The global protected area network does not harbor genetically diverse populations

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Abstract

Global biodiversity conservation targets include expanding protected areas and maintaining genetic diversity within species by 2030. However, the extent to which existing protected areas capture genetic diversity within species is unclear. We examined this question using a global sample of nuclear population-level genetic data comprising georeferenced genotypes from 2,513 local populations, 134,183 individuals, and 176 species of mammals and marine fish. We found that the existing protected area network does not capture populations with higher than average genetic diversity, and populations within protected areas are not more genetically differentiated than populations sampled elsewhere. This general trend does not preclude their effectiveness for specific species or regions currently, or in the future. While it may be desirable to prioritize regions with high genetic diversity when designating new protected areas, we caution that this will not be possible in many of the most at-risk regions of the world due to a lack of data. Continued focus on minimizing population decline and maintaining connectivity between protected areas remain essential considerations in area-based conservation for mediating genetic diversity loss.

Keywords: biodiversity, genetic diversity, genetic differentiation, effective population size, conservation policy

Main text

The Kunming-Montreal Global Biodiversity Framework (KMGBF) adopted in 2022 identified a series of urgent, action-oriented conservation targets for 2030 (CBD, 2022). Two key targets are to expand protected area coverage to 30% of land and sea (the ‘30 x 30’ target, i.e. KMGBF Target 3) and to conserve genetic diversity in all species (KMGBF Target 4). These targets intersect. Protected areas could strengthen the protection of genetic diversity in wild species, and the effectiveness of protected areas could be enhanced by encompassing genetically diverse populations as this would also protect the evolutionary processes that organize and sustain biodiversity (Arponen, 2012; Moritz, 2002). Intraspecific genetic diversity is the most fundamental level of biodiversity, underlying the microevolutionary processes that contribute to populations’ adaptive capacity and resilience to environmental change (Lande & Shannon, 1996). The growing human environmental footprint is associated with the erosion of genetic diversity across many species on land and in oceans (DiBattista, 2008; Karachaliou et al., 2024; Leigh et al., 2019; Pinsky & Palumbi, 2014; Schmidt et al., 2020). The expansion of protected areas buffering populations from environmental change and exploitation could be a powerful tool for limiting further genetic diversity losses.

While protected areas are a mainstay of conservation policy and a widely used tool to protect biodiversity in all its forms, their general effectiveness for conserving genetic diversity is not well understood (but see Figuerola-Ferrando et al., 2023 for marine habitat-forming invertebrates). From a conservation genetics standpoint, we consider a protected area to be effective if it captures genetically diverse or differentiated populations. We tested whether the current global protected area network overlaps with relatively genetically diverse or genetically distinct populations across terrestrial and marine realms. We repurposed publicly archived nuclear genetic data comprising georeferenced genotypes from 2,513 local populations, 134,183 individuals, and 176 species of mammals and marine fish (Fig. 1). Using a standardized analytical pipeline (see Methods), we assessed contemporary effective population size, which provides an estimate of the strength of genetic drift in each local population; gene diversity and allelic richness, which measure genetic diversity; and population-specific F_{ST}, a metric of genetic differentiation (see Methods). We used the World Database on Protected Areas (UNEP-WCMC and IUCN, 2022), which contains information on 293,754 protected areas on land and in oceans, to assess the effectiveness of the global protected area network for conserving intraspecific genetic diversity, genetically distinct populations, or both. We evaluated protected area effectiveness in two ways: by considering the protection status of sample locations (in- or outside of a protected area), and the proximity of sample locations to the nearest protected area.

We then explored whether protected area effectiveness was influenced by its area, International Union for Conservation of Nature (IUCN) designation (IUCN, 1994), or species body size. The IUCN designates protected areas as having strict protection of biodiversity (categories I-IV) or sustainable resource use (categories V-VI). Larger, biodiversity-focused protected areas may harbor larger, more genetically diverse or differentiated populations. In regard to body size, genetic diversity may be better captured for smaller bodied species as they could attain larger populations inside protected areas (Williams et al., 2022).

Protected area effectiveness for genetic diversity and differentiation

We found little evidence that the current terrestrial and marine protected area network captures genetically diverse or differentiated populations across mammal and fish species in a generalizable way. This could limit the ability of protected areas to sustain resilient populations in the long-term.

Spatially explicit Bayesian hierarchical models (see Methods) suggested that the genetic composition of terrestrial mammal and marine fish populations was not associated with whether they occurred within protected areas or with a local population's proximity to a protected area (Table 1, Fig. 2). Most sites in our analyses were located outside protected areas (75% of terrestrial data, 80% of marine). We detected a weak negative relationship between distance to protected area and genetic differentiation in terrestrial mammals, however this relationship appeared to be driven by a strong outlier species (*Dama dama*), and disappeared when this species was removed. Protected area effectiveness was generally similar for species of all body sizes, however smaller mammals tended to have slightly higher allelic richness inside protected areas (Table S2, Fig. S1). Protected area effectiveness in terms of a local population's nearness to a protected area was also unrelated to body size for both fish and mammals (Fig. S1). The size of protected areas did not influence effectiveness for any genetic metric or realm (Table S3, Figs. S2, S3). Finally, we found no differences between the effectiveness of terrestrial protected areas with restricted human access (IUCN categories I-IV) and those designated for sustainable use (V-VI; Table S3, Fig. S2).

Species-specific protected area effectiveness did not strongly deviate from the overall effect across species in any model (Fig. 2). This pattern likely reflects the fact that protected areas were haphazardly placed with respect to genetic diversity and population structure for these taxa. Historically, protected areas tended to be designated for the protection of landscapes important to people rather than expressly for the protection of biodiversity, and most often genetic diversity is not directly factored into design decisions (Jenkins et al., 2015; Phillips, 2004). However protected areas that were built around habitats and species, such as the

Europe-wide Natura 2000 network, may have been expected to better capture areas of high intraspecific genetic diversity. Such differences in management strategies and priorities at population, species, or landscape levels could have contributed to variation in protected area effectiveness at the tails of effect size distributions (Fig. 2). For example, the Belize Barrier Reef Reserve System protects nearly 75,000 hectares of mangrove forest (Cho-Ricketts & Cherrington, 2011), and also happened to capture a well-connected, genetically diverse local population of the Mangrove rivulus (*Kryptolebias marmoratus*). In contrast, the Laguna Atascosa National Wildlife Reserve, which protects ~18,000 hectares of intact brushland habitat in the Lower Rio Grande Valley, contains the largest remaining ocelot (*Leopardus pardalis*) population in the United States. This population is isolated and has notably low genetic diversity (Janecka et al., 2016). While some strategies have inadvertently protected high-diversity populations, protected areas are also used to manage at-risk populations with low genetic diversity. Because protected areas are important for both genetically diverse and depauperate populations, a focus on protecting critical habitat and maintaining stable population sizes could be a strategy that is broadly effective for conserving genetic diversity in species across a range of extinction risks.

Conserving genetic diversity and long-term maintenance of protected areas

In general, successes in halting population declines within protected areas have been mixed. In terms of population demography, protected areas, when effective, generally slow the pace of population declines rather than halt decline altogether (Geldmann et al., 2013; Nowakowski et al., 2023; Santangeli et al., 2023). While our results suggest that protected areas do not currently contain highly genetically diverse populations in general, they may still help to reduce future genetic diversity loss by reducing rates of population decline which will in turn slow genetic drift. After populations decline, they continue to lose genetic diversity due to genetic drift for many generations if they remain small. Given that most protected areas were recently established (90% of protected areas were established after 1990) this type of effectiveness would be difficult to detect (UNEP-WCMC and IUCN, 2022).

Our results do not preclude protected areas being effective for target species and the conservation of regions with high genetic diversity in the future (Minter et al., 2021; Paz-Vinas et al., 2018). Given the pressing timelines associated with 30 x 30 target commitments, it may be tempting to move forward with including genetic data in spatial prioritizations for the design of new protected areas. This strategy could considerably increase the effectiveness of protected areas, as it would not only preserve species and populations, but the evolutionary processes that contribute to biodiversity resilience (Arponen, 2012; Hanson, Marques, et al., 2020; Moritz, 2002). However, including genetic diversity in protected area design would require carefully balancing priorities for different aspects of biodiversity. For example, recent evidence suggests nuclear genetic diversity within species can be negatively related to species richness in some vertebrates (Kahilainen et al., 2014; Schmidt, Dray, et al., 2022; Schmidt, Munshi-South, et al., 2022).

Furthermore, while prioritizations including multi-species genetic data may be feasible for certain areas with sufficiently dense spatial and taxonomic data coverage (e.g., the California Conservation Genomics Project https://www.ccgproject.org/), this level of data availability is rare (Paz-Vinas et al., 2023), and as our own data suggest, largely confined to North America and Europe (Fig. 1). A recent survey of publicly available nuclear genetic data (microsatellites and genomic data) reported that only 24% of global protected areas contained at least 5 genetically sampled local populations (Paz-Vinas et al., 2023). The sparse and geographically unbalanced availability of genetic data suggests that at present we cannot robustly incorporate it into protected area prioritization for the vast majority of species and regions. Data gaps can potentially be circumvented with proxies for genetic diversity (Hanson, Veríssimo, et al., 2020; Hoban et al., 2022). However, we do not currently have reliable substitutes for genetic data to approximate the genetic composition of local populations or regional multi-species diversity could improve the efficacy of prioritization actions (Hanson, Veríssimo, et al., 2020; Schmidt, Hoban, et al., 2023).

