial genetic pattern. The link with latitude will be tested in the light of the bimodal species diversity pattern previously reported in marine species (Chaudhary et al., 2016). Then, owing to their ecological role and assuming that the genetic diversity of one MHF will be positively related to its abundance, which should positively impact associated communities (e.g., Reusch et al., 2005), we hypothesize a positive correlation between MHF species genetic diversity and species richness. Finally, considering the lack of enforcement in many marine protected areas (MPAs; e.g., Claudet

et al., 2020), we anticipate a limited effect of protection level on genetic diversity. To test for these hypotheses, we (a) characterize the global patterns of intraspecific genetic diversity and gain insights into the factors underlying those patterns with emphasis on geographic (latitude) and taxonomic (taxon) drivers; (b) test for the existence of a SGDC; and (c) estimate the overlap between the existing network of MPAs and the patterns of genetic diversity. Considering all the MHF species, we reveal a bimodal latitudinal pattern in genetic diversity. Yet this pattern is strongly influenced by taxonomy, as illustrated by the different patterns observed for MHF animals and plants. When considering the ecoregions, we report a significant and positive SGDC. The lack of differences in genetic diversity between protected and unprotected areas is alarming and contributes to the current call to strengthen the consideration of genetic diversity in biodiversity management and conservation plans. Overall, this study broadens our basic understanding of the macroscale patterns of genetic diversity of MHF taxa, providing some of the first insights into marine macrogenetics.

2 | METHODS

2.1 | Global genetic diversity database

The global genetic diversity database was built from a literature survey conducted on 28 October 2019 on the Institute for Scientific Information Web of Science following the method described in Supporting Information Appendix S1. From 809 articles, 261 microsatellite studies were included in the database (Supporting Information Appendix S1: Figure S1.1). We focused exclusively on microsatellites because they provide a relevant estimate of genome-wide diversity and are more appropriate than mitochondrial markers for the estimation of genetic diversity (Paz-Vinas et al., 2021). In the database, one record corresponds to one local population – considered as a group of individuals of the same species – in a specific geographic location defined by latitude and longitude coordinates and by a depth range. For each record, we: (a) added the variable 'taxon' (bryozoan, hexacoral, hydrozoan, octocoral, seagrass, seaweed and sponge) by using the World Register of Marine Species (WoRMS) Taxon Match tool (https://www.marinespecies.org/aphia.php?p=match); (b) assigned a marine ecoregion and province (the smallest-scale units and slightly larger areas in the Marine Ecoregions of the World – MEOW – system, respectively) according to Spalding et al. (2007), and (c) added a marine protected area (MPA) variable (protected versus non-protected) by using the Protected Planet database (https://www.protectedplanet.net) (Supporting Information Appendix S1: Figure S1.2).

For each record when available, we extracted the number of alleles (N_a), observed heterozygosity (H_o), expected heterozygosity (H_e), F_{IS} and allelic richness (Ar). We used only H_e in the subsequent analyses. Contrary to H_o, H_e is estimated from allele frequencies and not from individual genotypes and thus not biased by the level of inbreeding within a population (Ritland, 1996). Compared to N_a, H_e

is less influenced by the sampling effort (Toro et al., 2009). Finally, Ar was included in only 20% of the records. Despite this, it was positively correlated to H_e globally and when considering each taxon separately (Supporting Information Appendix S1: Figure S1.3).

2.2 | Mapping genetic diversity at a global scale

We mapped: (a) the number of records and mean H_e for each marine province using a *bubble* global map; and (b) the biogeographic distribution of the different studied taxa in each marine province using scatter pie plot maps in the R package 'scatterpie' (R Core Team, 2022; Yu, 2021; see Supporting Information Appendix S1: Figure S1.2; Appendix S4: Table S4.1).

2.3 | Genetic diversity predicted by latitude, taxon, and conservation status

We modelled the effects of latitude, taxon, and conservation status on genetic diversity, using H_e as a proxy. A series of statistical models were constructed using H_e as a dependent variable, and latitude, taxon and MPA as predictor variables (Supporting Information Appendix S2). Briefly, H_e was transformed with the Box–Cox function while the latitudinal effect was introduced as a smooth nonparametric predictor. Taxon was introduced first as a categorical factor with seven levels (bryozoan, hexacoral, hydrozoan, octocoral, seagrass, seaweed and sponge) and, additionally, in a separate model, as a two-level categorical factor (animals versus plants). MPA was defined as a categorical factor with two levels (protected versus non-protected; see Supporting Information Appendix S2).

