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RESEARCH

Genomic diversity in felids correlates with range and density, not census size

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Abstract

As the world is hit by the sixth mass extinction, it becomes increasingly important to understand the factors relevant to the conservation of species, so that we may protect biodiversity to the best of our abilities. Although genetic diversity is known to reflect population demography and contribute to genetic health and adaptability, it is not explicitly used as a criterion in assessments by the International Union for the Conservation of Nature (IUCN). Additionally, studies comparing diversity estimates between species often rely on summarizing results across studies, which use different methodologies and may not be suited for direct comparison. Here we performed a family-wide assessment of genomic diversity in Felidae, covering most extant species. We tested for correlations between autosomal heterozygosity and ecological traits across (sub)species, and whether a subspecies' genetic diversity was associated with its IUCN threat category. We found evidence for genetic diversity to be strongly positively correlated with both geographic range size and population density, but not with census size. Furthermore, although genetic diversity showed significant correlation with IUCN status, with threatened species exhibiting lower levels of genetic diversity, it was not possible to clearly distinguish between categories on this basis alone. Our results confirm the association of population parameters and assessment of extinction risk with genetic diversity in one of the most iconic and threatened families of land carnivores. While mechanisms and causality behind these associations will need to be the subject of further investigation, our study adds further credence to the importance of incorporating genomic information in risk assessment and conservation efforts.

Keywords Felidae · Heterozygosity · Conservation genomics · Global pattern

Introduction

Many species across the globe suffer reductions in population size and available habitat as a result of anthropogenic activity (Andermann et al. 2020). As these populations decline, so too does the genetic variation that exists within them (Willoughby et al. 2015). Genetic diversity is the key resource that allows species to adapt to novel conditions through natural selection (Sgrò et al. 2011). Loss of this genetic diversity will thus render species more vulnerable to extinction in the long term (Otto 2018). Declining populations are also likely to experience an increase in inbreeding, further reducing diversity in the gene pool, resulting in decreased fitness and reduced response to selection (Amos and Balmford 2001; Willi et al. 2022).

It is thus clear that genetic diversity is an important factor in the conservation of species and populations, and, accordingly, there have been increasing calls to collect more genetic data and increase the weight of genetic diversity in conservation assessments, something that is currently lacking in IUCN Red List assessments (Laikre et al. 2020; Hoban et al. 2020, 2024; Garner et al. 2020; Theissinger et al. 2023). Crucial topics of active debate are the relationship and potential predictive power of autosomal heterozygosity, a common measure of genetic diversity inferred from genomic data, with respect to a species' threat status (DeWoody et al. 2021; Teixeira and Huber 2021). Genomic

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data have been proven helpful in predicting a species' threat status or conservation priority (Fernandez-Fournier et al. 2021; Wilder et al. 2023), but not universally (Teixeira and Huber 2021; Kuderna et al. 2023). The latter studies found that no clear relationship could be determined between heterozygosity and a species' threat status across mammals and primates, respectively. However, it is equally possible that genetic data may be able to reveal species or populations at conservation risk that are currently not recognised using IUCN criteria (Willoughby et al. 2015; Jeon et al. 2024).

The cat family (Felidae) consists of at least 41 extant species, divided into two subfamilies, Felinae and Pantherinae (Kitchener et al. 2017) (Fig. S1). The family consists exclusively of hypercarnivores that fulfil important ecological roles in their environments, usually as mesopredators, while the larger species are generally apex predators and keystone species (Tensen 2018a, b). These top-down control effects, particularly from the larger apex predators, can exert substantial influences down the entire trophic chain (Ripple and Beschta 2006, 2008; Jorge et al. 2013; Sarasola et al. 2016). Beyond that, felids are typically charismatic species and score highly as favoured species for conservation with the public, making them suitable flagship species (Macdonald et al. 2015). Because of their ecological importance and charismatic appeal, felid research was an early adopter of using genomic data to further conservation research, as exemplified by studies on the Iberian lynx, Florida panther and cheetah (Pimm et al. 2006; Johnson et al. 2010; Abascal et al. 2016; O'Brien et al. 2017; Theissinger et al. 2023).

Today, there is an increasing number of studies using autosomal heterozygosity to investigate members of the Felidae family, often in a conservation context, including the above mentioned Iberian lynx (Abascal et al. 2016), pumas (Saremi et al. 2019) and cheetahs (Prost et al. 2022), as well as jaguars (Lorenzana et al. 2022), lions (Armstrong et al. 2020; de Manuel et al. 2020), leopards (Paijmans et al. 2021; Pečnerová et al. 2021), species of the genus *Leopardus* (Lescroart et al. 2023), bobcats (Lin et al. 2022), snow leopards (Solari et al. 2023), tigers (Cho et al. 2013; Liu et al. 2018; Armstrong et al. 2021), black-footed cats (Yuan et al. 2024), and clouded leopards (Yuan et al. 2023).

A few metastudies have also looked at trends in genetic diversity within the broader family, rather than individual species or genera, using microsatellite data (Azizan and Paradis 2021; Azizan et al. 2023). These metastudies found that there is a relationship between genetic diversity and both population density (Azizan et al. 2023) and threat status of a species (Azizan and Paradis 2021). However, these studies have two limitations. First, traditional markers, such as microsatellites used in these studies, focus on a small, biased set of polymorphic loci that are not representative of the average genetic diversity in the genome (Väli et al. 2008). In comparison, whole-genome sequencing (WGS) data yields estimates of population genetic parameters with greatly increased accuracy, because it derives from the genome in its entirety (Allendorf 2017; Fuentes-Pardo and Ruzzante 2017; Schmidt et al. 2021, 2024). Availability of WGS data has been rapidly increasing over the past decade, and for cats specifically, this type of data is now publicly accessible for almost all species. Second, metastudies aggregate genetic diversity estimates from multiple individual studies. However, such a comparison may not be justified if different methodologies are applied in different studies. This issue is especially apparent for estimates of heterozygosity from WGS data, which are sensitive not only to the choice of filter parameters and software, but also to the choice of reference genome (Brandt et al. 2015; Gopalakrishnan et al. 2017; Ros-Freixedes et al. 2018; Armstrong et al. 2020; Duchen and Salamin 2021; Prasad et al. 2022). Therefore, comparing estimates across studies may result in inaccurate conclusions and, instead, a single methodology should be applied to all genomic data. Some large-scale studies have carried out such analyses to look at whole-genome genetic diversity and how it relates to extinction risks in primates (Kuderna et al. 2023) and across placental mammals (Wilder et al. 2023). Previous studies applying such a unified approach to Felidae (Armstrong et al. 2020; Barnett et al. 2020; Lescroart et al. 2023; Solari et al. 2023) were limited in their taxonomic scope or the number of species included. As such, no study has applied a singular methodology to estimate and compare the heterozygosity across the majority of extant members of Felidae.

In the current study, we used previously published, raw whole-genome sequencing data to obtain estimates of genome-wide, autosomal heterozygosity for most members of the Felidae family (*sensu* Kitchener et al. 2017), covering all eight lineages of extant Felidae (Fig. S1). While past studies were often focused on specific subgroups of felids, such as the genera *Panthera* (Armstrong et al. 2020), *Leopardus* (Lescroart et al. 2023) or "big cat species" (Solari et al. 2023), and some used a limited amount of species (~15) across a wider taxonomic net (Barnett et al. 2020), our use of nearly all non-domesticated species of cats and a single methodological pipeline will allow, for the first time, for relatively unbiased comparisons between species across the Felidae family. We also compiled data on various species traits and population parameters at the species and subspecies level in order to uncover traits that may affect genetic diversity. We expected that larger population densities, geographic ranges and census sizes correlate positively with genetic diversity, as these parameters should relate to increased population mutation rate, reduced genetic drift and thus larger effective population sizes, an indicator of neutral genetic diversity (Frankham 2012; Leffler et al.