In the meantime, focusing on minimizing population decline and maintaining connectivity between protected areas remain essential considerations in area-based conservation for protecting genetic diversity. Genetic diversity is a lagging metric of population demography and a forward-looking metric of population resilience, meaning long-term maintenance of high-quality protected areas is critical. Isolation, low ecological representativeness, lack of resources, and mismanagement all could threaten the effectiveness and long-term potential of protected areas. Many protected areas across the globe are disappearing, shrinking, or reducing access restrictions, often for non-sustainable use of natural resources (Mascia & Pailler, 2011). The protected area network is a cornerstone of conservation practice, and continuing commitments to its expansion and maintenance serve as an important resource for preserving genetic diversity, evolutionary processes, the resilience of populations and species, and ultimately the future of biodiversity.

Methods

Genetic data

We used previously compiled databases of publicly archived, georeferenced microsatellite genetic data from terrestrial mammals and marine fish (Karachaliou et al., 2024; Schmidt, Mäkinen, et al., 2023). Detailed methods on database compilation can be found in (Karachaliou et al., 2024; Schmidt, Mäkinen, et al., 2023). Briefly, we obtained a list of species names for terrestrial mammals and marine fish from the IUCN Red List database (https://www.iucnredlist.org/). We then performed systematic searches for microsatellite datasets by querying DataONE (https://www.dataone.org/), a platform integrating and enabling comprehensive searching across different data repositories, and by directly querying the Dryad Digital Data Repository through its automated programming interface (API). We performed systematic searches in the R statistical software (R Core Team, 2021) using the ‘dataone’ package (M. B. Jones et al., 2017) and custom scripts to query Dryad with species names and ‘microsat*’ keywords. We evaluated each result for suitability according to pre-defined criteria, including: geo-referenced sample locations, genotype data available for neutral microsatellite loci, free-ranging (e.g., non-captive) populations, and study designs which did not affect genetic diversity (e.g., excluding studies on microsatellite development, parentage analyses, etc.). We note that precise sampling years were unavailable for a large portion of the data due to uneven reporting in the original datasets. Historical samples, where they could be identified, were removed. For studies with multiple temporal samples at the same spatial location, we retained only the most recent time point. We also removed sample sites with fewer than 5 sampled individuals.

We chose to work with microsatellites due to their wide availability and because they are appropriate markers for measuring neutral, genome-wide genetic diversity and population structure (Mittell et al., 2015). We did not use mitochondrial DNA markers because, despite their abundance, they are not neutral and do not capture genome-wide diversity (Galtier et al., 2009), thus are not appropriate for the questions we test here. Genetic diversity estimated from microsatellites and the typical number of single nucleotide polymorphisms (SNPs) used is ~80% correlated with genome-wide diversity for both marker types (Mittell et al., 2015). Although SNP data are used increasingly frequently, they are currently not as widely available geographically and taxonomically as microsatellites. Microsatellites are still commonly used markers in landscape genetics and thus are currently the best suited marker type for spatially-explicit macrogenetics analyses.

We analyzed four metrics of genetic composition. Gene diversity (Nei, 1973) is the probability of selecting two different alleles in a nonrandom mating population, and takes into account both the number and evenness of alleles. Allelic richness here is rarefied allelic richness, the number of alleles at each locus accounting for variable sample sizes across sites and studies (rarefied to 10 alleles, the minimum number of samples across all datasets). Effective population size is a contemporary effective size that estimates the strength of genetic drift in the parental generation of the sampled population. We estimated effective population size using the linkage disequilibrium method in NeEstimator v2 (Do et al., 2014) with an allele frequency cutoff of 0.1. Finally, we estimated population differentiation using a population-specific F_{ST} metric that we can interpret as a relative measure of how far sites have diverged from a common ancestor of all the sites in the sample (Weir & Goudet, 2017). A protected area might harbor low genetic diversity, but may be genetically–and thus potentially phenotypically–unique at the whole species level and important to protect (e.g., (Coleman et al., 2013).

Protected areas

We obtained a shapefile of global protected areas available from the World Database on Protected areas (WDPA) in November 2022. This is a comprehensive database including spatial locations and metadata for terrestrial and marine protected areas and other effective area-based conservation measures. We cleaned protected area data using the ‘wdpar’ package (Hanson, 2022) which provides an R interface to the WDPA database. We followed best practices described in (Butchart et al., 2015; Runge et al., 2015; UNEP-WCMC and IUCN, 2022) to clean the data. This involved repairing invalid geometries, removing protected areas with status listed as “proposed” or “unknown”, removing United Nations Educational, Scientific and Cultural Organization (UNESCO) Biosphere reserves, and buffering protected areas denoted by point locations using their reported spatial extent to generate a circular area.

We performed a spatial join using the R package ‘sf’ (Pebesma, 2018) to identify genetic sites located within protected areas to create a binary predictor variable, hereafter *protected area status* (0 = outside a protected area; 1 = within a protected area). We used decimal degrees in the WGS84 coordinate system for both genetic and WDPA data. Populations may use and benefit from protected areas even if the sample location was not within protected area boundaries. We accounted for this by additionally recording the distance between each sample site and the nearest protected area. We measured the geodesic distances (m) between genetic sample sites and protected areas using the ‘geosphere’ package (Hijmans, 2019). The geodesic distance is a highly accurate distance measure for two points along a curved surface. If a site was located inside a protected area, we set this distance to 0.

Analysis

We used Bayesian generalized linear mixed models to test for relationships between protected area status or distance from protected area and genetic composition. We scaled and centered all variables before analysis so that effect sizes were comparable across models and genetic metrics. We log-transformed effective population size, which naturally varies across orders of magnitude across species. We fit models using the integrated nested Laplace approximation implemented in the ‘INLA’ package version 22.5.3 (Lindgren & Rue, 2015; Rue et al., 2009). Unlike Markov Chain Monte Carlo (MCMC) based methods for fitting Bayesian models, INLA deterministically approximates marginal posterior distributions and allows for faster and more flexible fitting of complex model structures (Beguin et al., 2012). All analyses were performed in R version 4.1.2.

Effect of protected area status and distance to protected area. We fit a series of models, one for each metric of genetic composition (gene diversity, allelic richness, population-specific F_{ST}, and effective population size) and for each predictor variable (protected area status or distance to nearest protected area), for a total of 8 models. We used normally distributed priors on fixed effect slope coefficients with mean 0 ± 10 standard deviation (0.1 precision in INLA) and default priors for other parameters. These are weakly informative priors that do not assume any directionality of effect. We performed analyses in parallel for terrestrial and marine realms.

Our data were hierarchical, with multiple observations recorded for species. Thus, we used a random effect structure to account for species-level variation in the data. We modeled differences in the means of each genetic metric using random intercepts for species. Because protected areas likely have different relationships with genetic composition across species, we allowed the relationships between predictor (status or distance) and response to vary according to species with random slopes. We also accounted for the spatial structure of the data with a Besag-York-Mollié-type spatial random effect. For the spatial random effect, we defined the connectivity matrix of the sample sites using the k-nearest neighbor method. We fit models for each genetic metric without a spatial effect, and with 8 connectivity matrices (k = 1 to k = 8 neighbors) and selected the best performing model based on deviance information criterion (DIC) and the Watanabe-Akaike criterion (WAIC; Gelman et al., 2014). In fitting spatial random effects our main goal was to capture spatial autocorrelation in model residuals that may violate our models' assumptions, and not to further analyze spatial structure.

Effect of area and IUCN category. We next tested whether attributes of protected areas moderated their effectiveness for genetic composition. For genetic sample sites located within protected areas (353 terrestrial sites, 195 marine), we recorded the area (km^2) and IUCN category of the protected area. Some sites were located within multiple protected areas (nested protected areas), and in these instances we used metadata associated with the larger protected area. We log-transformed, scaled, and centered area before analysis. The IUCN has designated 6 categories of protected area that describe increasing levels of human interference (IUCN, 1994): category I is strict protection, including nature reserves and wilderness areas, and category VI is designated for sustainable resource use. After excluding observations where IUCN category was listed as not applicable, not assigned, or not reported, categories were available for 214 of the terrestrial, and 79 marine sites located in protected areas. We then classified IUCN categories into 2 groups based on purpose for analysis. Categories I-IV are specifically for biodiversity protection, while categories V and VI are designated for multiple use (IUCN, 1994). We then fit a series of hierarchical models relating area or IUCN category to each metric of genetic composition with random slopes and intercepts for species, and accounting for spatially autocorrelated residuals when necessary. Due to small sample size and low replication within species, we did not test the effect of IUCN category on genetic composition of marine sites.

Relationships between protected area effectiveness and body size. We performed a post hoc analysis testing whether the effectiveness of protected areas for genetic diversity varied with respect to species body size. To do this, we took a meta-regression approach, using species' estimated effect sizes (random slopes) from hierarchical regressions of protected area effectiveness (status or distance) on genetic composition. These random slopes describe the magnitude and direction of the effect of protected areas for each species, and are thus a species-specific measure of protected area effectiveness for genetic composition. We then compiled body mass (g) for terrestrial vertebrate species from the PanTHERIA database (K. E. Jones et al., 2009) via the R package ‘traitdata’ (RS-eco, 2022). For marine fish, we used body length (cm) as a measure of body size obtained through the ‘rFishbase’ package (Boettiger et al., 2012). We used body size as a predictor variable in a series of simple linear regressions (‘lm’ function in R) for each genetic metric with species effect sizes as a response. We performed analyses in parallel for terrestrial and marine species.