We fitted all the models using the *gam* and the *gamm4* functions, from the R packages 'mgcv' (Wood, 2011) and 'gamm4' (Wood & Scheipl, 2014), respectively. The best model was selected by the largest absolute value of the relative maximum likelihood obtained in the model fit procedure (see Supporting Information Table S2.1). Because in the selected model there was a significant interaction between taxon and MPA, we performed a post-hoc least significant difference (LSD) test to assess the differences between the groups resulting from the combinations of levels of the two factors. We conducted the analysis of variance of the selected model with the *Anova* function from the 'car' R package (Fox & Weisberg, 2018). The LSD test was performed with the *LSD test* function from the 'agricolae' R package (De Mendiburu, 2014).

2.4 | Species genetic diversity correlation

A set of models was fit to predict H_e as a function of species diversity. Occurrence data of MHF species were obtained from previous work (Pagès-Escolà, 2019), which combined species occurrence data obtained from the Global Biodiversity Information Facility system (GBIF.org, 2022) and the Ocean Biodiversity Information

System (OBIS, 2020). The dataset was filtered for duplicate records, records non-available at species levels, and records without geographic coordinates. Then, we included the variable taxon by using the WoRMS Taxon match tool, reviewed the non-accepted species extracted from the original publications, and removed the extinct taxa (e.g., the cnidarian subclass Ceriantharia). The species diversity in each raster cell (5×5 degree) was estimated using the: (a) species diversity (i.e., the count of species per cell), (b) corrected species diversity (i.e., accounting for sample sizes using a rarefaction function), (c) Shannon diversity index and, (d) Simpson diversity index. Then, we computed the mean value per ecoregion or province for each of the four measures (Supporting Information Appendix S1: Figure S1.2). Considering alternatively the whole genetic diversity database or each of the five taxa with a number of occurrences higher than 30 (i.e., hexacoral, octocoral, seagrass, seaweed and sponge), we generated 72 different models by combining the three ways of grouping spatial data (raster 5×5 degrees grid cells, ecoregions, and provinces) with the four measures of species diversity. The best models were selected according to: (a) the diagnostic plots for normal distribution, linear relationship, residual homogeneity and lack of autocorrelation; and (b) the 95% confidence intervals of the model predictions. 'Corrected species richness' reported by 'ecoregions' was the proxy for species diversity that better fit genetic diversity in our models (Supporting Information Appendix S3: Table S3.1). Two outliers according to the Bonferroni test (i.e., ecoregions nos. 82 and 88) were removed. Considering each taxon separately, none of the model alternatives succesfully fit the SGDC (Supporting Information Appendix S3: Table S3.2).

3 | RESULTS

3.1 | Overview of the genetic diversity database

We extracted data from 261 different studies representing 9,306 local populations (i.e., records) of 140 species that belong to seven different taxa: bryozoans (28 populations of 3 species), hexacorals (4,652 populations of 55 species), hydrozoans (22 populations of 7 species), octocorals (1,309 populations of 15 species), seagrasses (1,687 populations of 16 species), seaweeds (1,211 populations of 32 species) and sponges (397 populations of 12 species). Data were heterogeneously distributed as shown in Figure 1a,b (see Supporting Information Appendix S4).

3.2 | Genetic diversity estimated by the expected heterozygosity

The global mean genetic diversity, based on H_e, was $.51 \pm .21$ (Supporting Information Appendix S4: Table S4.1). The Warm Temperate Northwest Atlantic province showed the highest genetic diversity (mean $H_e \pm SD$: $.74 \pm .18$), followed by the Bay of Bengal ($H_e = .67 \pm .27$) and the Cold Temperate Northwest Atlantic

($H_e = .63 \pm .19$). The lowest values of genetic diversity were found in the Warm Temperate Southwestern Atlantic ($H_e = .38 \pm .29$) and Gulf of Guinea ($H_e = .38 \pm .40$; Supporting Information Appendix S4: Table S4.1, Figure S4.4). The hexacorals *Zoanthus sansibaricus*, *Galaxea fascicularis* and *Acropora muricata* ($H_e = .89 \pm .08$, $.83 \pm .08$ and $.82 \pm .23$, respectively), and the sponge *Spongia officinalis* ($H_e = .85 \pm .11$) were the species showing the highest values. Contrastingly, the species with the lowest H_e were the bryozoan *Myriapora truncata* ($H_e = .03 \pm .00$), and the seaweeds *Ulva prolifera*, *Fucus guiryi* and *Sargassum muticum* ($H_e = .044 \pm .02$, $.08 \pm .06$ and $.11 \pm .10$, respectively; Supporting Information Appendix S4: Table S4.2).