2012; Hague and Routman 2016; Myhre et al. 2016; Grundler et al. 2019; Jeon et al. 2024). On the other hand, we expected species with a larger body size or mass to have lower levels of genetic diversity than small-bodied species, because larger species typically maintain smaller population sizes (Silva et al. 2001; White et al. 2007; Grundler et al. 2019). Larger species are also more likely to suffer greater reductions in gene flow due to habitat fragmentation than do smaller species (Figueiredo et al. 2015). Finally, we compared genetic diversity to IUCN threat classification at subspecies level, testing the hypothesis that threatened subspecies have lower levels of genetic diversity.

Materials and methods

Data collection

To enable comparison of genetic diversity across a broad range of felid species, we compiled a dataset consisting of 100 individuals across 39 felid species, covering most extant felids, with the notable exceptions of the domestic cat (*Felis catus*), the Sunda leopard cat (*Prionailurus javanensis*) and African golden cat (*Caracal aurata*). A bay cat sample (*Catopuma badia*) was included in the initial dataset, but excluded from the final set of heterozygosity estimates due to poor data quality. Samples were selected by querying the Sequence Read Archive and European Nucleotide Archive databases for short-read whole-genome sequencing data. We limited our query to samples of non-domesticated, extant Felidae species sequenced to medium or high depth of genomic coverage from fresh material (Table S1). Sequences and metadata were downloaded with fastq-dl v2.0.4 (Petit et al. 2023). Samples were classified at the subspecies level according to taxonomic and geographic information in the metadata. For samples for which we could not infer subspecies classification, we opted to approximate ecological variables for statistical analysis by assigning it the values recorded for the subspecies with the largest range, rather than species-level sum totals that are an overestimation for any of the subspecies (e.g., range, census size) or artificial averages (e.g., density, body size). We clearly indicated where this approximation applies (Fig. 2 and Table S2). Classification followed the reference work *Felids and hyenas of the world* (José and Castelló 2020), which itself largely follows the revised Felidae taxonomy published by the IUCN Cat Specialist Group (Kitchener et al. 2017), but distinguishes some additional populations of particular interest below the subspecies level. Samples were also labelled as captive, when obtained from, e.g., a zoo population, or non-captive when obtained from the wild (Table S2, see also supplementary text).

Data on species traits and population parameters (body mass, body size, gestation, litter size, lifespan, census size, range and density) was compiled at the species and subspecies level by consulting the following sources: *Felids and hyenas of the world* (José and Castelló 2020), the *Handbook of the mammals of the world* (Wilson and Mittermeier 2009), the IUCN Red List of Threatened Species (IUCN 2023), and information made available by the IUCN/SSC Cat Specialist Group (www.catsg.org) (Table S3). Body sizes refer to measurements from the tip of the muzzle to the base of the tail. Geographic ranges were extracted from spatial distribution data made available by the IUCN Red List of Threatened Species, excluding all polygons in the categories *Extinct* and *Possibly Extinct*. Subspecies ranges were obtained by subdividing the species ranges in QGIS v3.0 (QGIS Development Team 2021) according to the geographic information listed in Kitchener et al. (2017). Surface areas were then calculated with custom Python code (see 'Data availability').

Mapping and variant calling

We aligned the raw reads of each sample to two reference genomes, applied filtering steps and called variant sites to obtain one set of genome-wide variants for each reference genome, using a custom pipeline (see 'Data availability'). We used two publicly available, highly contiguous genome assemblies as references, representing both subfamilies in Felidae: for Felinae, a domestic cat (*Felis catus*) genome (GenBank accession: GCA_018350175.1) (Bredemeyer et al. 2023) and for Pantherinae, a tiger (*Panthera tigris*) genome (GenBank accession: GCA_018350195.2) (Bredemeyer et al. 2023). This strategy allowed us to detect reference bias that may be introduced due to different genetic distances between the various samples and the reference genomes of both subfamilies (Prasad et al. 2022).

We created indices of the reference genomes using BWA v0.7.17 (Li and Durbin 2009) and SAMtools v1.14 (Danecek et al. 2021). Raw sequence reads of the sample set were then mapped to both reference genomes using the BWA-MEM algorithm. Using SAMtools, the aligned reads were tagged with mate scores and sorted by leftmost coordinates. We then marked duplicate reads, created an index for the Binary Alignment Map (BAM) file of each sample and obtained basic statistics for each alignment. BAM files were then compressed with Crumble v0.8.3 (Bonfield et al. 2019). We called bases jointly for all samples using BCFtools v1.14 (Danecek et al. 2021) and indexed the resulting Binary Call Format (BCF) file. We filtered the call set using BCFtools and custom Python code, retaining sites with mean mapping quality >50, <10% mapped reads with quality zero, allelic balance >20%, depth of coverage <150%

of the genome-wide average, and <20% missing genotype calls. We recorded the coordinates of all the sites that passed the filtering criteria using BEDTools v2.30.0 (Quinlan and Hall 2010) and further refer to this fraction of the genome as the 'accessible genome'. We then selected all biallelic single nucleotide polymorphism (SNP) variants located in the accessible genome from the call set, which were stored in Variant Call Format (VCF).

Heterozygosity estimates

For each sample in the VCF file, we counted the number of homozygous, heterozygous and missing genotypes in each autosome with a custom Python script (see 'Data availability'). We calculated heterozygosity as the number of heterozygous sites, taking into account a corresponding fraction of missing genotypes, and normalizing our count with the size of the accessible genome. Variance around the mean heterozygosity of each sample was calculated as the weighted standard deviation of estimates obtained from each of the 18 autosomes. Specifically, our estimator of heterozygosity is given as:

$$heterozygosity = \frac{sites_{heterozygous} + sites_{missing}}{size\ of\ accessible\ genome} \times \left(\frac{sites_{heterozygous}}{sites_{heterozygous} + sites_{homozygous}} \right)$$

Under the assumption of random mating, the heterozygosity as normalised here is an estimator of a population's nucleotide diversity π (i.e., the average number of nucleotide differences between two sequences per site) (Nei and Li 1979), a common measure of genetic diversity. This usage is consistent with much of population genetic literature, but we note that it differs from the measures of heterozygosity commonly used in microsatellite studies, which report heterozygosity values for loci known to be polymorphic. The latter measures can detect deviations from Hardy-Weinberg equilibrium (e.g., due to inbreeding), but given the conditioning on loci being polymorphic, they are not suited to assess overall genetic diversity.

Statistical analysis

We performed statistical analyses to test for biases in our heterozygosity estimates and to detect correlations between heterozygosity and various species and population characteristics or threat status. All analyses were conducted using custom R code (see 'Data availability'). Exploration of the data revealed a significant correlation between mean coverage and heterozygosity best explained by a power correlation of the formula: $heterozygosity = 0.006251 * coverage^{-0.556245}$ (adjusted $R^2 = 0.343$; $p < 0.001$), with the samples with the lowest coverage showing high heterozygosity (Fig. S2). When compared to our overall heterozygosity estimates and to other samples of the same species, the estimates for these low-coverage samples appeared inflated. We therefore excluded samples from further analysis if their average genome coverage was below 7× for both reference genomes (Cat_bad_PBA2; Lyn_ruf_mLynRuf1.p; Her_yag_HJA5, Aci_jub_EH_ID75, Aci_jub_DZ_ID42 and Aci_jub_AJU173) (Table S4; see Table S5 for a full list of samples and datapoints removed from various parts of the analysis).

We explored potential effects of reference bias in our heterozygosity estimates by calculating the strength of correlation between the estimates derived from mapping to the two distinct reference assemblies. In addition, we directly compared the estimate of each sample obtained from mapping to its phylogenetically closest reference (same subfamily) to the estimate obtained from the more distant reference (different subfamily).