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Table 1. Model summaries for the relationships between protected area status or distance (predictors) and the genetic composition of terrestrial and marine sites. Mean overall effect sizes for each predictor are given with 95% credible intervals. The model marginal log likelihood and Watanabe-Akaike information criterion (WAIC) are presented for model comparison. Credible intervals for all models overlap 0, suggesting neither protected area status nor distance generally affect genetic composition across terrestrial mammal or marine fish species.

	predictor	**mean (95% CI)**	**marginal log likelihood**	**WAIC**
terrestrial				
effective population size	status	-0.06 (-0.20 - 0.08)	-1266.35	2595.87
	distance	0.02 (-0.06 - 0.09)	-1554.28	2497.20
gene diversity	status	-0.06 (-0.15 - 0.03)	-1491.50	944.12
	distance	0.04 (-0.00 - 0.09)	-1092.89	1074.33
allelic richness	status	0.01 (-0.08 - 0.11)	-1480.01	1639.72
	distance	0.02 (-0.03 - 0.06)	-1609.61	1210.80
population-specific F_{ST}	status	0.07 (-0.05 - 0.19)	-1856.58	2172.28
	distance	-0.06 (-0.12 - -0.00)	-1613.95	2171.92
marine				
effective population size	status	-0.09 (-0.34 - 0.16)	-979.27	1532.71
	distance	0.07 (-0.05 - 0.19)	-982.72	1505.78
gene diversity	status	0.05 (-0.07 - 0.17)	-443.23	1147.78
	distance	0.00 (-0.06 - 0.05)	-192.01	1071.17
allelic richness	status	-0.01 (-0.14 - 0.12)	-1084.60	1482.13
	distance	0.02 (-0.04 - 0.08)	-1012.98	1433.98
population-specific F_{ST}	status	-0.05 (-0.23 - 0.12)	-896.11	2130.08
	distance	0.00 (-0.07 - 0.08)	-621.49	2162.52

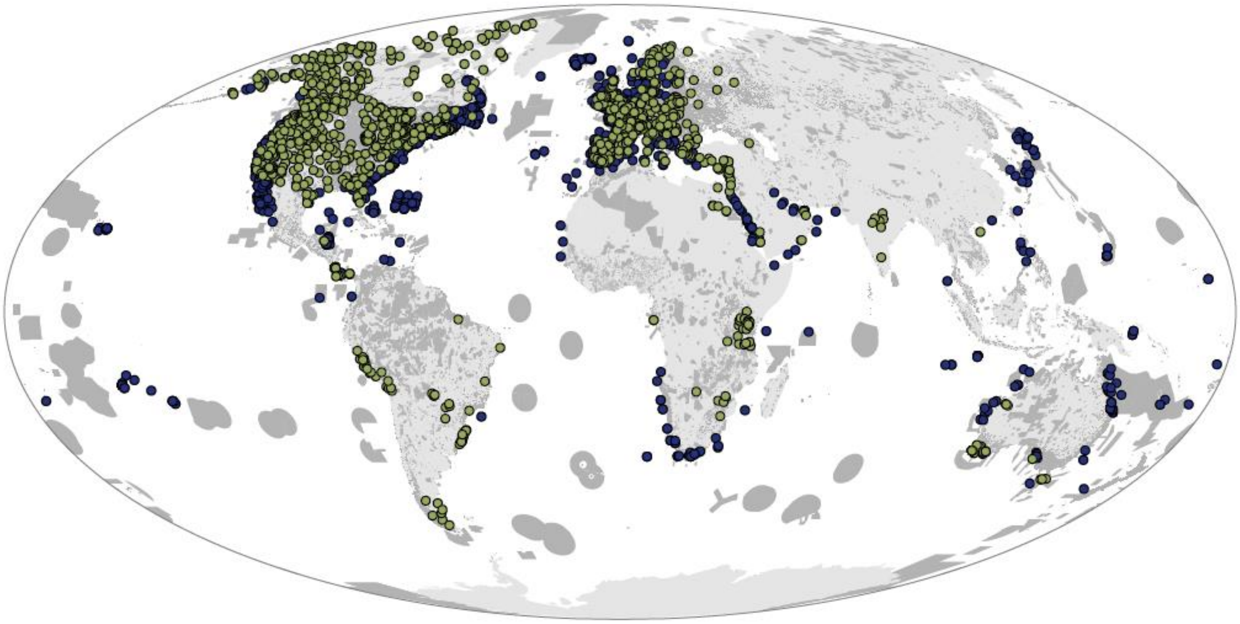

Figure 1. Map of genetic sample sites for terrestrial mammals (green) and marine fish (blue). Protected areas are shown in dark grey. Each point represents a location where multiple individuals of a single species were sampled to obtain estimates of effective population size, genetic diversity, and genetic differentiation.

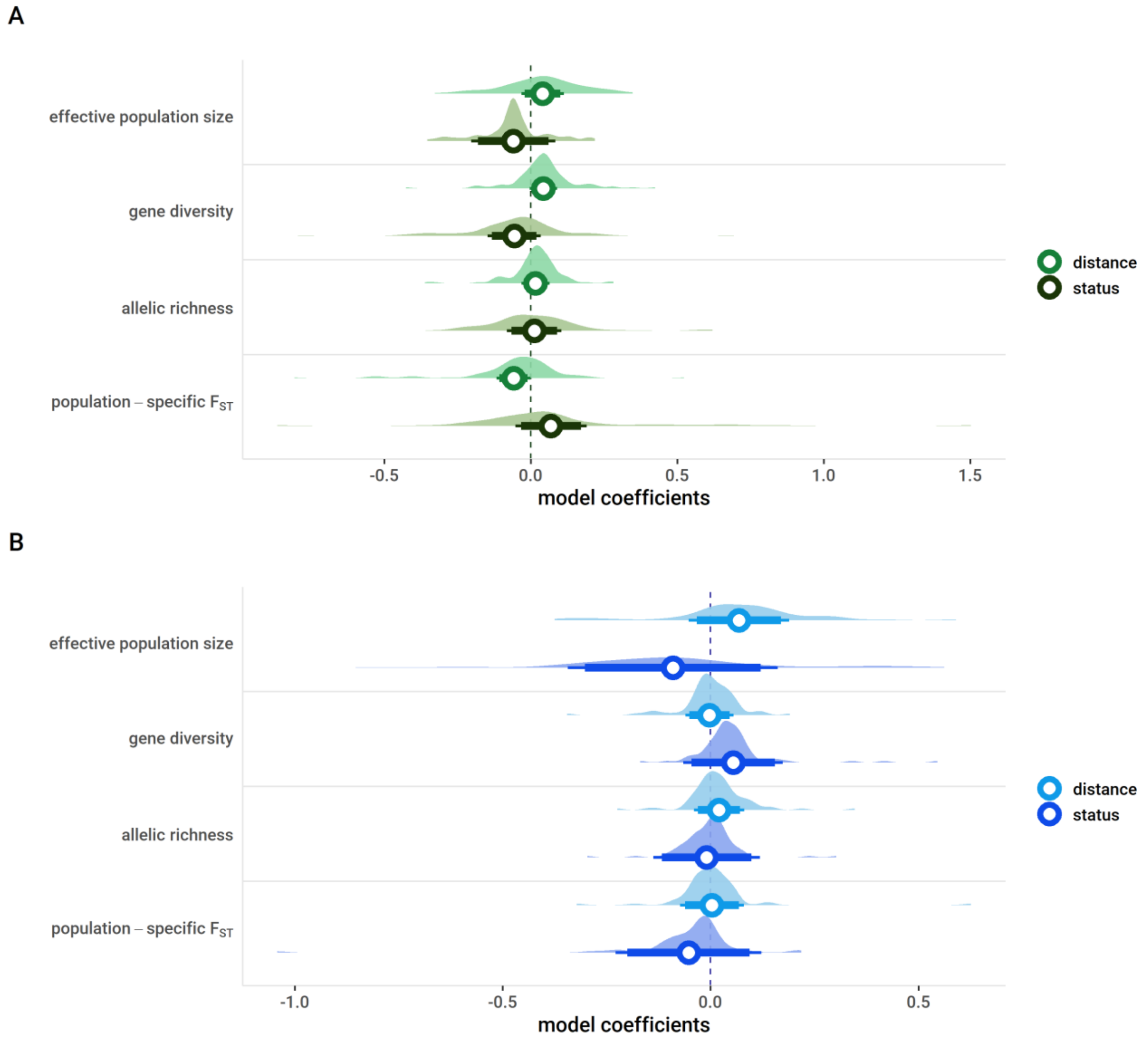

Figure 2. Model summaries of generalized linear mixed models for terrestrial mammal (a) and marine fish (b) genetic composition with distance to protected area or protected area status (in or outside a protected area) as predictors. Open circles are estimates of the overall mean effect of distance or status, shown with 90% (thick lines) and 95% (thin lines) credible intervals (see Table 1). Credible intervals significantly overlapping 0 (dashed lines) suggest no detectable effects of the predictor variables. Density plots show the distribution of species-specific random slopes for each model. Species-specific effects tended to aggregate near the overall

effect, indicating that genetic composition in most species was unrelated to distance to protected area or protected area status.