3.3 | Statistical analysis

The best model is summarized by the following equation (Supporting Information Appendix S2: Table S2.1):

$$\text{Genetic diversity} (H_e) \sim \text{smoothed latitude} + \text{taxa}^* \text{ MPA} \qquad (1)$$

The genetic diversity pattern determined by the smoothed latitude (estimated degrees of freedom $= 8.52$; p-value $< .01$, Figure 2a) showed reasonable confidence intervals, especially between -40 and $60°$, but not at higher latitudes, likely because of smaller sample size (Figure 2a). The model slightly differs when separating marine habitat forming animals (MHFA; estimated degrees of freedom $= 7.46$; p-value $< .01$, Supporting Information Appendix S2: Figure S2.2a) and plants (MHFP; estimated degrees of freedom $= 8.41$; p-value $< .01$, Supporting Information Appendix S2: Figure S2.2b). While it peaks at mid-latitudes in the Southern Hemisphere, the genetic diversity of MHFA plateaus around the equator, then sharply increases at lower latitudes, slightly plateaus and increases again in the Northern Hemisphere. The genetic diversity of MHFP shows a complex and wiggly pattern with an overall flat trend only slightly peaking at intermediate latitudes in the Northern Hemisphere (Supporting Information Appendix S2: Figure S2.2).

The effect of taxon on H_e was significant ($F = 99.562$, p-value $< .001$, Figure 2b, Supporting Information Appendix S2: Table S2.2). When compared against the bryozoan reference level, this result is mainly driven by seagrasses (t-test $= -4.11$, p-value $< .001$; Figure 2b; Supporting Information Appendix S2: Table S2.3), seaweeds (t-test $= -5.09$, p-value $< .001$; Figure 2b; Supporting Information Appendix S2: Table S2.3) and octocorals (t-test $= -0.23$, p-value $< .01$; Figure 2b; Supporting Information Appendix S2: Table S2.3). The mean H_e of MHFP was lower (seaweed $H_e = .43 \pm .21$; seagrass $H_e = .51 \pm .22$) than the mean H_e of MHFA (hydrozoan $H_e = .54 \pm .09$, hexacoral $H_e = .55 \pm .25$, octocoral $H_e = .61 \pm .21$, sponge $H_e = .64 \pm .21$ and bryozoan $H_e = .66 \pm .13$; Figure 2b). These differences were also corroborated by the model considering two categories of taxa (MHFA versus MHFP; Supporting Information Appendix S2: Tables S2.2, S2.3 and S2.4). Noteworthily, leverage plots by taxon showed homogeneity in their distribution (Supporting Information Appendix S2: Figure S2.3). MHFA and MHFP responded
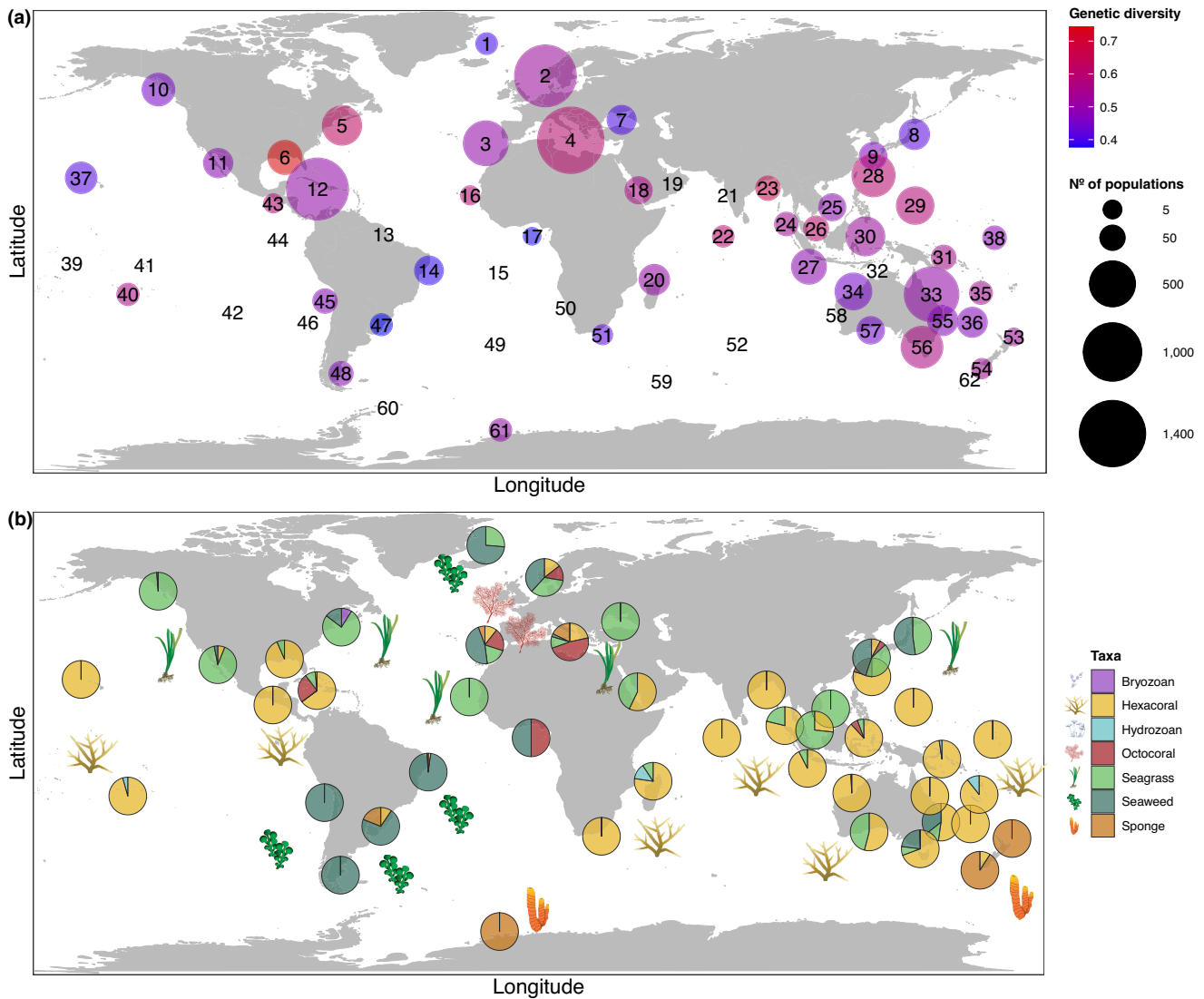
FIGURE 1 Spatial patterns of genetic diversity at global scale. (a) Genetic diversity in each of the 62 marine provinces is estimated based on the mean expected heterozygosity (H_e) value represented by the colour scale from blue ($H_e = .38$) to red ($H_e > .7$). The number of populations inside each marine province is represented by the bubble width. The numbers inside bubbles indicate the marine province identity, according to Spalding et al. (2007) (see Supporting Information Table S4.1 for details). Note that empty bubbles represent marine provinces without genetic diversity occurrences. (b) The global biogeographic distribution of each taxon is represented by equal size scatter pies. Colours represent the proportion of each studied taxon (bryozoans, hexacorals, hydrozoans, octocorals, seagrasses, seaweeds and sponges) inside a particular marine province. Note that only marine provinces with genetic diversity are shown. Includes symbols from integration and application network Library of Symbols, University of Maryland.