To enable regression analysis, heterozygosity was averaged at the subspecies level for body mass, body size and geographical range, while for gestation time, litter size and lifespan, estimates were averaged at species level. For population density and census size, data was averaged at the subspecies level where possible, and at the species level otherwise. To test for phylogenetic signal in the data, we used the multiphylosignal function in the picante v1.8.2 package (Kembel et al. 2010), which calculates Blomberg's K, a statistic that compares observed trait values to expectations based on a Brownian motion model of evolution. The phylogenetic scale of the test matched the scale at which estimates of heterozygosity were averaged. Due to how the data was used, heterozygosity, population density and census size were tested at both species and subspecies level. Phylogenies were based on the published phylogeny by Li et al. (2016) (Fig. S1). For the tests at subspecies or population level, the phylogenetic tree was adapted by splitting each species node into lower-level nodes with an arbitrary branch length of 0.5 (subspecies) or 0.3 (e.g. African and Indian populations of *Panthera leo leo*) (Fig. S3). We then performed a simple linear regression to test the correlation between heterozygosity, the dependent variable, and each ecological variable separately, as the independent variable. P-value, sample size (n), correlation coefficient (R) and the coefficient of determination (adjusted R^2) of the linear regression were added to the plots using ggpmisc v0.6.1 (Aphalo 2024). We subsequently produced diagnostic plots for each correlation to verify adherence to the model assumptions, particularly looking for signs of heteroscedasticity and

potentially influential outliers, as these will have the greatest effect on model accuracy (Schmidt and Finan 2018). Outliers were considered influential when the Cook's distance exceeded 5 (Table S5). We redid the linear regression after transforming the data or removing influential outliers, where appropriate. As an additional method to assess the effect of phylogeny, we created linear mixed-effects models (Table S6 and supplementary text).

We also performed a multiple regression analysis in order to assess the relative predictive value of each ecological variable in relation to heterozygosity. First, we assessed intercorrelation between the ecological variables at the subspecies level using the Kendall rank correlation coefficient (Kendall's Tau), visualised with the GGally package v2.2.1 (Schloerke et al. 2024). We then constructed a multiple regression model with the variables that showed significant correlation with heterozygosity, but not with any other variable included in the model. The lack of multicollinearity of independent variables in the model was verified by calculating the variance inflation factor using the car package v3.1-3 (Fox and Weisberg 2019). Lastly, we determined the relative predictive value of each ecological variable in the multiple regression model by calculating their coefficient of partial determination (R^2) using the Sensemakr v0.1.6 package (Cinelli et al. 2024).

To evaluate the difference in heterozygosity between threat categories, we used the IUCN Red List Categories classification and averaged heterozygosity by subspecies before applying a Welch's t-test to compare between threatened (Vulnerable, Endangered and Critically Endangered) and non-threatened (Least Concern and Near Threatened). We also applied an ANOVA test followed by Tukey's Honest Significant Difference test to evaluate differences between the separate IUCN categories. We then used ordinal regression to evaluate how much of the variation across IUCN categories is explained by heterozygosity using the ordinal v2023.12-4.1 package (Christensen 2024). We carried out an analogous binomial logistic regression to evaluate the amount of variation that heterozygosity could explain across the threatened and non-threatened group. McFadden's pseudo-R^2 was then used to evaluate improvement of the model fit between the null model and the full model using heterozygosity as an explanatory variable. McFadden's pseudo-R^2 are typically much lower than traditional R^2 values, and values between 0.2 and 0.4 are considered good performance (McFadden 1979). The McFadden's pseudo-R^2 values were determined using the *nagelkerke* function in the rcompanion package v2.5.0 (Mangiafico 2025).

Finally, we explored potential differences between samples obtained from captive or wild-collected individuals by comparing the two groups across the entire family and within the *Panthera* lineage using Welch's t-tests. The latter lineage was chosen for its large representation of both groups compared to the other lineages. Results were visualised with boxplots. Plots were generated using the ggplot2 (v3.5.1) and ggpubr (v0.6.0) packages (Wickham 2016; Kassambara 2023). The significance threshold for all analyses was set at $p < 0.05$.

Results

Mapping and base calling

We mapped the raw sequencing reads of each sample (94 million − 1 billion reads per sample, see Table S1) to both reference genomes and applied a series of filter steps, resulting in accessible genome sizes of 78% (1.78 Gbp) of the domestic cat assembly and 80% (1.82 Gbp) of the tiger assembly. Base calling yielded 270 and 275 million variant sites in the total sample set after filtering. The number of variants retained per sample varied between 1.9 and 35.2 million biallelic SNPs (Table S7).

Minor effect of reference genome on heterozygosity estimates

Heterozygosity estimates obtained with reference assemblies of both subfamilies were highly correlated ($R = 1.00$; $p < 0.001$) (Fig. 1a). Estimates were also consistent when comparing between those using a phylogenetically close and more distantly related reference genome (Fig. 1b). In those cases where estimates were noticeably different, it was typically an increase in heterozygosity when mapped to the distant reference genome (Fig. 1c). This occurred primarily in tigers (*Panthera tigris*) and members of the wildcat lineage (genus *Felis*), particularly the Afro-Asiatic wildcat (*F. lybica*) (Fig. S4). The largest difference was found in an Afro-Asiatic wildcat individual (FLI4) and constitutes an absolute increase in heterozygosity by 0.047% percentage points, or a 21.7% increase when mapped to the more distant reference genome relative to the closer reference (Table S8). Overall, our results suggest that, with our variant filtering, the choice of reference genome is of minor importance at the phylogenetic scale of this study. Because of the high similarity between both sets of heterozygosity estimates, the remainder of the analysis was performed using the domestic cat set.

54-fold variation in heterozygosity estimates across the cat family

Our estimates of heterozygosity range from 0.006% (SD = 0.002%) in a sample from the Indian population of