Supplementary Information: The global protected area network does not harbor genetically diverse populations

Contents:

Table S1. Data summarized for species within each realm (terrestrial mammal or marine fish). *Individuals* is the number of individuals summed across all sites; *sites total* is the total number of spatial locations sampled; *sites in PAs* denotes the number of sample sites that were located inside a protected area; *median distance* is the median distance to the nearest protected area in meters (note that sites located inside protected areas have distance set to 0). Summary statistics are reported for each genetic metric, with mean and standard deviation given for gene diversity and population-specific F_{ST} (standard deviations and F_{ST} are NA when only a single site was sampled), and median and range are reported for allelic richness and effective population size. Effective population size is NA when it was inestimable. Note for single sites, range minima and maxima are equal to the median value.

realm	**species**	**individuals**	**sites (total)**	**sites (in PAs)**	**median distance**	**gene diversity**	**allelic richness**	**population-specific F_{ST}**	**effective population size**
terrestrial	*Alces alces*	961	23	5	2822.43	0.64 (0.09)	4.1 (2.41 - 4.55)	0.04 (0.06)	56.4 (18.1 - 3617.9)
terrestrial	*Antilocapra americana*	175	1	0	433.48	0.67 (NA)	4 (4 - 4)	NA	39.3 (39.3 - 39.3)
terrestrial	*Apodemus flavicollis*	879	19	10	0	0.73 (0.15)	6.02 (3.54 - 6.43)	0.04 (0.06)	75.4 (6.5 - 227.4)
terrestrial	*Artibeus jamaicensis*	386	24	4	2525.04	0.71 (0.03)	4.97 (4.3 - 5.14)	0.01 (0.03)	78.3 (30.2 - 1000.6)
terrestrial	*Bettongia penicillata*	231	4	1	4258.12	0.76 (0.09)	5.19 (3.54 - 5.81)	0.12 (0.1)	58.2 (36.1 - 312.7)
terrestrial	*Bison bison*	184	8	4	135.99	0.47 (0.03)	2.63 (2.46 - 2.85)	0.13 (0.05)	63.3 (3 - 437.9)
terrestrial	*Bradypus pygmaeus*	10	1	0	16087.7	0.23 (NA)	1.77 (1.77 - 1.77)	NA	19.8 (19.8 - 19.8)
terrestrial	*Bradypus variegatus*	69	4	0	22666.82	0.42 (0.12)	2.75 (1.73 - 3.48)	0.35 (0.19)	41 (21.8 - 43)
terrestrial	*Canis latrans*	392	43	1	4819.93	0.77 (0.03)	5.8 (4.3 - 13.7)	0.02 (0.03)	19.5 (1.2 - 439.3)
terrestrial	*Canis lupus*	312	5	0	2487.4	0.72 (0.04)	4.65 (3.85 - 6.61)	0.05 (0.04)	15.8 (8 - 55.1)
terrestrial	*Capra ibex*	152	1	1	0	0.44 (NA)	2.37 (2.37 - 2.37)	0.04 (NA)	153.2 (153.2 - 153.2)
terrestrial	*Capreolus capreolus*	690	16	6	900.08	0.63 (0.05)	3.46 (2.88 - 4.58)	0.13 (0.1)	110.25 (11 - 679.8)
terrestrial	*Carollia castanea*	348	24	4	2746.04	0.69 (0.02)	4.33 (4.05 - 4.62)	0.01 (0.02)	97.6 (15 - 891.5)
terrestrial	*Cervus elaphus*	1591	30	14	101.36	0.64 (0.09)	4.18 (2.14 - 4.78)	0.16 (0.13)	54.95 (2.1 - 495.1)
terrestrial	*Ctenomys minutus*	323	25	1	9558.86	0.55 (0.11)	3.21 (1.83 - 4.21)	0.32 (0.13)	11.4 (0.5 - 39)
terrestrial	*Cynomys leucurus*	801	1	1	0	0.32 (NA)	2.15 (2.15 - 2.15)	NA	2.9 (2.9 - 2.9)
terrestrial	*Cynopterus sphinx*	81	1	0	185885.85	0.71 (NA)	4.37 (4.37 - 4.37)	NA	472.8 (472.8 - 472.8)
terrestrial	*Dama dama*	340	10	3	910.72	0.3 (0.09)	1.92 (1.5 - 2.25)	0.49 (0.15)	36.8 (2 - 313.4)
terrestrial	*Diceros bicornis*	553	3	2	0	0.5 (0.01)	2.72 (2.61 - 2.73)	0.01 (0.01)	26.6 (21.2 - 49.7)
terrestrial	*Dipodomys ingens*	558	7	2	4848.99	0.88 (0.04)	7.15 (6.58 - 7.37)	0.02 (0.01)	35.15 (22.9 - 354.3)
terrestrial	*Eptesicus serotinus*	694	34	13	388.5	0.59 (0.05)	3.57 (2.96 - 4.24)	0.06 (0.07)	42.1 (5.6 - 1843.2)
terrestrial	*Erinaceus europaeus*	7	1	0	651.9	0.4 (NA)	2.7 (2.7 - 2.7)	0.19 (NA)	2.8 (2.8 - 2.8)

terrestrial	*Felis silvestris*	620	15	6	760.39	0.66 (0.04)	4.2 (3.18 - 4.86)	0.1 (0.05)	41.45 (2.6 - 497.1)
terrestrial	*Gazella arabica*	114	4	1	40474.03	0.66 (0.11)	4.53 (3.15 - 5.58)	0.12 (0.15)	8.2 (2.5 - 42.4)
terrestrial	*Glaucomys volans*	278	8	1	816.06	0.75 (0.05)	5.23 (4.67 - 6.61)	0.03 (0.04)	39.8 (24.2 - 111.6)
terrestrial	*Lama guanicoe*	223	12	3	10443.2	0.68 (0.06)	4.1 (3.08 - 4.59)	0.1 (0.07)	15.7 (1.9 - 81.5)
terrestrial	*Lasionycteris noctivagans*	87	1	0	31026.22	0.83 (NA)	5.47 (5.47 - 5.47)	NA	353.9 (353.9 - 353.9)
terrestrial	*Lasiurus cinereus*	132	1	0	31026.22	0.88 (NA)	6.51 (6.51 - 6.51)	NA	1495.5 (1495.5 - 1495.5)
terrestrial	*Lemmus lemmus*	276	13	4	329.6	0.72 (0.04)	4.59 (4.22 - 5.2)	0.04 (0.04)	47.15 (22.2 - 163.3)
terrestrial	*Leopardus pardalis*	100	3	2	0	0.55 (0.17)	2.86 (2.2 - 4.21)	0.19 (0.27)	13 (8.2 - 40.2)
terrestrial	*Lepus americanus*	853	39	6	5799.94	0.66 (0.08)	4.47 (2.93 - 5.16)	0.16 (0.1)	30.35 (1.1 - 231.8)
terrestrial	*Lepus europaeus*	630	7	3	406.32	0.51 (0.06)	3.37 (2.87 - 3.78)	0.09 (0.07)	62.7 (7.1 - 701.6)
terrestrial	*Lepus granatensis*	194	8	3	669.88	0.36 (0.03)	2.5 (2.27 - 2.82)	0.04 (0.09)	10.5 (3 - 26.2)
terrestrial	*Lepus timidus*	161	3	1	78.24	0.5 (0.02)	3.54 (2.96 - 3.88)	0.1 (0.03)	71.05 (66.2 - 75.9)
terrestrial	*Lontra longicaudis*	28	1	0	3714.67	0.72 (NA)	4.31 (4.31 - 4.31)	NA	4.8 (4.8 - 4.8)
terrestrial	*Loxodonta africana*	974	13	12	0	0.7 (0.07)	4.31 (3.58 - 5.37)	0.02 (0.02)	50.1 (30 - 324.7)
terrestrial	*Lycaon pictus*	211	7	4	0	0.66 (0.05)	3.81 (3.54 - 4.3)	0.18 (0.06)	12.2 (0.8 - 18.2)
terrestrial	*Lynx canadensis*	1258	33	3	8462.56	0.72 (0.05)	4.47 (2.65 - 4.68)	0.03 (0.07)	58.45 (11.4 - 3175.7)
terrestrial	*Lynx pardinus*	104	2	2	0	0.37 (0.11)	2.14 (1.81 - 2.48)	0.44 (0.17)	12.45 (9.9 - 15)
terrestrial	*Lynx rufus*	2208	65	10	5808.76	0.73 (0.04)	4.46 (3.18 - 5.1)	0.06 (0.05)	100.6 (10.4 - 3544.8)
terrestrial	*Macropus eugenii*	226	2	0	2962.69	0.41 (0.31)	2.99 (1.72 - 4.26)	0.44 (0.42)	213.5 (213.5 - 213.5)
terrestrial	*Martes americana*	653	29	2	8264.45	0.63 (0.03)	3.87 (3.32 - 4.12)	0.02 (0.04)	75.45 (4.9 - 1362.4)
terrestrial	*Martes martes*	140	1	1	0	0.62 (NA)	3.3 (3.3 - 3.3)	NA	28.1 (28.1 - 28.1)
terrestrial	*Meles meles*	1060	31	8	966.99	0.56 (0.07)	3.49 (2.5 - 5.78)	0.18 (0.1)	48.05 (8.2 - 284.2)
terrestrial	*Mephitis mephitis*	345	1	0	4203.81	0.81 (NA)	5.23 (5.23 - 5.23)	NA	1290.5 (1290.5 - 1290.5)
terrestrial	*Microdipodops megacephalus*	180	3	0	18209.88	0.78 (0.05)	4.97 (4.69 - 5.23)	0.09 (0.06)	159.4 (100.4 - 173.9)
terrestrial	*Microdipodops pallidus*	105	2	0	29167.68	0.73 (0)	4.59 (4.42 - 4.76)	0.08 (0)	333.65 (95.4 - 571.9)
terrestrial	*Microtus arvalis*	717	33	11	718.32	0.65 (0.21)	4.89 (1.64 - 6.4)	0.23 (0.24)	15 (2 - 8003.8)
terrestrial	*Microtus duodecimcostatus*	60	10	2	4546.6	0.41 (0.09)	2.65 (2.11 - 4.23)	0.29 (0.16)	8.4 (2.1 - 207.3)
terrestrial	*Microtus lusitanicus*	42	5	3	0	0.6 (0.09)	3.41 (3.21 - 4.87)	0.13 (0.12)	2.5 (1.6 - 45.3)
terrestrial	*Miniopterus schreibersii*	312	22	7	175.18	0.41 (0.02)	2.75 (2.52 - 3.02)	0.06 (0.05)	15.9 (3.4 - 231.8)
terrestrial	*Mustela nivalis*	126	1	1	0	0.8 (NA)	5.21 (5.21 - 5.21)	NA	32.7 (32.7 - 32.7)
terrestrial	*Myodes glareolus*	492	14	8	0	0.78 (0.05)	5.21 (4.5 - 6.4)	0.05 (0.03)	38 (14.9 - 105.3)
terrestrial	*Myotis blythii*	12	1	1	0	0.72 (NA)	4.9 (4.9 - 4.9)	NA	11.7 (11.7 - 11.7)