similarly to the model, thus strengthening their differences in genetic diversity (Supporting Information Appendix S2: Figure S2.3).

The effect of MPA on H_e was not significant, neither considering all the taxa ($F = 0.939$, p-value $= .333$) nor considering the MHFA versus MHFP ($F = 0.81$, p-value $= .37$; Supporting Information Appendix S2: Table S2.2). Yet, the interaction between the factors 'taxon' and 'MPA' was significant in the two models (all taxa: $F = 20.588$, p-value $< .001$; MHFA versus MHFP: $F = 10.89$, p-value $< .01$; Supporting Information Appendix S2: Table S2.2). The LSD post-hoc test performed to compare between the levels defined by the interaction between taxon and MPA showed that the situation differs between each taxon (Supporting Information Appendix S2: Figure S2.4).

Octocorals showed higher genetic diversity inside MPAs (t-test $= 0.17$, p-value $< .05$, Supporting Information Appendix S2: Table 2.3). While the differences were not significant, bryozoans, hexacorals and hydrozoans showed lower genetic diversity inside MPAs and seagrasses, seaweeds and sponges showed higher genetic diversity inside MPAs (Supporting Information Appendix S2: Figure S2.4).

3.4 | Species–genetic diversity correlation

The SGDC was significantly positive ($r^2 = .38$, p-value $< .001$; Figure 3) when considering the whole dataset and the rarefied