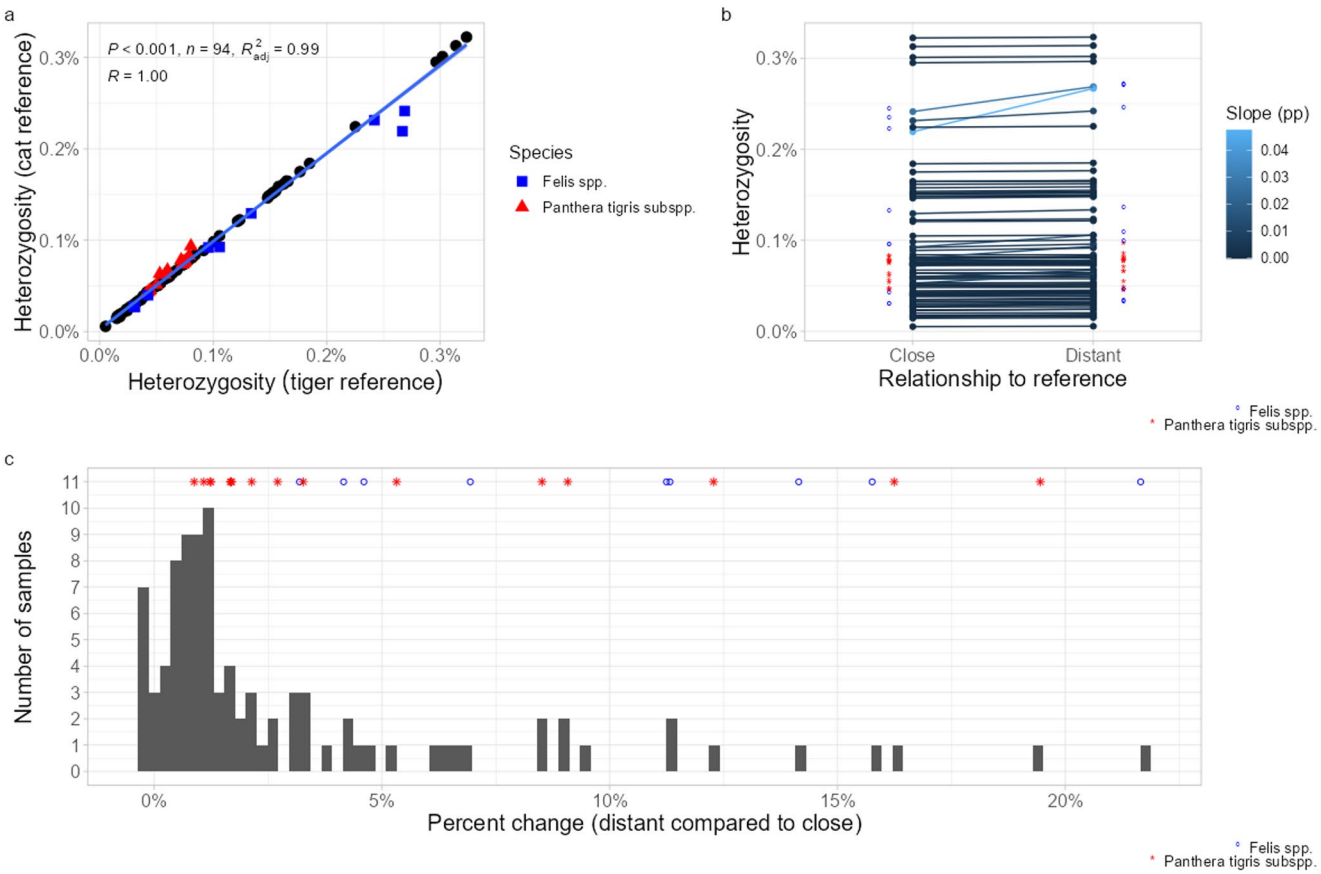

Fig. 1 Effect of using different reference genomes on heterozygosity estimates. **a** Correlation between heterozygosity estimates using a reference genome belonging to a tiger and a domestic cat. **b** Estimates of heterozygosity obtained from mapping against the reference genome from the same subfamily versus the reference genome from the other subfamily. Data points derived from the same sample are connected with a line, the slope of which indicates percentage point difference. **c** Histogram showing the difference in heterozygosity estimates given as a percent increase from estimates derived from the close reference to estimates derived from the distant reference. Species of the genus Felis are marked with a blue square (**a**) or open circle (**b-c**); subspecies of the tiger (Panthera tigris) are marked with a red triangle (**a**) or asterisk (**b-c**)

lions, *Panthera leo leo*, to 0.322% (SD = 0.012%) in an ocelot, *Leopardus pardalis*, revealing a 53.7-fold difference across the cat family (Fig. 2, grouped by subspecies, Fig. S5, grouped by species). Other species with high levels of heterozygosity are the serval (*Leptailurus serval*) (0.295%), and African/Asiatic wildcats (*Felis lybica lybica/ornata*) (0.219–0.231%), while other species with notably low levels of heterozygosity were the Andean cat (*Leopardus jacobita*) (0.014%) and the snow leopard (*Panthera uncia*) (0.017–0.019%).

We found no significant difference in heterozygosity estimates between captive and non-captive samples across the entire family ($t_{(89.4)}$ = -0.927; p = 0.357), but within the Panthera lineage, there was a significant difference ($t_{(39.2)}$ = -2.83; p = 0.007), with captive samples exhibiting lower genetic diversity on average (Fig. S6). Heterozygosity values vary greatly both across and within the different felid lineages, and vary noticeably even between samples of the same species. For instance, heterozygosity differs between African leopards and the Asiatic subspecies (resp., *Panthera pardus pardus* and *P. p. orientalis/fusca*), between North/Central and South American pumas (resp., *Puma concolor cougar* and *P. c. concolor*), and within North/Central American pumas (*P. c. cougar*) (Fig. 2). Of the eight suprageneric lineages commonly referred to in Felidae, none was uniformly high or low in genetic diversity.

Heterozygosity is significantly correlated with geographic range size and population density

The simple linear regressions (Fig. 3) indicated a clear positive relationship between heterozygosity and range (R = 0.47; p < 0.001). Population density initially showed no significant correlation with heterozygosity (R = 0.15; p = 0.369). Outlier analysis, however, revealed the presence of two strong outliers, the guigna (*Leopardus guigna*) and jungle cat (*Felis chaus*) (Fig. S7 a-d). Removal of the outliers revealed a strong positive correlation with heterozygosity

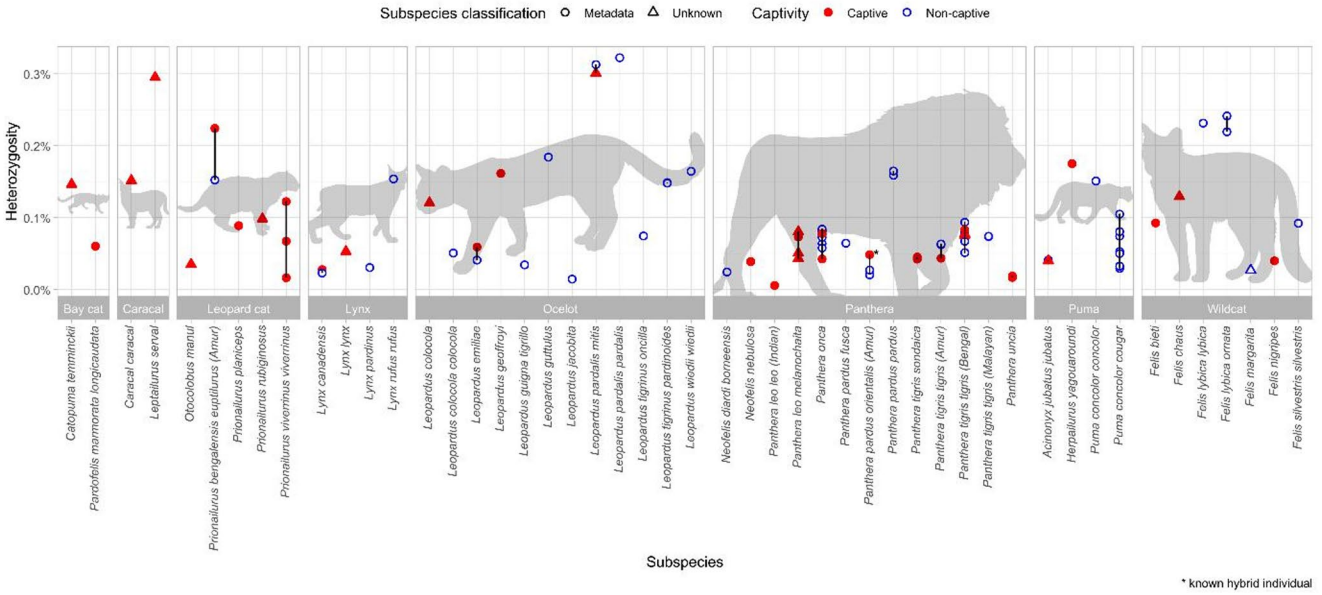

Fig. 2 Estimates of heterozygosity for all samples using the cat reference genome, grouped per lineage and subspecies. Red filled shapes denote samples from captive populations; blue open shapes denote samples from wild populations. Circles denote samples where subspecies classification is retrieved from the metadata; triangles denote samples without such information. Silhouettes obtained from PhyloPic (www.phylopic.org)

($R=0.52$; $p=0.001$). Alternatively, using a more conservative estimate for guigna population density also resulted in a significant positive relationship ($R=0.36$; $p=0.025$) (Fig. S8).

Census size showed no significant relationship with heterozygosity, both before ($R=0.24$; $p=0.182$) and after outlier removal (R = -0.07; $p=0.719$) (Fig. 3h; see also Fig. S7 e-h). Average lifespan, also, showed no correlation with heterozygosity ($R<0.01$; $p=0.99$). Litter size (R = -0.23; $p=0.162$), body size (R = -0.28; $p=0.055$), body mass (log-transformed) (R = -0.21; $p=0.147$) and gestation time (R = -0.25; $p=0.144$) all showed weak, non-significant negative relationships with heterozygosity (Fig. 3). Results using only non-captive samples were similar overall, but with lower levels of statistical confidence (Fig. S9, Table S9).