terrestrial	*Myotis dasycneme*	112	3	0	47.77	0.76 (0.02)	5.18 (4.91 - 5.21)	0.02 (0.02)	36.5 (11.3 - 275.9)
terrestrial	*Myotis daubentonii*	106	1	1	0	0.73 (NA)	4.56 (4.56 - 4.56)	NA	55.5 (55.5 - 55.5)
terrestrial	*Myotis escalerai*	442	15	3	1228.28	0.81 (0.04)	5.57 (4.26 - 6.07)	0.04 (0.04)	21.9 (3.8 - 470.4)
terrestrial	*Myotis lucifugus*	3104	66	6	5441.66	0.82 (0.04)	5.86 (4.81 - 9.24)	0.01 (0.02)	117.1 (16 - 53777.4)
terrestrial	*Myotis myotis*	140	1	1	0	0.76 (NA)	5.27 (5.27 - 5.27)	NA	28.4 (28.4 - 28.4)
terrestrial	*Myotis septentrionalis*	954	17	4	3550.02	0.86 (0.03)	6.61 (5.12 - 6.75)	0 (0.02)	96.7 (11.6 - 3569.6)
terrestrial	*Myotis thysanodes*	29	2	0	1574.29	0.65 (0.01)	4.36 (4.12 - 4.6)	0.05 (0.06)	172.7 (172.7 - 172.7)
terrestrial	*Ningaui timealeyi*	274	1	0	23009.48	0.79 (NA)	5.48 (5.48 - 5.48)	NA	514.5 (514.5 - 514.5)
terrestrial	*Nomascus hainanus*	9	1	0	249678.27	0.42 (NA)	2.14 (2.14 - 2.14)	NA	14.7 (14.7 - 14.7)
terrestrial	*Nyctalus lasiopterus*	191	4	2	3326.79	0.74 (0.02)	4.55 (4.46 - 4.85)	0.02 (0.03)	173.55 (84.9 - 262.2)
terrestrial	*Nyctalus leisleri*	183	14	4	1000.51	0.72 (0.04)	4.6 (4.1 - 5.33)	0.03 (0.03)	107.85 (2.9 - 136861.7)
terrestrial	*Odocoileus hemionus*	2332	67	10	8973.89	0.62 (0.09)	3.71 (1.65 - 4.37)	0.11 (0.14)	87.35 (1.1 - 1348.9)
terrestrial	*Odocoileus virginianus*	2069	64	0	3242.84	0.81 (0.01)	5.51 (5.12 - 5.87)	0.01 (0.01)	192.5 (23.9 - 7931.3)
terrestrial	*Oreamnos americanus*	102	1	0	6628.71	0.52 (NA)	2.9 (2.9 - 2.9)	NA	111.8 (111.8 - 111.8)
terrestrial	*Otospermophilus beecheyi*	205	3	0	4042.7	0.75 (0.03)	4.94 (4.68 - 5.5)	0.13 (0.04)	54.1 (38.6 - 63.1)
terrestrial	*Ovis canadensis*	1071	16	12	0	0.61 (0.05)	3.38 (2.54 - 3.91)	0.12 (0.08)	24.9 (14.6 - 530.7)
terrestrial	*Panthera onca*	176	9	4	2694.06	0.64 (0.07)	3.9 (2.85 - 4.29)	0.08 (0.1)	19 (4.8 - 58.5)
terrestrial	*Panthera tigris*	165	7	0	282451.2	0.65 (0.08)	4.1 (3.24 - 10.2)	0.15 (0.09)	2.65 (0.9 - 16.2)
terrestrial	*Papio anubis*	93	6	0	8645.16	0.73 (0.03)	4.81 (4.68 - 6.97)	0.06 (0.02)	24.95 (18.4 - 76.1)
terrestrial	*Papio cynocephalus*	354	5	3	0	0.73 (0.05)	4.61 (4.01 - 5.62)	0.07 (0.05)	63.5 (10.4 - 6595.8)
terrestrial	*Parantechinus apicalis*	196	6	6	0	0.63 (0.08)	3.77 (2.96 - 3.91)	0.05 (0.1)	34.15 (2 - 61.2)
terrestrial	*Pekania pennanti*	722	34	2	5031.26	0.62 (0.03)	3.59 (2.98 - 4.01)	0.07 (0.05)	38.75 (8.3 - 1372.8)
terrestrial	*Peromyscus leucopus*	775	36	8	2054.58	0.82 (0.03)	5.82 (4.67 - 10.1)	0.05 (0.04)	40.85 (9.8 - 259.6)
terrestrial	*Peromyscus maniculatus*	136	10	9	0	0.77 (0.02)	5.54 (5.3 - 5.68)	0.08 (0.02)	13.8 (2.2 - 41.3)
terrestrial	*Procyon lotor*	330	1	0	2209.44	0.84 (NA)	5.57 (5.57 - 5.57)	NA	2159.3 (2159.3 - 2159.3)
terrestrial	*Pseudocheirus occidentalis*	145	7	3	98.59	0.58 (0.03)	3.16 (2.93 - 3.3)	0.04 (0.05)	14.6 (8.8 - 33.8)
terrestrial	*Pseudomys chapmani*	110	1	0	21519.08	0.88 (NA)	6.81 (6.81 - 6.81)	NA	305.7 (305.7 - 305.7)
terrestrial	*Pseudomys hermannsburgensis*	227	1	0	13942.34	0.84 (NA)	6.14 (6.14 - 6.14)	NA	761.5 (761.5 - 761.5)
terrestrial	*Puma concolor*	2010	14	2	5004.55	0.5 (0.09)	2.73 (1.97 - 4.14)	0.17 (0.14)	32.75 (1.9 - 124.5)
terrestrial	*Rangifer tarandus*	2637	82	26	4232.56	0.77 (0.07)	5.22 (2.29 - 6.54)	0.06 (0.08)	122.05 (6.3 - 12930.2)
terrestrial	*Rhinolophus ferrumequinum*	950	27	10	142.15	0.73 (0.04)	4.62 (3.47 - 4.79)	0.04 (0.05)	137.4 (30.8 - 6270.7)
terrestrial	*Rhynchonycteris naso*	198	3	3	0	0.87 (0)	6.46 (6.46 - 6.53)	0.01 (0)	105.4 (51.8 - 187.1)

terrestrial	*Rousettus aegyptiacus*	490	34	4	11161.49	0.61 (0.05)	3.75 (3.03 - 5.26)	0.13 (0.06)	70.65 (1.3 - 754.3)
terrestrial	*Saguinus geoffroyi*	59	3	1	1073.67	0.59 (0.03)	3.25 (2.86 - 3.41)	0.05 (0.07)	5.65 (2.4 - 8.9)
terrestrial	*Sarcophilus harrisii*	60	3	1	554.28	0.41 (0.02)	2.26 (2.23 - 2.35)	0.08 (0.04)	6.5 (3 - 13.1)
terrestrial	*Sorex antinorii*	213	17	2	1054.55	0.78 (0.03)	5.54 (4.66 - 5.94)	0.06 (0.03)	67.35 (11.4 - 2395.8)
terrestrial	*Sus scrofa*	1834	24	8	843.96	0.63 (0.07)	3.76 (2.72 - 6.7)	0.09 (0.07)	32.35 (1.8 - 405.7)
terrestrial	*Sylvilagus transitionalis*	157	3	1	184.99	0.42 (0.09)	2.53 (1.87 - 2.63)	0.15 (0.14)	17.75 (3.7 - 31.8)
terrestrial	*Tadarida teniotis*	41	1	1	0	0.79 (NA)	5.14 (5.14 - 5.14)	0.01 (NA)	NA
terrestrial	*Tamiasciurus douglasii*	186	14	8	0	0.65 (0.03)	4.11 (3.69 - 4.43)	0.03 (0.04)	48 (8.8 - 193.5)
terrestrial	*Tamiasciurus hudsonicus*	188	12	0	3030.4	0.66 (0.08)	4.51 (4.17 - 5.7)	0.07 (0.09)	67.75 (20.8 - 190.3)
terrestrial	*Taxidea taxus*	1500	15	3	3986.98	0.73 (0.1)	4.58 (2.52 - 5.33)	0.08 (0.12)	59.5 (6.3 - 1780.2)
terrestrial	*Thyroptera tricolor*	766	2	1	2999.29	0.82 (0.01)	5.7 (5.61 - 5.78)	0.02 (0.01)	158.55 (153.5 - 163.6)
terrestrial	*Ursus americanus*	3600	43	9	2657.52	0.72 (0.11)	4.68 (1.95 - 7.15)	0.13 (0.12)	45.2 (1 - 534.2)
terrestrial	*Ursus arctos*	3716	24	7	2190.23	0.69 (0.07)	4.09 (2.93 - 4.84)	0.1 (0.09)	30.95 (11.3 - 133.9)
terrestrial	*Ursus maritimus*	3640	35	7	53156.94	0.69 (0.06)	4.13 (3.55 - 5)	0.04 (0.03)	138.6 (6.3 - 1692.2)
terrestrial	*Vicugna vicugna*	374	14	3	21467.18	0.48 (0.08)	3.08 (2.07 - 4.15)	0.17 (0.13)	29.2 (2.7 - 443.9)
terrestrial	*Vulpes lagopus*	36	2	1	5482.39	0.69 (0.01)	4.61 (4.43 - 4.78)	0.04 (0.05)	80 (80 - 80)
terrestrial	*Vulpes vulpes*	298	6	0	4097.73	0.7 (0.04)	4.4 (3.58 - 4.46)	0.03 (0.05)	133.45 (3.3 - 572.3)
marine	*Aetobatus narinari*	572	3	0	47198.51	0.87 (0.01)	6.57 (6.51 - 6.8)	0 (0.01)	25.1 (19.6 - 31.9)
marine	*Alopias pelagicus*	326	6	2	43644.37	0.72 (0.02)	5.38 (5.34 - 5.56)	0.04 (0.02)	24.7 (11.1 - 344.7)
marine	*Alosa aestivalis*	1478	27	1	28963.06	0.6 (0.09)	3.52 (2.64 - 3.93)	0.1 (0.06)	167.85 (15.7 - 2451.6)
marine	*Alosa pseudoharengus*	5346	56	5	20271.23	0.63 (0.08)	3.02 (2.43 - 3.59)	0.09 (0.05)	139.2 (3.4 - 215642.3)
marine	*Alosa sapidissima*	4354	33	3	28833.74	0.75 (0.04)	5.18 (3.83 - 5.43)	0.04 (0.05)	360.6 (58.1 - 17953.9)
marine	*Alticus arnoldorum*	204	6	0	22976.26	0.74 (0.01)	5.15 (5.05 - 5.44)	0.01 (0.02)	631.7 (112.8 - 966.5)
marine	*Amphiprion bicinctus*	991	19	0	266176.72	0.75 (0.02)	5.02 (4.58 - 5.18)	0 (0.02)	894.7 (515.4 - 19560.5)
marine	*Amphiprion chrysopterus*	46	1	0	420583.66	0.6 (NA)	4.5 (4.5 - 4.5)	NA	30.2 (30.2 - 30.2)
marine	*Amphiprion melanopus*	426	12	12	0	0.51 (0.03)	3.35 (3.08 - 3.48)	0.02 (0.03)	155.35 (3.1 - 271.4)
marine	*Amphiprion sandaracinos*	160	1	0	420583.66	0.3 (NA)	2.49 (2.49 - 2.49)	NA	61.4 (61.4 - 61.4)
marine	*Anguilla anguilla*	1336	30	5	373113.6	0.77 (0.03)	6.07 (5.82 - 8.05)	0 (0.01)	313.2 (2.7 - 4228.4)
marine	*Anguilla rostrata*	2160	38	2	40332.17	0.79 (0.03)	6.21 (5.77 - 6.36)	0 (0.01)	563.6 (74.6 - 23663.9)
marine	*Atractoscion aequidens*	396	2	0	381165.6	0.9 (0)	7.21 (7.19 - 7.23)	0.05 (0)	317.4 (317.4 - 317.4)
marine	*Carcharhinus amblyrhynchos*	112	9	9	0	0.76 (0.02)	5.57 (5.48 - 6.28)	0 (0.02)	106.4 (13.4 - 469.8)
marine	*Carcharhinus isodon*	369	6	0	50630.95	0.66 (0.01)	4.37 (4.29 - 4.44)	0.01 (0.01)	145.95 (113.8 - 178.1)