FIGURE 2 Biogeographic patterns and marine protected areas (MPAs). The generalized additive model (GAM; red solid curve) of genetic diversity predicted by the smoothed latitude (a), where blue dashed lines indicate the 95% confidence intervals and green vertical line the equator; the taxa (b), where a red asterisk indicates significant differences (*p-value < .01, and **p-value < .001; see Supporting Information Table S2.3); and protection (c), expressed as the database records inside and outside MPAs according to Protected Planet. Genetic diversity was estimated based on expected heterozygosity (H_e). Data density is represented on the x axes by tick marks. The y axis in (a) represents the spline function for latitude of the GAM model and in (b) (c) the linear coefficients for the independen variables 'Taxa' and 'MPA'. Includes symbols from integration and application network Library of Symbols, University of Maryland.
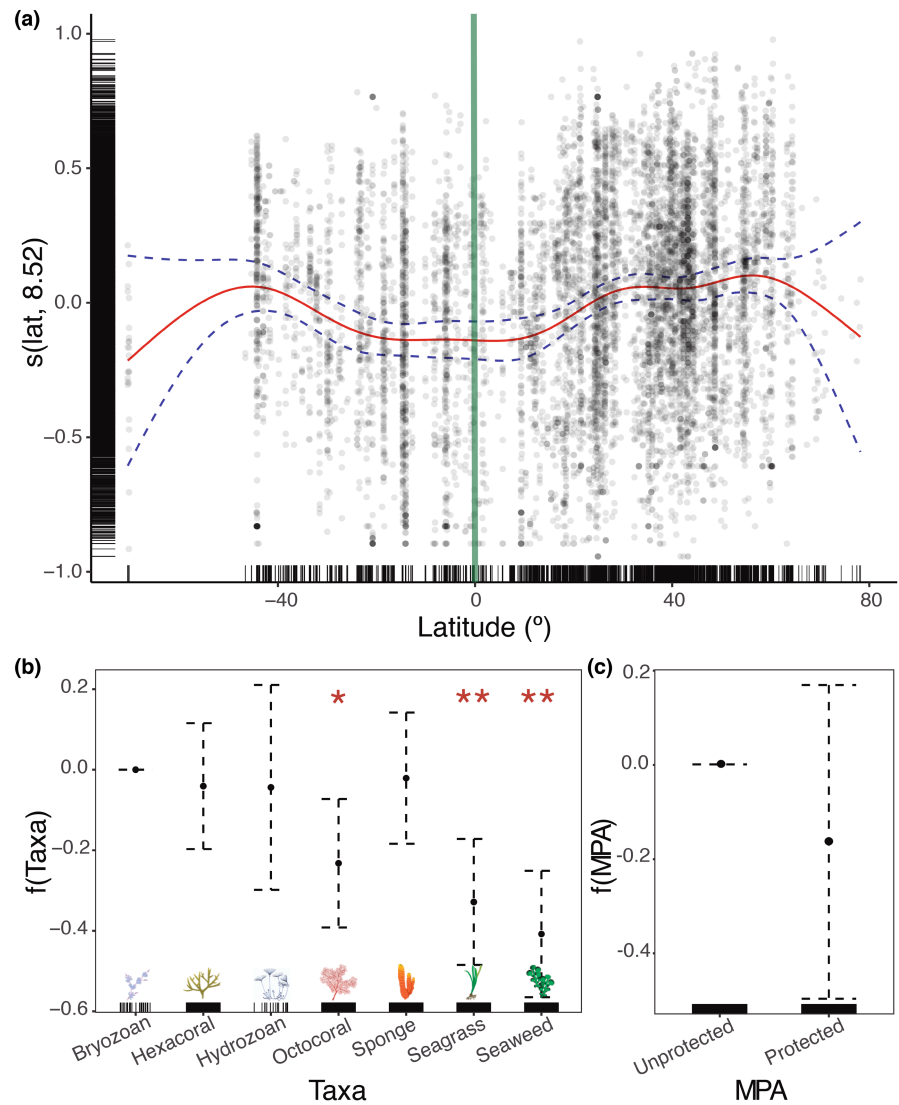
estimate of species richness at the scale of marine ecoregions (see also Supporting Information Appendix S3: Table S3.1).

4 | DISCUSSION

This study provides the first macrogenetic exploration of global patterns and drivers of genetic diversity in an ecologically important functional group, the MHF species (> 9,000 populations of 140 species; Figure 1). Further, it provides baseline macrogenetic data that may help guiding future genetic monitoring and conservation actions. We analysed this dataset to reveal a heterogeneous distribution of the genetic diversity with a significant biogeographic pattern characterized by a bimodal latitudinal trend and influenced by taxonomy. In addition, we show a significant and positive correlation between species and genetic diversity (SGDC) at the scale of the marine ecoregions. Alarming, the levels of genetic diversity are not related to the protection status.

4.1 | Marine habitat-forming animals display higher genetic diversity than marine habitat-forming plants