We found no evidence of significant phylogenetic signal in estimates of heterozygosity at the species level ($K=0.102$, $p=0.324$), and only very weak phylogenetic signal at the subspecies level ($K=0.098$, $p=0.002$). At the species level, both litter size and gestation time showed significant phylogenetic signal, with litter size having a relatively weak signal ($K=0.231$, $p=0.002$) while gestation time had a strong signal ($K=1.045$, $p<0.001$), indicating that the trait is distributed as expected under Brownian motion. At the subspecies level, both male size and male mass showed significant phylogenetic signal in the weak-moderate range (resp. $K=0.284$, $p<0.001$; $K=0.497$, $p<0.001$) (Table S10). As the significant variables only showed weak or no phylogenetic signal, corrections for phylogenetic non-independence were not incorporated into the models.

To build the multiple regression model, we selected only the independent variables that significantly correlated with heterozygosity at the subspecies level and lacked significant correlation with other such independent variables (Fig. S10). This resulted in a model with two explanatory variables: range and population density (τ_B range ~ density = 0.040 (filtered; $p=0.98$); 0.003 (conservative; $p=0.73$)). Because the population density data was less complete at the subspecies level than the geographic range data, we summarized the range data to match the sample size of the density data (see: "Statistical analysis"). The model explains 29.3% of the variation in heterozygosity (adjusted $R^2=0.2933$). The low Variance Inflation Factor ($VIF=1.001$) confirmed absence of multicollinearity in the model. Range was a more important predictor (partial $R^2=0.230$; $p=0.003$) compared to population density (partial $R^2=0.155$; $p=0.016$) when the conservative density estimate was used for guigna. However, density increased in importance when the guigna datapoint was omitted entirely (Range: partial $R^2=0.201$; $p=0.007$, Density: partial $R^2=0.275$, $p=0.001$). The overall model that omitted the guigna and jungle cat datapoints also explained more of the variation in heterozygosity (adjusted $R^2=0.3845$; $p<0.001$; $VIF=1.017$; see also Table S11).

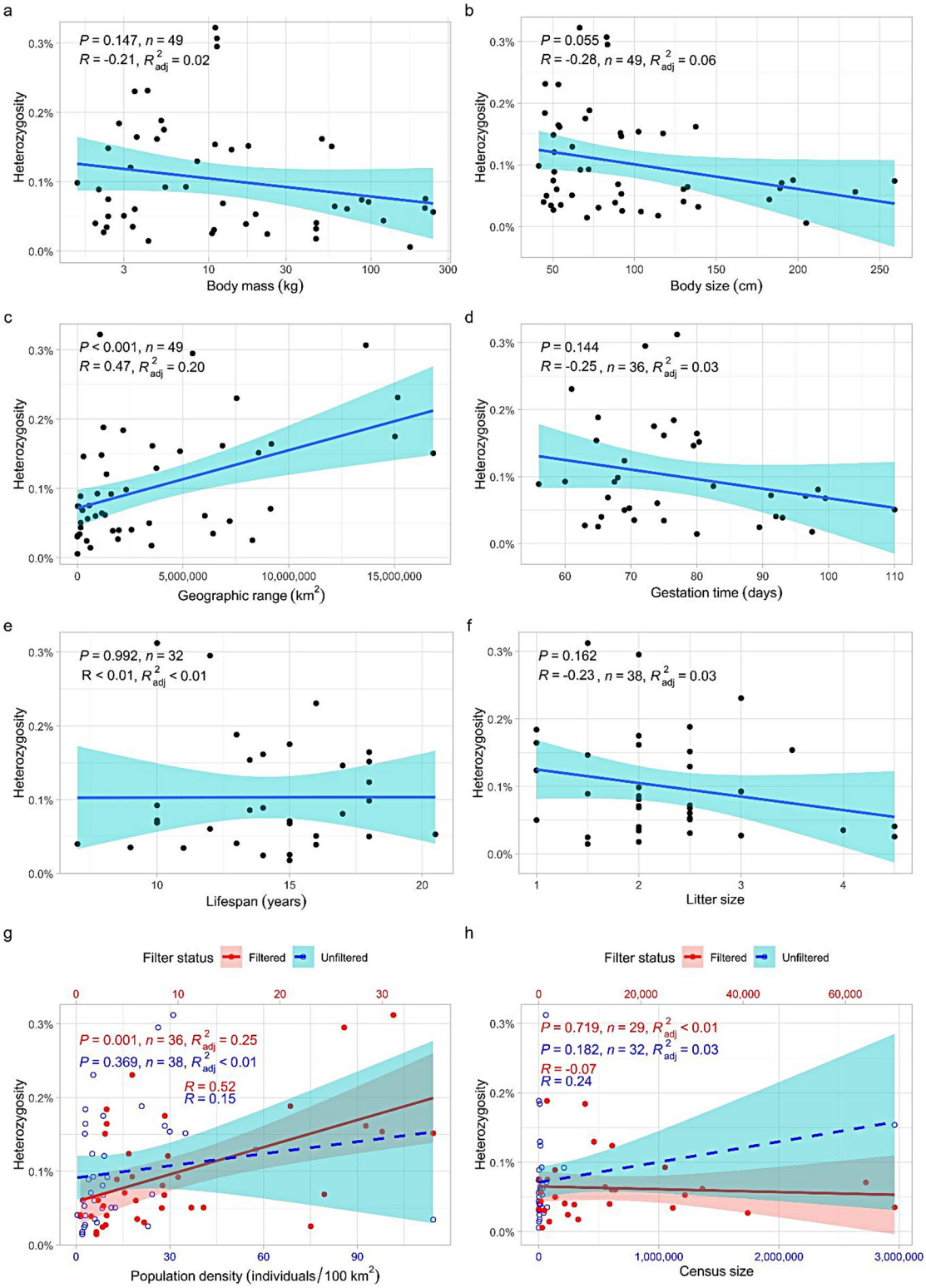

Fig. 3 Simple linear regressions between heterozygosity and ecological traits. Heterozygosity as a function of **a** log-transformed body mass, **b** body size, **c** geographic range, **d** average gestation time, **e** average lifespan, **f** average litter size, **g** average population density, **h** average census size. Averaging is at subspecies level (**a-c**), species level (**d-f**), or both depending on data availability (**g-h**). **g** and **h** show regression with (blue; open circles; dashed line) and without (red; filled circles; solid line) outliers. Datapoints were transformed (red) and imposed on a secondary axis (red; top) for clarity