marine	*Carcharhinus limbatus*	812	10	0	174395.61	0.7 (0.03)	4.37 (4.06 - 5.13)	0.02 (0.02)	168.25 (39.8 - 2485.6)
marine	*Carcharhinus melanopterus*	1388	31	3	302456.19	0.54 (0.06)	3.44 (2.65 - 4.58)	0.09 (0.13)	55.7 (3.3 - 1096.8)
marine	*Carcharhinus sorrah*	700	6	0	137371.8	0.67 (0.02)	4.21 (4.04 - 4.92)	0.01 (0.02)	679.8 (78.1 - 5476.2)
marine	*Carcharodon carcharias*	166	2	0	129024.25	0.67 (0.04)	4.05 (3.92 - 4.18)	0.1 (0.06)	109.35 (16.1 - 202.6)
marine	*Centroscymnus coelolepis*	478	7	2	41140.65	0.79 (0.06)	5.46 (3.94 - 5.7)	0.03 (0.07)	156.4 (117.3 - 2136.5)
marine	*Chaetodon capistratus*	79	10	2	7869.94	0.71 (0.03)	5.33 (5.13 - 5.75)	0.02 (0.04)	38.5 (32 - 45)
marine	*Chaetodon guttatissimus*	43	2	0	279167.94	0.72 (0.01)	5.26 (5.18 - 5.34)	0.01 (0.01)	110.9 (110.9 - 110.9)
marine	*Chaetodon lunulatus*	263	7	3	132545.25	0.78 (0.02)	5.76 (4.99 - 6.07)	0.01 (0.02)	513.25 (110.4 - 1229.1)
marine	*Chaetodon punctatofasciatus*	25	2	0	259499.02	0.77 (0.05)	5.93 (5.82 - 6.03)	0.01 (0.02)	NA
marine	*Chaetodon trifascialis*	209	5	3	0	0.83 (0)	6.02 (5.81 - 6.09)	0.01 (0)	319.85 (73 - 566.7)
marine	*Chaetodon trifasciatus*	71	3	0	291186.27	0.8 (0.03)	6.13 (6.05 - 6.18)	0 (0.02)	NA
marine	*Clupea pallasii*	3600	18	14	0	0.86 (0.03)	6.28 (5.3 - 7.03)	0.03 (0.03)	552.4 (70.2 - 4239.3)
marine	*Diplodus vulgaris*	310	12	3	16899.28	0.82 (0.03)	6.15 (5.15 - 6.69)	0.03 (0.03)	113.65 (16.8 - 4618.6)
marine	*Elacatinus lori*	300	10	3	3990.19	0.83 (0.01)	6.38 (6.04 - 6.51)	0.01 (0.01)	142.35 (89.7 - 1102.3)
marine	*Engraulis encrasicolus*	724	17	0	15850.64	0.74 (0.03)	4.91 (4.26 - 5.52)	0.01 (0.04)	161.3 (28.4 - 2124)
marine	*Entosphenus tridentatus*	965	20	10	2309.49	0.58 (0.03)	3.27 (2.73 - 3.54)	0.02 (0.04)	66.1 (14.7 - 337.9)
marine	*Fundulus parvipinnis*	182	23	2	10173.58	0.46 (0.05)	3.64 (2.71 - 4.4)	0.2 (0.11)	34.1 (8 - 109.9)
marine	*Gadus morhua*	1236	13	4	1174.81	0.76 (0.01)	5.6 (5.36 - 5.77)	0 (0.01)	281.8 (100.5 - 3111.4)
marine	*Galeocerdo cuvier*	380	10	0	178983.31	0.64 (0.06)	4.45 (3.7 - 4.88)	0.09 (0.09)	218.5 (8.8 - 620.7)
marine	*Gasterosteus aculeatus*	545	14	0	8715.2	0.82 (0.05)	6.2 (5 - 6.73)	0.03 (0.05)	223.65 (53.2 - 470.5)
marine	*Gillichthys mirabilis*	311	29	5	10173.58	0.4 (0.17)	2.27 (1.44 - 4.65)	0.23 (0.28)	15.5 (3.2 - 122.1)
marine	*Gobiusculus flavescens*	10	1	0	2228.28	0.81 (NA)	6.16 (6.16 - 6.16)	0.02 (NA)	14.5 (14.5 - 14.5)
marine	*Gymnosarda unicolor*	73	6	4	0	0.62 (0.04)	4.32 (3.68 - 5.46)	0.02 (0.05)	27.9 (19.3 - 92.4)
marine	*Haemulon flavolineatum*	69	9	1	5443.93	0.74 (0.03)	5.41 (5.23 - 7.82)	0.01 (0.03)	79.35 (20.3 - 159.7)
marine	*Hypoplectrus nigricans*	66	9	1	7035.9	0.74 (0.02)	5.71 (5.22 - 6.06)	0 (0.03)	78.85 (32.1 - 454.8)
marine	*Kryptolebias marmoratus*	388	14	2	5687.48	0.44 (0.16)	2.94 (1.34 - 4.37)	0.43 (0.23)	10.7 (0.5 - 194.6)
marine	*Lethrinus nebulosus*	350	4	3	0	0.7 (0.04)	5.02 (4.81 - 5.11)	0.01 (0.03)	5.4 (3.6 - 501.6)
marine	*Limanda limanda*	3006	15	6	2465.93	0.73 (0.01)	5.59 (5.44 - 5.67)	0 (0.01)	3446.35 (159.4 - 15552.2)
marine	*Lithognathus lithognathus*	50	3	1	3696.26	0.81 (0)	5.5 (5.47 - 5.55)	0 (0.01)	NA
marine	*Merluccius capensis*	1477	9	0	53334.19	0.61 (0.03)	4.37 (4.22 - 4.96)	0.04 (0.04)	905.05 (71.7 - 5556.6)
marine	*Merluccius paradoxus*	1452	9	0	53334.19	0.69 (0.01)	4.92 (4.79 - 4.98)	0 (0.01)	4231.9 (2494.2 - 8249)
marine	*Naso unicornis*	562	7	0	23186.47	0.82 (0.01)	5.92 (5.81 - 6.14)	0 (0.01)	278.75 (26.6 - 638)