Overall, the mean value of H_e for MHF species was moderate (.51 ± .21) compared to values reported in other marine species (e.g., fishes > .7 based on microsatellites; Pinsky & Palumbi, 2014). This genetic diversity was not homogeneously distributed between MHFP (H_e = .47) and MHFA (H_e = .57). This result echoes those of a recent study that found lower genetic diversity in terrestrial plants compared to terrestrial animals (vertebrates and molluscs), which was explained by their respective effective population sizes (N_e; De Kort et al., 2021). Interestingly, the heterozygosity values for MHFP and MHFA recorded here are within the range of values for terrestrial plants (.21) and animals (.72) [obtained from amplified fragment length polymorphisms (AFLPs) and microsatellites; De Kort et al., 2021]. One can wonder whether this increase in H_e results from an increase in N_es, from terrestrial plants, MHFP, MHFA to terrestrial animals. Noteworthily, the order of magnitude of N_e is still
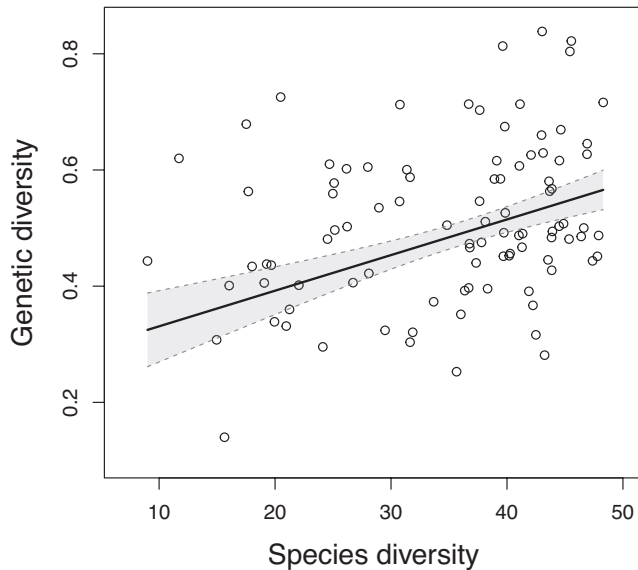
FIGURE 3 Species–genetic diversity correlation. The trend line is modelled as the output of a linear model of the correlation between the mean expected heterozygosity (H_e) and the mean corrected species diversity per ecoregion (Pearson's correlation $r^2 = .38$ $p < .001$). The shaded area corresponds to the standard error of the linear model.

a matter of debate in marine species (Hare et al., 2011). Marine invertebrates, which include MHFA, are usually considered as highly fecund species with high long-term species-wide N_es (Romiguier et al., 2014), while published studies on MHFP point toward lower N_es (Jahnke et al., 2019; but see Jueterbock et al., 2018). The characterization of the life-history traits driving variations in N_e is challenging (Luikart et al., 2021). A recent study highlighted that the trade-offs among survival, development and reproduction in the evolution of terrestrial and aquatic (including marine) species are the same, but with some differences in life-history strategies (Capdevila et al., 2020). In the case of terrestrial plants and animals, De Kort et al. (2021) identified the highly contrasted reproductive strategies (active search for compatible mate versus passive reproduction), mating systems (outcrossing versus self-fertilization) and longevity (short versus long-live species) as the main drivers of the differences in N_es. By comparison, MHFA and MHFP are sessile taxa relying on passive reproduction and sharing a variety of reproductive strategies [e.g., asexual and sexual reproduction ranging from hermaphroditic to fully gonochoric mating systems; see Kerr et al. (2011) in corals; Arnaud-Haond et al. (2020) in seagrasses]. Moreover, many MHFA and MHFP are long-lived species with long generation times (> 10 years) and life spans of several hundreds of years (e.g., Montero-Serra et al., 2019). In this context, we first hypothesize that the high fecundity and higher reproductive frequency of MHFA increase their N_e leading to higher genetic diversity compared to MHFP. Then, the shared (e.g., sessile, long-lived species) but also highly variable (e.g., reproduction) life-history traits observed in MHFP and MHFA may buffer the difference in their respective N_e compared to the difference observed between terrestrial plants

and animals, putting MHFP and MHFA in an intermediate position. The high stochasticity in reproduction and recruitment reported for many MHFA, known as sweepstakes reproductive success (see Pudovkin & Hedgecock, 2011), will also decrease N_e in comparison to their census population size. In addition to the complex reproductive strategies previously mentioned, this sweepstakes reproductive success can potentially explain the lowest H_e of MHFA compared to terrestrial and strictly outcrossing animals considered by De Kort et al. (2021). Noteworthily, H_e reported in fish (.7 with microsatellites; Pinsky & Palumbi, 2014) is similar to the value reported in terrestrial animals (.72; De Kort et al., 2021), strengthening the idea that specific reproductive strategies in MHFA may drive their low N_e. A formal test of these different hypotheses cannot be done until the knowledge gaps regarding life-history traits for many of the 140 MHF species under study are filled (Capdevila et al., 2020).

4.2 | The impact of latitude on the pattern of genetic diversity

We revealed a significant bimodal latitudinal trend of genetic diversity with mid-latitude smoothed peaks and a small dip at the equator. This pattern excludes a unimodal latitudinal gradient of the genetic diversity in MHF species. Considering MHFA and MHFP separately, the influence of latitude remains significant. Yet the global bimodal trend is mostly driven by the genetic diversity of MHFA while the diversity of MHFP shows a flatter latitudinal pattern. Contrasting genetic diversity patterns among taxa have also been reported among terrestrial species. A strong latitudinal genetic gradient was observed in terrestrial mammals and amphibians (mitochondrial data by Miraldo et al., 2016; but see Gratton et al., 2017), and in birds and fishes (mitochondrial data by Millette et al., 2020), while the gradient was weak in vertebrates and molluscs (AFLP and microsatellite data by De Kort et al., 2021) and absent in insects (Millette et al., 2020) and plants (De Kort et al., 2021).