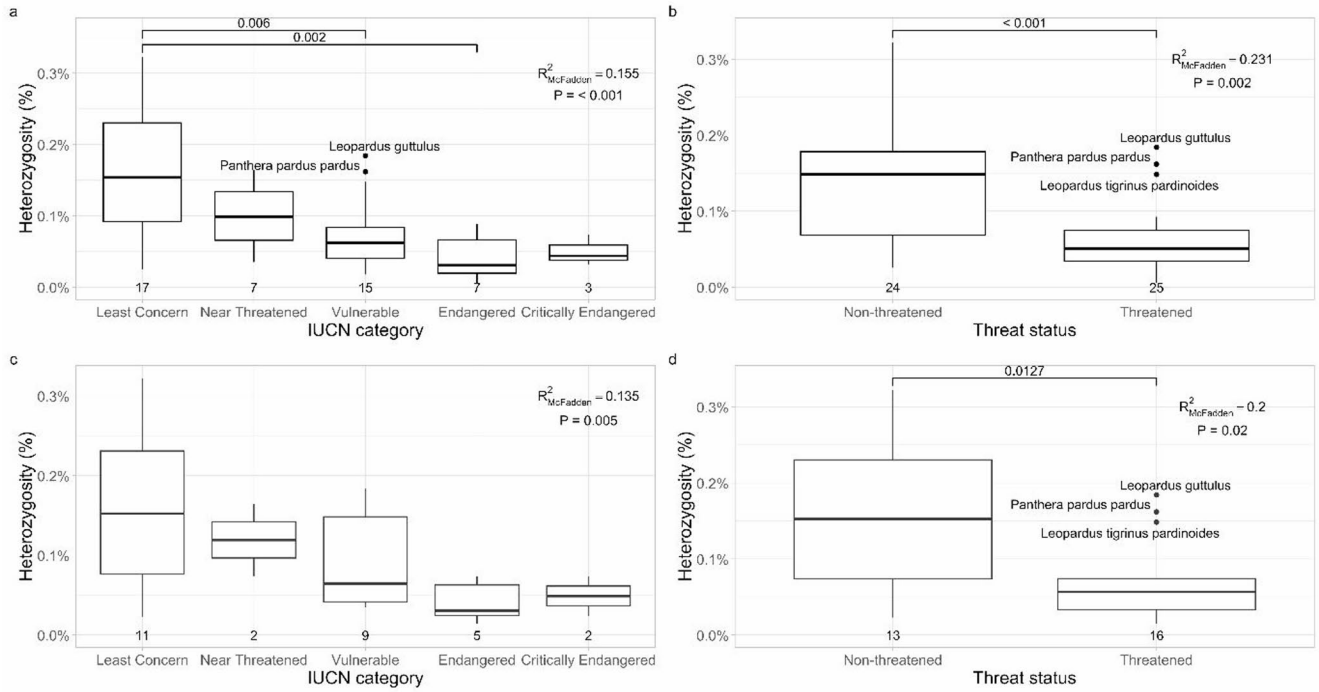

Fig. 4 Differences in average heterozygosity of subspecies between **a** the different IUCN categories, **b** threatened and non-threatened subspecies, **c** the different IUCN categories using only non-captive samples, **d** threatened and non-threatened subspecies using only non-captive individuals. Comparisons between threat categories were carried out using a Welch's t-test. Comparisons between IUCN categories were carried out using a Tukey HSD test after rejection of an ANOVA test. McFadden's pseudo-R^2 is given as a measure of the variation in heterozygosity explained by threat status. Sample sizes per category are shown below each box

Heterozygosity is significantly lower in threatened species

There was a noticeable trend of declining heterozygosity estimates going from Least Concern to Critically Endangered categories (with the exception of Critically Endangered showing slightly higher heterozygosity than Endangered) (mean heterozygosity: LC = 0.162%; NT = 0.099%; VU = 0.075%; EN = 0.042%; CR = 0.050%). Overall, heterozygosity estimates differed significantly between IUCN categories ($F_{(4;44)} = 5.91$; $p < 0.001$). Pairwise comparisons revealed that significant differences only existed between subspecies classified as Least Concern and Vulnerable ($p = 0.006$) and Least Concern and Endangered ($p = 0.002$) (Fig. 4a). Ordinal regression analysis confirmed that heterozygosity correlates significantly with IUCN status and that its inclusion constitutes a moderate improvement of the overall model fit, both when all samples were considered (estimate = -2074.1 ± 535.8; $p < 0.001$; McFadden's pseudo-$R^2 = 0.16$) as well as when only non-captive samples were used (estimate = -1687 ± 604; $p = 0.005$; McFadden's pseudo-$R^2 = 0.13$) (see also supplementary table S12).

When splitting the data into threatened and non-threatened categories, heterozygosity was higher on average in the non-threatened (0.144%) than in the threatened (0.063%) subspecies ($p < 0.001$) (Fig. 4b).

Heterozygosity did not exhibit significant differences between IUCN categories when only non-captive individuals were considered ($p = 0.066$). The difference between threatened and non-threatened subspecies, however, remained significant ($p = 0.0127$) (Fig. 4c and d). Binomial logistic regression further established the significance of the relationship between heterozygosity and a subspecies' status as threatened or non-threatened and again confirmed that the inclusion of heterozygosity as an explanatory variable improved the model fit (all samples: estimate = 1946.6 ± 624.9; $p = 0.002$; McFadden's pseudo $R^2 = 0.23$; non-captive samples: estimate = -1519.4 ± 652.3; $p = 0.020$; McFadden's pseudo-$R^2 = 0.20$) (Table S13).

Discussion

Choice of reference genome has little effect on heterozygosity estimates in felids

Reference bias may affect estimates of genetic diversity in complex and contrasting ways, dependent on features of the genome assembly and the phylogenetic relation of the

reference species to the focal taxa. Increased phylogenetic distance to the reference genome may both inflate (Prasad et al. 2022) or underestimate (Degner et al. 2009; Sousa and Hey 2013; Ros-Freixedes et al. 2018; Duchen and Salamin 2021) heterozygosity through misalignments between the reference and the sample of interest. Estimates may further be impacted by the quality of the reference genome (Gopalakrishnan et al. 2017; Prasad et al. 2022) or the software and filtering strategy employed (Brandt et al. 2015; Duchen and Salamin 2021).

Considering all these caveats, it becomes clear that comparisons of estimates obtained from different studies may very well lead to inaccurate results. To address these issues, we subjected WGS data of nearly all extant Felidae species to a single heterozygosity estimation pipeline, thereby ensuring identical treatment of each sample in terms of mapping, quality filtering and estimation of heterozygosity. Our resulting set of heterozygosity estimates (Fig. 2, Table S4; see Tables S8 & S14 for different layouts) offer a largely unbiased view of the relative differences in genetic diversity found in individual samples across the cat family. Ideally, estimates of heterozygosity would be determined with high-quality, species-specific reference genomes. Since this resource has not yet been developed for all species, we instead used two high-quality, ultra-contiguous assemblies, representing both subfamilies, (*Felis catus* with N50 of 148.5 Mbp and 39 gaps, and *Panthera tigris* with N50 of 146.9 Mbp and 65 gaps), allowing us to assess potential reference bias in terms of phylogenetic distance to the samples of interest.

We found that estimates were generally consistent between reference genomes (Fig. 1), contrasting previous studies (Armstrong et al. 2020; Prasad et al. 2022). This may reflect the high quality of both reference genomes and the high level of synteny among felid genomes (Davis et al. 2009; Cho et al. 2013; Armstrong et al. 2020). Clear signs of reference bias, considered as >5% difference between same-sample estimates ($n=18$; see Table S8), mostly concerned samples closely related to one of the reference species ($n=12$), i.e., tigers (*Panthera tigris*) which share a common ancestor 7.5–9.2 kya (Armstrong et al. 2021) and species in the domestic cat lineage (*Felis spp.*) with a common ancestor ~3 mya and ubiquitous post-speciation gene flow (Yuan et al. 2024). Large relative differences between references may also be an artefact of low absolute heterozygosity (likely in samples of fishing cat and Canadian lynx; $n=3$), possibly compounding true reference bias (*Panthera* samples with low diversity, i.e., Asiatic lion and snow leopard; $n=3$). Where biased, heterozygosity was generally overestimated with the more distant reference, in line with the findings of Prasad et al. (2022), who surmised that this might be the result of misalignments.

Genetic diversity across Felidae

The sample with the lowest heterozygosity (0.006 ± 0.002%) among our set of felids was an Asiatic lion (*Panthera leo leo*; formerly *P. l. persica*), consistent with previous findings (Azizan and Paradis 2021). The Asiatic lion once roamed across most of India, its range possibly extended as far west as Anatolia (Jhala et al. 2019). Habitat loss and hunting during the second half of the 19th century eventually reduced the Asiatic lion population to less than 50 individuals in the Gir forest in India (Jhala et al. 2019). Its negative population trend has since been reversed as a result of conservation measures implemented during the 20th century, elevating the species from Critically Endangered to Endangered status (Jhala et al. 2019). Regardless, the severe bottleneck the population experienced is more than likely still showing its effects in the estimates of heterozygosity determined in this study. Other (sub)species with severely depleted levels of heterozygosity (<0.03%) were the Andean cat (*Leopardus jacobita*), snow leopard (*Panthera uncia*), Amur leopard (*Panthera pardus orientalis*), Canada lynx (*Lynx canadensis*), Bornean clouded leopard (*Neofelis diardi borneensis*) and Arabian sand cat (*Felis margarita thinobia*). These (sub) species have previously been reported to harbour exceedingly low genetic diversity (Paijmans et al. 2021; Bursell et al. 2022; Lescroart et al. 2023; Solari et al. 2023; Yuan et al. 2024), with the exception of Canada lynx. Studies on the Canada lynx have typically found high levels of heterozygosity (Campbell and Strobeck 2006), although heterozygosity was lower in peripheral and insular populations (Schwartz et al. 2003; Prentice et al. 2019). Another species from the Lynx lineage, the Iberian lynx (*Lynx pardinus*), is often brought forward as an example of extremely low heterozygosity among vertebrates (Abascal et al. 2016). With an estimate of 0.031 ± 0.005% for Iberian lynx, our family-wide comparison demonstrates that there are several other felids species that have lower levels of genetic diversity.