marine	*Nerophis lumbriciformis*	155	2	0	8257.92	0.79 (0.02)	5.28 (5.08 - 5.48)	NA	309.65 (274.7 - 344.6)
marine	*Oncorhynchus nerka*	1338	10	0	155265.82	0.72 (0.09)	4.98 (2.7 - 5.85)	0.06 (0.1)	83 (16.7 - 166.5)
marine	*Pachymetopon blochii*	50	2	0	26232.74	0.88 (0)	6.79 (6.77 - 6.81)	0 (0)	156.1 (156.1 - 156.1)
marine	*Paracirrhites arcatus*	264	7	5	0	0.83 (0.01)	5.94 (5.83 - 6.02)	0 (0.01)	1358.9 (619.1 - 11757.6)
marine	*Phycodurus eques*	49	6	4	0	0.33 (0.1)	2.08 (1.59 - 2.53)	0.36 (0.2)	1.1 (0.7 - 7.3)
marine	*Plectropomus leopardus*	1204	8	8	0	0.73 (0.02)	5.13 (4.84 - 5.26)	0 (0)	107.25 (48.7 - 663.7)
marine	*Plectropomus maculatus*	2477	7	7	0	0.79 (0)	5.33 (5.28 - 5.43)	0 (0)	147.1 (115.3 - 170.1)
marine	*Pomatomus saltatrix*	218	4	0	67646.37	0.75 (0.03)	5.66 (5.51 - 6.69)	0.1 (0.03)	93.5 (39 - 474)
marine	*Prionace glauca*	226	7	2	54375.59	0.74 (0.02)	5.16 (4.88 - 5.64)	0.01 (0.01)	91.45 (32.8 - 167.7)
marine	*Pristipomoides zonatus*	292	8	1	51354.46	0.32 (0.07)	2.33 (2.06 - 2.6)	0.01 (0.06)	43.25 (36.4 - 50.1)
marine	*Quietula y-cauda*	182	28	3	20138.06	0.56 (0.12)	5.48 (2.12 - 10.12)	0.19 (0.17)	32 (20.9 - 41.7)
marine	*Rhincodon typus*	406	7	0	91555.14	0.64 (0.02)	3.95 (3.53 - 4.16)	0.01 (0.03)	193.9 (37.3 - 303.1)
marine	*Rhizoprionodon acutus*	294	2	0	137371.8	0.56 (0.01)	3.64 (3.62 - 3.67)	0 (0.02)	79321.7 (79321.7 - 79321.7)
marine	*Salmo salar*	19740	279	36	26802.71	0.81 (0.06)	6.01 (2.21 - 13.18)	0.04 (0.03)	106.1 (6.3 - 10087.9)
marine	*Scomberomorus niphonius*	945	9	6	0	0.74 (0.01)	5.12 (5.11 - 5.34)	0 (0.01)	163 (52.6 - 600)
marine	*Scyliorhinus canicula*	834	10	2	18569.16	0.59 (0.03)	3.39 (3.24 - 3.96)	0.04 (0.05)	441.5 (55.2 - 1479.4)
marine	*Sebastes mentella*	117	8	0	130475.97	0.77 (0.04)	5.67 (5.19 - 6.27)	0.01 (0.04)	579.55 (75.5 - 1083.6)
marine	*Serranus cabrilla*	330	11	1	12559.7	0.71 (0.04)	4.71 (4.37 - 5.06)	0.03 (0.05)	94.7 (39.5 - 265.8)
marine	*Siganus fuscescens*	248	6	1	26711.81	0.71 (0.05)	5 (4.34 - 5.34)	0.1 (0.07)	128.1 (1.8 - 468)
marine	*Solea solea*	342	4	2	1900.45	0.77 (0.01)	5.05 (4.94 - 5.08)	0 (0.01)	370 (205.2 - 471.2)
marine	*Sparus aurata*	171	5	1	6062.13	0.86 (0.01)	6.42 (6.22 - 6.75)	0 (0.01)	72.75 (27.2 - 1424.1)
marine	*Sphyrna lewini*	233	2	0	137371.8	0.76 (0.01)	5.13 (5.13 - 5.14)	0 (0.01)	405.6 (405.6 - 405.6)
marine	*Sprattus sprattus*	1285	13	2	6709.18	0.83 (0.03)	6.05 (5.47 - 6.65)	0.03 (0.03)	274.6 (125 - 658.2)
marine	*Stegastes partitus*	3463	14	2	11297.83	0.84 (0.04)	6.97 (6.1 - 7.08)	0.01 (0.02)	85.4 (18.5 - 2448.7)
marine	*Thalassoma bifasciatum*	81	11	1	7035.9	0.85 (0.02)	7.56 (6.99 - 14.09)	0.01 (0.02)	36.4 (36.4 - 36.4)
marine	*Totoaba macdonaldi*	310	5	0	135496.23	0.67 (0.01)	4.32 (4.19 - 4.39)	0 (0.01)	670.5 (306.9 - 1034.1)

Table S2. Model summaries for meta-regressions between species-specific protected area effectiveness (species random slopes from models in Table 1) and species body size. The number of species for which body size information was available is reported in parenthesis after each genetic metric. The predictor column indicates from which model (protected area status or distance) species-specific slope coefficients were summarized. Mean effect sizes are given with 95% confidence intervals. R^2 is the variation in each genetic metric explained by the predictors, an indicator of model fit. Confidence intervals overlapping 0 suggest that the effectiveness of protected areas (in terms of status or distance) is unrelated to species body size across terrestrial mammal or marine fish species. The effectiveness of protected area status on allelic richness appears to decrease with respect to body size in terrestrial mammals.

	predictor	**mean (95% CI)**	**R^2**
terrestrial			
effective population size (*84*)	status	-0.01 (-0.05 - 0.01)	0.01
	distance	-0.02 (-0.04 - 0.00)	0.02
gene diversity (*103*)	status	-0.03 (-0.07 - 0.00)	0.04
	distance	0.01 (-0.01 - 0.03)	0.01
allelic richness (*103*)	status	-0.04 (-0.08 - -0.02)	0.08
	distance	0.01 (-0.01 - 0.03)	0.01
population-specific F_{ST} (*102*)	status	0.04 (-0.02 - 0.10)	0.02
	distance	-0.02 (-0.06 - 0.01)	0.02
marine			
effective population size (*70*)	status	0.03 (-0.03 - 0.09)	0.01
	distance	-0.00 (-0.04 - 0.04)	0.00
gene diversity (*73*)	status	-0.00 (-0.03 - 0.02)	0.00
	distance	-0.00 (-0.02 - 0.01)	0.00
allelic richness (*73*)	status	0.00 (-0.01 - 0.02)	0.00
	distance	-0.01 (-0.03 - 0.00)	0.04
population-specific F_{ST} (*70*)	status	0.02 (-0.01 - 0.06)	0.02
	distance	-0.01 (-0.03 - 0.02)	0.00

Table S3. Model summaries for relationships between the area and IUCN category of protected areas (predictors) on the genetic composition of terrestrial and marine sites. Sites were excluded if they were located outside protected areas or if they had missing data for area or IUCN status (i.e., *Not Applicable*, *Not Assigned*, or *Not Reported*). Sample size for each model are given in parentheses after each predictor. Mean overall (across-species) effect sizes for each predictor are given with 95% credible intervals. The model marginal log likelihood and Watanabe-Akaike information criterion (WAIC) are indicators of model fit. Credible intervals overlapping 0 suggest neither the area nor IUCN category of protected area are related to the genetic composition of populations across terrestrial mammal or marine fish species. The significant relationship between area and allelic richness in marine fish was driven by an outlier species with a strong negative effect; this relationship disappears when this species is removed.

	predictor	**mean (95% CI)**	**marginal log likelihood**	**WAIC**
terrestrial				
effective population size	area (*353*)	0.03 (-0.11 - 0.18)	-433.74	811.16
	IUCN category (*214*)	0.04 (-0.30 - 0.38)	-276.39	515.35
gene diversity	area (*353*)	0.03 (-0.07 - 0.14)	-267.62	372.25
	IUCN category (*214*)	0.15 (-0.13 - 0.44)	-264.16	410.85
allelic richness	area (*339*)	0.07 (-0.03 - 0.16)	-259.66	523.14
	IUCN category (*205*)	0.10 (-0.15 - 0.36)	-231.48	311.07
population-specific F_{ST}	area (*300*)	0.02 (-0.11 - 0.15)	-462.52	811.62
	IUCN category (*186*)	0.16 (-0.18 - 0.50)	-296.49	562.97
marine				
effective population size	area (*195*)	0.06 (-0.14 - 0.25)	-191.66	328.83
gene diversity	area (*195*)	0.11 (-0.08 - 0.31)	-173.06	217.66
allelic richness	area (*194*)	-0.23 (-0.43- -0.02)	-181.96	-740.23
population-specific F_{ST}	area (*195*)	0.01 (-0.25 - 0.27)	-234.83	419.44