These idiosyncratic patterns in genetic diversity contrast with the prevalence of the latitudinal gradient in terrestrial species diversity. Indeed, the increase in species richness from high latitudes toward the tropics reaching a single (unimodal) peak at the equator is one of the most pervasive patterns characterizing terrestrial biodiversity (Gaston, 2000). In the marine realm, recent studies have shown the pattern of species diversity generally follows a bimodal distribution that peaks close to mid-to-tropical latitudes (e.g., Chaudhary et al., 2016; Pagès-Escolà, 2019). Interestingly, the global and the MHFA genetic patterns fit this pattern of species diversity. A recent effort to provide a diversity-gradient synthesis accounting for the different levels of diversity in terrestrial species confirmed the complex link between latitudinal genetic and species diversity patterns. This was explained by the strong influence of historical and contemporary factors, in particular, taxon-specific life-history traits, on genetic diversity gradients (Lawrence & Fraser, 2020). Our results expand these conclusions to MHF species. First, the idiosyncratic nature of latitudinal genetic diversity patterns is likely a feature

shared by terrestrial and marine species. Additionally, the MHFA but not the MHFP genetic pattern is related to the marine species diversity pattern corroborating the taxon-specific influences of life-history traits on genetic gradients.

4.3 | Positive correlation between species and genetic diversity

In line with the shared latitudinal patterns between genetic and species diversity, a positive and significant SGDC was revealed when considering the whole dataset at the scale of marine ecoregions. The mean H_e of MHF species increases with the number of MHF species per ecoregion. This positive SGDC expands the positive correlations already reported in different taxa such as terrestrial mammals (Theodoridis et al., 2020; but see Schmidt, Dray, & Garroway, 2022) and marine and freshwater fishes (Manel et al., 2020). In the marine realm, yet on regional scales, positive SGDCs were also reported in temperate (e.g., Cahill et al., 2017) and tropical sessile communities (e.g., Selkoe et al., 2016). In recent years, the interactions between these two levels of diversity (genetic and species) have been the focus of renewed interest, owing to their basic (e.g., identification of the drivers of biodiversity patterns) and applied (e.g., simultaneous estimation of the diversity at different levels) implications (Lawrence & Fraser, 2020; Vellend & Geber, 2005). Most of the studies characterizing SGDCs to date have been conducted at a regional scale (but see Manel et al., 2020; Theodoridis et al., 2020). Yet, these studies reported contrasting results, with positive (e.g., Vellend & Geber, 2005), non-significant (e.g., Reisch & Schmid, 2019) and even negative correlations (e.g., Marchesini et al., 2018). These results, combined with recent theoretical developments (Lawrence & Fraser, 2020), point toward the multifactorial nature of the underlying processes (e.g., mutation rate, local competition, site carrying capacity; Laroche et al., 2015). When considering the global scale, the occurrence of a positive SGDC in terrestrial mammals has been linked to three complementary hypotheses: the 'evolutionary speed' (Gillman et al., 2009), 'time and area' (Mittelbach et al., 2007) and 'Red Queen' (Brown, 2014) hypotheses (Theodoridis et al., 2020). Yet, the bimodal latitudinal genetic diversity pattern previously discussed questions these three hypotheses in the case of MHF species, since they rely on unimodal distributions of genetic and species richness peaking at the equator. Alternatively, the SGDC reported here may result from a direct ecological effect of the genetic diversity of MHF species, for instance on habitat complexity, with positive impacts on associated communities (e.g., Reusch et al., 2005; see also Raffard et al., 2019). The identification of the drivers of the positive SGDC revealed here is challenging. It will require significant efforts in acquiring and compiling taxonomic and phylogenetic diversity and palaeoclimatic data for MHF species to further test the first three hypotheses. Testing the direct ecological effects, albeit at small spatial scale, require the development of experimental approaches manipulating genetic diversity in MHF species (e.g., Reusch et al., 2005).

4.4 | The pattern of genetic diversity is disconnected from the network of protected areas

No significant difference in the level of genetic diversity was observed between protected and unprotected areas, although some taxa (octocorals, seagrasses, seaweeds and sponges) showed larger values inside MPAs. Accordingly, protected areas do not support higher genetic diversity, contrary to previous expectations (Roberts et al., 2017). These results are in line with previous studies revealing the contrasting impacts of protected areas on genetic diversity. Higher genetic diversity in protected populations was observed in different marine invertebrate species, albeit on very local spatial scales (e.g., Ledoux et al., 2021), while no effect was reported in some terrestrial species (e.g., Guzmán et al., 2015). At the macro-scale, similar contrasting patterns were confirmed in 44 vertebrates (including mammals, reptiles and amphibians) studied across North America with a higher genetic diversity of protected populations in only 48% of the species (Thompson et al., 2021).