The highest estimates of heterozygosity in this study all belong to the ocelot (*Leopardus pardalis*), which is in concordance with past studies that have looked at genetic diversity in *Leopardus* and other felid species (Ramirez et al. 2022; Lescroart et al. 2023). Plausible explanations for the high diversity of the ocelot are its occurrence at high densities and broad distribution as well as higher levels of gene flow between populations compared to larger species such as jaguars (*Panthera onca*) (Figueiredo et al. 2015; de Oliveira et al. 2022; Lombardi et al. 2022; Lescroart et al. 2023). Other (sub)species with high heterozygosity values (>0.2%) include the serval (*Leptailurus serval*), the leopard cat (*Prionailurus bengalensis*) and the Afro-Asiatic wildcat (*Felis lybica)*. The leopard cat and the Afro-Asiatic wildcat have previously been shown to have high degrees of genetic

diversity compared to other cat species (Barnett et al. 2020; Azizan and Paradis 2021; Yuan et al. 2024), while we were unable to find any earlier estimates of heterozygosity for the serval. It should also be noted that both the serval and the leopard cat sample were derived from captive individuals, which may affect genetic diversity.

The incorporation of multiple samples per species or, where available, per subspecies, revealed relatively uniform heterozygosity in some species and considerable intraspecific variation in others. Species such as ocelot, Afro-Asiatic wildcat, jaguar and tiger all exhibited low variation across samples, while high variation was observed in puma and leopard samples, in accordance with the findings of the studies that originally published the data (Kim et al. 2016; Saremi et al. 2019; Paijmans et al. 2021). Several other species showed considerable variation in heterozygosity, such as the fishing cat (*Prionailurus viverrinus*) (Fig. 2). However, as for some species we are partly or entirely dependent on data from captive individuals with little information on pedigree or origin, it is not possible to ascertain whether this variation is representative for natural populations, or the result of in- or outbreeding in captivity. For instance, the amur leopard (*Panthera pardus orientalis*) with the highest heterozygosity was confirmed to be a 30% hybrid with a North Chinese leopard (*P. p. orientalis*, *formerly P. p. japonensis*) (Kim et al. 2016). In other instances, such as the puma samples, the variation matches natural patterns of population structure. The highest level of heterozygosity in this species (0.15%), belongs to the South American puma (*Puma concolor concolor*), which has larger and better-connected populations than their northern conspecifics. In North America, populations were drastically reduced as a result of habitat destruction and hunting, until regulations were put in place during the mid-20th century (Saremi et al. 2019). Genetic diversity in North American pumas ranges from 0.03% in an inbred and threatened population in Florida (Pimm et al. 2006; Johnson et al. 2010; Saremi et al. 2019), up to 0.08% and 0.10% in larger and outbred populations, respectively (Saremi et al. 2019). In general, diversity in puma populations, appears to match their degree of isolation (Riley et al. 2014; Saremi et al. 2019) (see also supplementary text).

Heterozygosity correlates with population density and geographic range

We tested for correlations between average heterozygosity of subspecies and various ecological traits of the subspecies using simple linear regression. We found that a subspecies' heterozygosity was highly positively correlated with geographic range (Fig. 3c), conform with some studies that have previously found significant relationships between these two variables in *Drosophila* as well as threatened mammals (Leffler et al. 2012; Doyle et al. 2015), but in contrast with findings from Romiguier et al. (2014) and Azizan and Paradis (2021). Romiguier et al. examined a broad host of metazoan taxa, whereas the current study is limited to the Felidae family. Our observed correlation between heterozygosity and range may break down at larger phylogenetic scales owing to differences in life history traits or other aspects of biology that do not vary within a single family. On the other hand, Azizan and Paradis (2021) focused specifically on Felidae, yet did not observe a correlation between range and genetic diversity, which is likely a consequence of our different treatment of the spatial data available through the IUCN Red List. In their study, the authors used the range data as it is presented, i.e., at the level of species, whereas we carried out manual division of the spatial polygons to instead conform to the ranges of subspecies. Our approach allows for a more nuanced correlation analysis of geographic range and genetic diversity data, because the subspecies level more accurately approximates the population structure that shapes genetic diversity.

Average population density initially showed no significant correlation with genetic diversity values, in contrast with expectations based on earlier findings (Azizan et al. 2023). Exploring the data revealed the presence of two outliers (Fig. S7a-c), removal of which results in a significant positive relationship (Fig. 3g). These outlier data points belong to the guigna (*Leopardus guigna*) and jungle cat (*Felis chaus*), both having relatively low levels of genetic diversity and high estimates for their population density. The outliers are indicative of a general limitation of the population density data: a lack of estimates from different regions and/or populations. For both species, the number of available estimates is limited and both have estimates derived from pristine habitats (Belousova 1993; Dunstone et al. 2002), where one can expect density to be higher and thus not representative for the situation across the species' range. Alternatively, using another, more conservative estimate for the guigna also resulted in a significant positive relationship (Fig. S7d & S8), bringing it more in line with the findings of Azizan et al. (2023). Our finding of a positive relationship between population density and genetic diversity in felids aligns with the prediction from neutral theory. The relationship supports earlier notions about explanatory factors in genetic diversity, such as the difference in population density between the ocelot and jaguar, and is in agreement with empirical observations in other taxa, e.g., in lizards (Hague and Routman 2016).

We also found that there were no significant relationships ($P > 0.05$) between genetic diversity and body size, or genetic diversity and body mass, unlike what was reported in earlier studies across metazoan taxa (Romiguier et al.

2014), butterflies (Mackintosh et al. 2019), mammals (Wooten and Smith 1985; Lino et al. 2019), tanagers (Brüniche-Olsen et al. 2019) and birds in general (Eo et al. 2011), but in agreement with an earlier study on felids (Azizan and Paradis 2021) and another in mammals (Doyle et al. 2015). It thus appears that measures of body size are not strong predictors of genetic diversity in felids. That said, we do observe a negative trend in felids between genetic diversity and body size (R = -0.28) or body mass (R = -0.27), as did Azizan and Paradis (2021). As argued by these authors, measures of body size are associated to other factors that might have causal links with heterozygosity. Indeed, larger-bodied species tend to have lower population sizes, a phenomenon known as Damuth's rule (Damuth 1981), and thus generally lower N_e, as well as lower rates of molecular evolution (Martin and Palumbi 1993; Eo et al. 2011). Interestingly, measures of body size did not show any notable correlation with the two significant variables– population density and geographic range (Fig. S10). This may be the result of relatively low sample sizes and lack of availability of population density data. On the other hand, relationships between measures of body size and both population density and geographic range have been found to be more complex than expected (Silva et al. 2001; White et al. 2007; Willig et al. 2009; Smith and Lyons 2013; Lyons et al. 2019).

Census size also showed no correlation with autosomal heterozygosity, contrary to our hypothesis that larger population sizes are linked to increased genetic diversity, as it has previously been shown that census size can be used as a proxy for effective population size with an N_e/N_c ratio of around 0.11–0.14 (Frankham 1995, 2012; Palstra and Ruzzante 2008). Some past studies did manage to uncover a significant correlation with genetic diversity (Frankham 2012; Hague and Routman 2016), but many others were similarly unable to establish such correlation (Nabholz et al. 2008; Perry et al. 2012; Leffler et al. 2012). A possible explanation for the lack of correlation is the nature of the census data. The census data here represents the sum total of all mature individuals of a species or subspecies, which may be far greater than the true census sizes of individual, reproductively connected populations, thus masking potential correlations. Additionally, some studies have found evidence of a negative relationship between N_e/N_c and N_c, particularly in very small populations, which may further muddle the relationship (Palstra and Ruzzante 2008; Myhre et al. 2016). A more fine-grained analysis with accurate estimations of census data at the population level would thus greatly help in uncovering how population size relates to genetic diversity in cats.