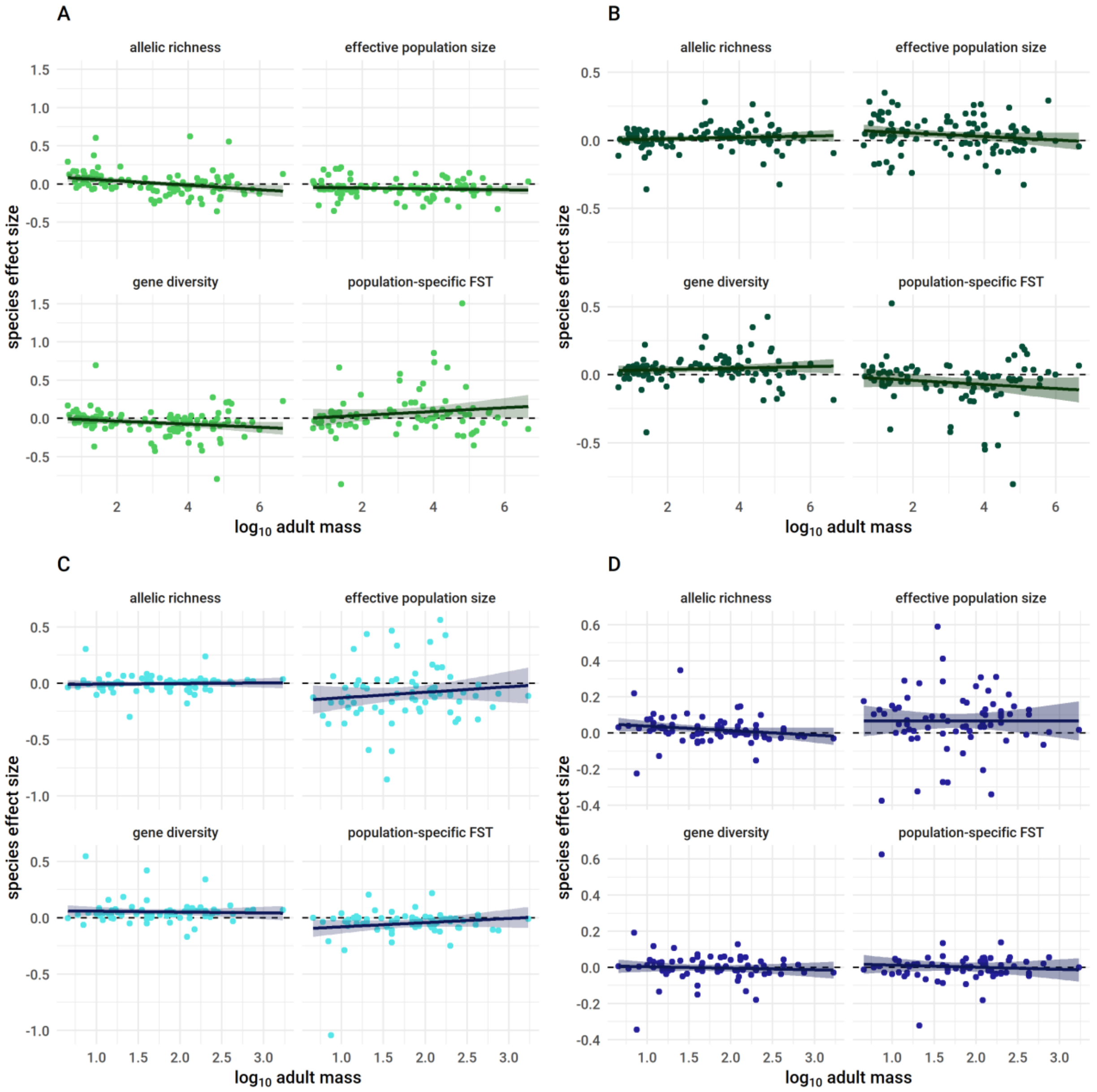

Figure S1. Body size of terrestrial mammal and marine fish species vs. protected area effectiveness for terrestrial (A, B) and marine realms (C, D). Points represent species-specific effect sizes (random slopes) of protected area status (A, C) or distance to protected area (B, D) for each genetic metric. The dashed horizontal line indicates an effect size of 0 (no relationship between genetic composition and protected area status or distance). Positive effect sizes indicate the genetic metric was higher inside protected areas, or increased with increasing distance from protected areas. Body size was weakly negatively related to the effectiveness of protected area status for allelic richness (A), i.e., smaller species tended to have higher allelic richness inside protected areas. Body size was unrelated to effectiveness for other genetic metrics across both realms (see Table S3).

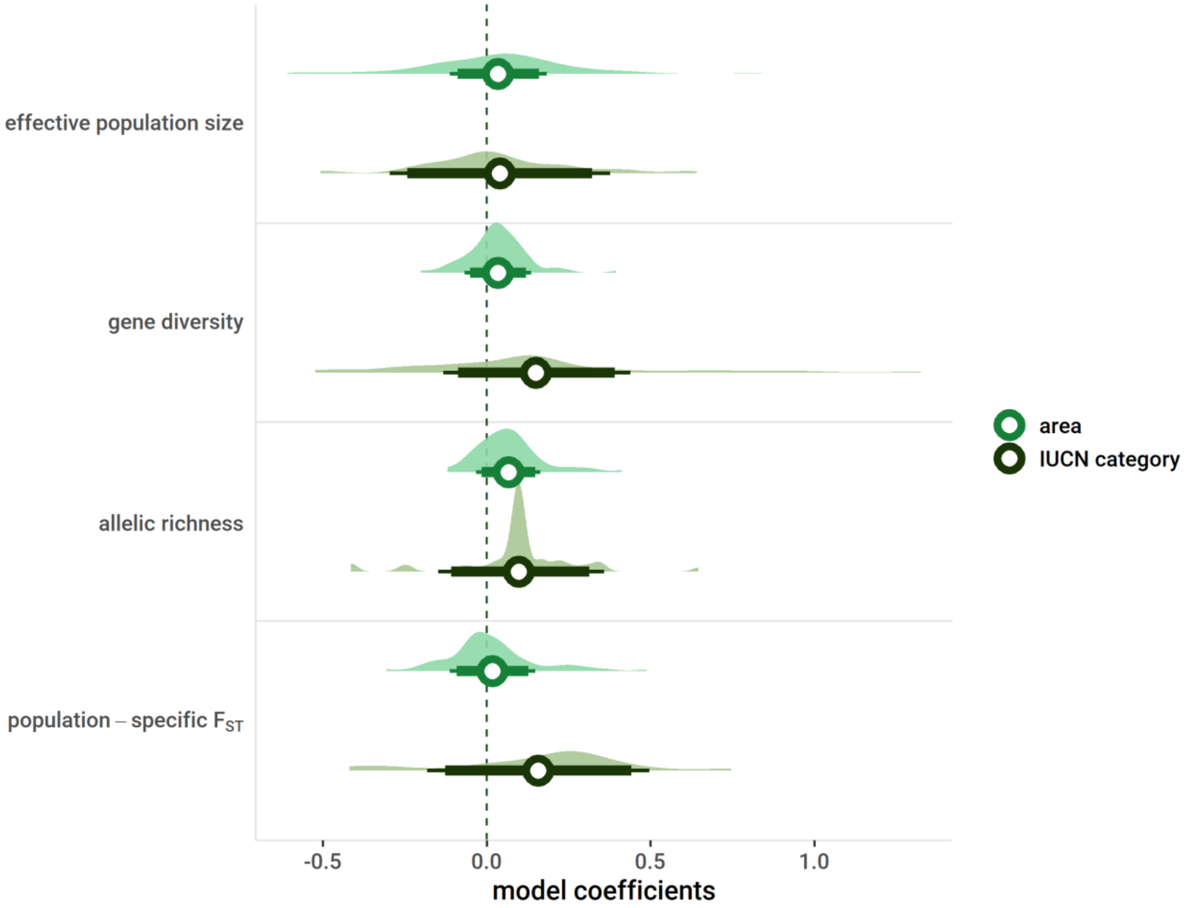

Figure S2. Plotted model coefficients for the effects of protected area size and IUCN category (related to the extent of human influence) on the genetic composition of terrestrial mammal populations. Open circles indicate the overall effect size across species, flanked by 90 (bold lines) and 95% (narrow lines) credible intervals. Densities behind the open circle show the distribution of species-specific effects for each genetic metric. Area had a small negative effect on population-specific F_{ST}, however this was likely due to species- and site-specific factors driving strong negative effects. Neither area nor IUCN category was related to other genetic metrics for terrestrial mammal species.

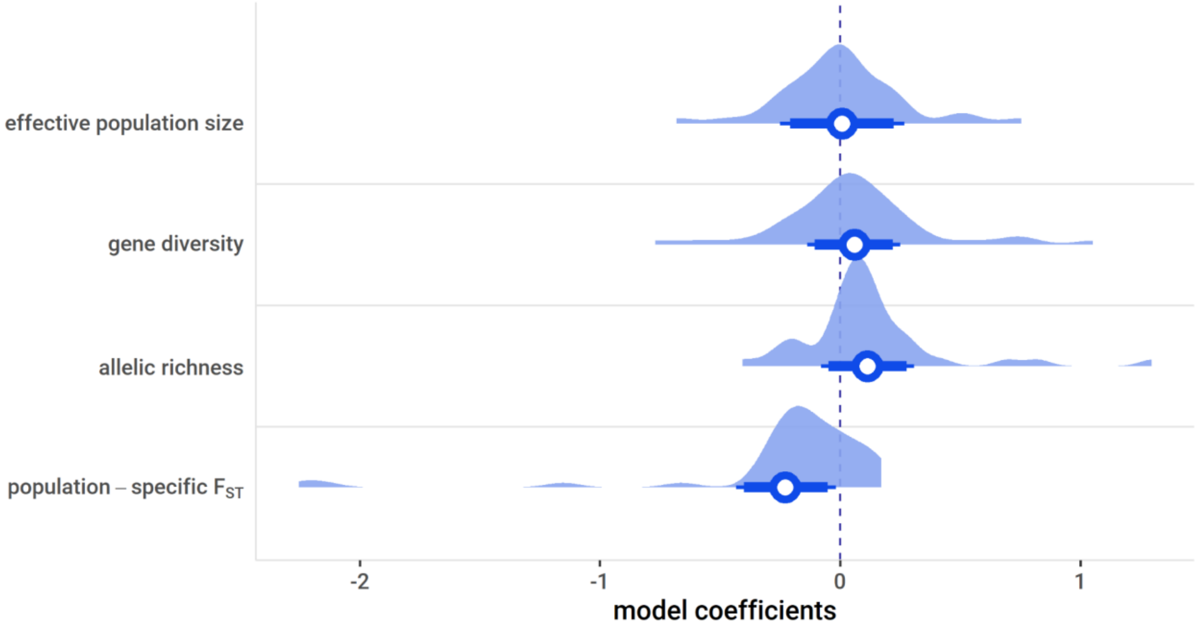

Figure S3. Plotted model coefficients for the effects of protected area size on the genetic composition of marine fish populations. Open circles indicate the overall effect size across species, flanked by 90 (bold lines) and 95% (narrow lines) credible intervals. Densities behind the open circle show the distribution of species-specific effects for each genetic metric. Area had a small negative effect on population-specific F_{ST}, however this was due to the presence of a strong outlier species; no effect is apparent when this species is removed. The size of protected areas was not related to other genetic metrics for marine fish species.