Owing to the critical roles of genetic diversity in genetic adaptability and responses to climate change, this lack of differences between protected and unprotected areas is concerning. It may result from the low priority of genetic diversity in conservation planning (Hoban et al., 2020). Recent methodological improvements are likely to help with the inclusion of genetic diversity and related metrics in biodiversity management (e.g., Paz-Vinas et al., 2018). Yet, considering that some protected areas were established several decades ago, genetic diversity should have indirectly benefited from existing conservation planning. Low levels of regulation may potentially explain why many protected areas globally have failed to promote higher genetic diversity (see Claudet et al., 2020), strengthening the recent calls to ensure that genetic diversity is considered in conservation planning and to enforce existing regulations (Hoban et al., 2021).

4.5 | Potential limitations and future directions

In spite of the 9,000 records coming from 140 species, we evidenced an important disparity in population genetic efforts worldwide, with both overlooked taxa (e.g., bryozoans), underrepresented marine provinces (e.g., Western Africa, Tropical East Pacific) and the combination of the two (e.g., octocorals in tropical provinces). This disparity is mostly linked to biased sampling strategies both at the taxonomic and geographic levels. Regarding the seven taxa considered here, the sampling efforts mostly reflect the traditionally studied species or phyla in each area. For instance, most of the studies conducted in Australia were focused on hexacorals, although octocorals and sponges are also abundant (e.g., Chin et al., 2020). Besides, some taxa such as bryozoans and hydrozoans have been overlooked by population geneticists (five studies in total), most likely because of the challenges linked to the identification of molecular markers (Lee et al., 2011). While our dataset includes more than 70% of the marine provinces (Figure 1a; Supporting Information Appendix S4: Table S4.1), we

also evidenced how the population genetics knowledge in MHF species remains scarce in various provinces (e.g., Gulf of Guinea), and even non-existent in other ones (e.g., Subantarctic New Zealand) (Figure 1a; Supporting Information Appendix S4: Table S4.1). Prioritizing future sampling efforts on these overlooked taxa and regions will be key to furthering our understanding regarding MHF species macrogenetics.

Besides the sampling gaps, the lack of ecological data in many of the targeted species precludes digging deeper into the potential impact of life-history traits on the reported patterns. Gathering these data is particularly challenging and still an ongoing endeavour in many marine species (Capdevila et al., 2020). Yet, the development of global demographic databases (e.g., COMPADRE and COMADRE Plant and Animal Matrix Database, respectively; Salguero-Gómez et al., 2015, 2016) is promising. It should for instance allow formal testing of the influence of reproductive strategies, longevity and effective population size on the genetic patterns.

Our assessment of macrogenetic patterns in MHF species using microsatellites is of particular conservation interest, as previous studies were based on mitochondrial DNA (e.g., Manel et al., 2020; Millette et al., 2020; Theodoridis et al., 2020; see also Paz-Vinas et al., 2021). Yet, the use of microsatellites induced a focus on neutral diversity putting aside adaptive variation in spite of its critical role in the context of global change. The ongoing development of genomic resources to conduct population genomic studies in MHF species will open new perspectives for macrogenetics.

Refining our knowledge regarding macrogenetics in MHF species is a prerequisite to improving the efficiency of large-scale conservation and management efforts (Leigh et al., 2021). It requires enhanced collaboration among population geneticists and ecologists to overcome the existing sampling, ecological and genomic gaps in knowledge. In the meantime, protecting the results established by the baseline set by our study should be a priority. Hopefully, this ambitious objective will benefit from the recently adopted 'Kunming-Montreal Global Biodiversity framework' within the Convention on Biological Diversity, which aims to maintain genetic diversity within populations of wild species, safeguarding their adaptive potential (CBD/COP/15/L25, 2022).

AUTHOR CONTRIBUTIONS

Ignasi Montero-Serra, Cristina Linares and Jean-Baptiste Ledoux conceived the study. Laura Figuerola-Ferrando, Ignasi Montero-Serra, Marta Pagès-Escolà and Jean-Baptiste Ledoux collected the data. Laura Figuerola-Ferrando, Ignasi Montero-Serra, Marta Pagès-Escolà, Aldo Barreiro and Jean-Baptiste Ledoux performed the statistical analyses. Laura Figuerola-Ferrando, Aldo Barreiro and Jean-Baptiste Ledoux wrote the paper with inputs from all co-authors.

CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in 'CORA. Repositori de Dadeds de Recerca' at https://doi.org/10.34810/data213.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.