Finally, we found no relationship between genetic diversity and the life history traits of average litter size, lifespan and gestation time. Gestation time and litter size did both show a noticeable negative trend, however. The negative trend shown by gestation time is likely related to the negative trend noticed in body size and mass, as gestation time has been shown to be strongly correlated to body mass in carnivores (Danis and Rokas 2024). The negative trend in litter size on the other hand conflicts with earlier findings by Romiguier et al. (2014), who found a strong positive correlation between measures of genetic diversity and fecundity. It should be noted, however, that Romiguier et al. used a large variety of metazoan taxa, and thus had a much larger range of fecundity data compared to our taxonomically limited scale. Their study also revealed a negative correlation with lifespan where we found none. This too might be explained by the difference in taxonomic scope and the associated variability in lifespans.

A multiple linear regression model, which was created using the variables that were significant in the simple linear regression analysis (population density and geographic range), suggested that geographic range was a better predictor of heterozygosity than population density, unlike the conclusion by Azizan et al. (2023), who identified population density as the main predictor of genetic diversity in felids. Factors leading to these different outcomes are likely our use of genome-wide estimates of diversity, our improved resolution in range data and inclusion of a higher number of species. It should be noted that the relative importance of both variables is reversed when the guigna data is removed. Future studies investigating these relationships would benefit greatly from improved estimates of population characteristics, especially population density.

Threatened species have significantly lower levels of autosomal heterozygosity

We tested the relationship between genetic diversity and IUCN threat status within a single family, Felidae, using whole-genome sequence data. When deciding on conservation priorities, genome-wide variation is thought of as a suitable proxy for variation with adaptive potential, as demonstrated in yellow warblers and lodgepole pines (Fernandez-Fournier et al. 2021). While our results do show that heterozygosity correlates significantly with IUCN categories, with lower heterozygosity indicating a higher threat category, it remains difficult to distinguish between categories based on heterozygosity alone (Fig. 4a). These findings confirm those of earlier studies where heterozygosity was similarly unable to distinguish between IUCN categories (Teixeira and Huber 2021; Schmidt et al. 2023; Kuderna et al. 2023), while also supporting findings that there is a general, albeit sometimes weak, relationship between declining heterozygosity and increasing extinction risk (Schmidt et al. 2023; Jeon et al. 2024). We also found that estimates of

heterozygosity performed better as a predictor of extinction risk when the categories were summarized as "threatened" (LC, NT) and "non-threatened" (VU, EN, CR), as was the case in previous studies (Willoughby et al. 2015; Azizan and Paradis 2021; Wilder et al. 2023; Kuderna et al. 2023; Jeon et al. 2024).

There are several possible reasons that may explain the difficulty in differentiating between IUCN classifications based on genetic diversity measures. Most importantly, it takes time for genetic diversity to reflect changes in a population's demography. Current estimates of heterozygosity may be inaccurate due to population structure or failure to capture recent, sudden population decline or fragmentation and instead represent historic population size and connectivity (Willoughby et al. 2015; Schmidt et al. 2023). The IUCN Red List also does not make use of genetic diversity data in its assessment criteria, meaning that species that might qualify for a threatened status from a genetic point of view are potentially overlooked by the IUCN criteria (Willoughby et al. 2015; Schmidt et al. 2023; Jeon et al. 2024). Finally, the non-threatened categories, LC and NT, tend to have a much wider range of heterozygosity values compared to the threatened categories, VU, EN and CR, as well as more species listed, as has been reported elsewhere (Schmidt et al. 2023).

We have shown above that the high variability of genetic diversity estimates in North American pumas can be explained by the conditions and demographic history of the populations that each of the samples belong to. The wide variation in heterozygosity estimates present in non-threatened categories may therefore in part result from the sampling of threatened populations of an otherwise non-threatened (sub)species. For example, prior to the revision of the Felid taxonomy by Kitchener et al. (2017), the Florida puma, which exhibits the lowest levels of heterozygosity among puma samples here, was categorised as an endangered subspecies and currently still is listed as an endangered subpopulation (Nielsen et al. 2016).

Genomic diversity in conservation

We have shown that in felids, threatened species have significantly lower levels of genetic diversity than non-threatened species and that this heterozygosity can be linked to various species or population traits, among which are geographical range and population density, presumably because these traits reflect the effective population size to some degree (Myhre et al. 2016; Birzu et al. 2019; Jeon et al. 2024). In that regard, the lack of correlation between genetic diversity and census size in our sample set was unexpected, as lower population sizes are expected to lead to increased genetic stochasticity and inbreeding, and thus lower N_e. However, as discussed above, this may simply be a limitation of the available data. The IUCN Red List criteria focus largely on census size, geographic distribution and the reduction thereof to establish whether a species belongs in a threatened category (IUCN Standards and Petitions Committee 2024).

Therefore, it appears the lack of correlation between census data and heterozygosity compromises the predictive capability of genetic diversity in classifying a species or subspecies as threatened, while any legitimate predictive power relies at least partly on geographic distribution as a common determinant of both genetic variation and threat assessment.

Our results suggest that genetic diversity may serve as a useful diagnostic tool in future conservation assessments, with the caveat that changes in genetic diversity are delayed compared to the immediate changes in population parameters such as geographic range or population size (Epps and Keyghobadi 2015; Gargiulo et al. 2024). Beyond its utility as a measure for monitoring population viability, genetic diversity is critically important in its own right to maintain healthy populations capable of adapting to new threats (Slate et al. 2000; Reed and Frankham 2003; Charpentier et al. 2005; Markert et al. 2010; Takahashi et al. 2018; Clarke et al. 2024). Low levels of genetic diversity have repeatedly been linked to various health issues in wild cat populations. In pumas, genetic impoverishment has been shown to result in kinked tails, cryptorchidism and teratospermia (Huffmeyer et al. 2022). Similarly, cheetahs were also found to have malformed sperm alongside an overall lower sperm count, as well as a lack of variation in the immune system (O'Brien et al. 2017). These examples illustrate the relevance of measuring genetic diversity for wildlife conservation, and our heterozygosity estimates may help to identify the felid species and subspecies that are most at risk.

Overall, our study bolsters the call for genomic data and diversity measures to constitute an essential aspect of conservation efforts, and steps should be taken to formally incorporate such data in the Red List assessments. To improve future analyses, several issues warrant attention, particularly regarding data availability and bias. For many of the samples used in this study, metadata detailing the sample's origin was hard to find or unavailable, making it difficult to correctly assign subspecies labels and associated species characteristics, limiting the accuracy of the analyses. Thus, including this type of data (sampling location, subspecies classification, pedigree,…) with the submission of genomic data should be a priority in order to improve the accuracy of future studies. Furthermore, there exists a clear bias in data availability (genetic and non-genetic) and studies towards the larger and often more recognisable species in the family (Brodie 2009; Pérez-Irineo and Santos-Moreno 2013;

Zanin et al. 2015; Tensen 2018a; Azizan and Paradis 2021). Additional field and genomic research on the small and inconspicuous species of cats will allow for a better understanding of the processes that determine genetic diversity and extinction risk in cats and, by extension, other taxa, so that we may push for increasingly competent prioritization strategies to better preserve global biodiversity.

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Author contributions CRediT author statement — M.P.M.: Data Curation, Formal Analysis, Methodology, Software, Writing - original draft. J.L.: Conceptualization, Methodology, Validation, Writing - review and editing. H.S.: Supervision, Methodology, Writing - review and editing.

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Data availability We accessed and re-used publicly available whole-genome sequencing data (Table S1). Custom R and Python code used in this study are available on an archived GitHub repository (https://doi.org/10.5281/zenodo.15360989). Variant call sets (VCF format) and spatial polygons of subspecies ranges (shape files) are shared on the Open Science Framework (http://osf.io/5pkue).

Declarations

Competing interests The authors declare no competing interests.

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