

Population density and genetic diversity are positively correlated in wild felids globally

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Abstract

Aim: Insights into the biological and evolutionary traits of species, and their ability to cope with global changes, can be gained by studying genetic diversity within species. A cornerstone hypothesis in evolutionary and conservation biology suggests that genetic diversity decreases with decreasing population size, however, population size is difficult to estimate in threatened species with large distribution ranges, and evidence for this is limited to few species. To address this gap, we tested this hypothesis across multiple closely related species at a global scale using population density which is a more accessible measure.

Location: Global.

Time Period: Contemporary.

Major Taxa Studied: Wild felids in their natural habitats.

Methods: We obtained data from published estimates of population density assessed via camera trap and within-population genetic diversity generated from microsatellite markers on 18 felid species across 41 countries from 354 studies. We propose a novel method to standardize population density estimates and to spatially join data using K-means clustering. Linear mixed-effect modelling was applied to account for confounding factors such as body mass, generation length and sample size used for the genetic estimates.

Results: We found a significant positive correlation between population density and genetic diversity, particularly observed heterozygosity and allelic richness. While the confounding factors did not affect the main results, long generation length and large sample size were significantly associated with high genetic diversity. Body mass had no effect on genetic diversity, likely because large-bodied species were over-represented in our data sets.

Main Conclusions: Our study emphasizes how recent demographic processes shape neutral genetic diversity in threatened and small populations where extinction vortex is a risk. Although caution is needed when interpreting the small population density effect in our findings, our methodological framework shows promising potential to identify which populations require actions to conserve maximal genetic variation.

Emmanuel Paradis and Sébastien Devillard co-last authors.

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KEYWORDS

carnivore, Felidae, generation length, genetic diversity, SECR

1 | INTRODUCTION

Maintenance of high intraspecific genetic diversity (GD) is critical to sustaining the evolutionary potential of species facing ongoing changes in their ecosystems (Frankham et al., 2002). Similarly, maintaining population density (PD) above a viable threshold is a crucial target for demographic sustainability in any threatened species (Sanderson, 2006). Neutral theory predicts that GD and effective population size, N_e , covary positively as the rate of inbreeding and the strength of genetic drift tend to increase in small populations; thus, both GD and N_e should be considered to characterize the extinction risk of species (Lande, 1988). N_e , which is a measure of the size of an ideal population contributing to the observed genetic changes in the population under consideration, remains challenging to quantify as it requires specific information such as the breeding structure (e.g., sex ratio in a population), pedigree data or past population sizes (Frankham, 1995). Under the assumption that census population size, N_c , is a proxy of N_e , previous studies have demonstrated the prevalence of positive relationship between GD and N_c within species, namely through experiments and meta-analyses, but which also are highly dependent on the molecular markers used (Frankham, 2012 and references herein). Alternatively, several species-specific indicators of N_c can also significantly affect GD such as species conservation status (lower GD in threatened species, Flight, 2010), body size (lower GD in species with larger body size, Mackintosh et al., 2019) and distribution range (higher GD in species with wider range, Doyle et al., 2015).

Another way of measuring the local demographic status of species is in the form of PD. Defined as the number of individuals within a focal area, PD varies widely over time and space throughout a species' range. This variation is driven primarily by the interaction among ecological laws, habitat quality and resource availability, while accounting for species-specific metabolic and dispersal needs (Carbone & Gittleman, 2002; Stephens et al., 2019). Where reliable N_c is challenging to estimate from empirical data, PD has the potential to serve as a surrogate of N_c . Additionally, because density-dependent factors impact species dispersal and survival rate, it can be assumed that differences in PD could influence N_e and subsequently, determine the levels of GD within and among populations (Birzu et al., 2019; Myhre et al., 2016). Empirically testing the relationship between PD and GD across multiple species with wide and continuous distribution, as well as to those with small and scattered populations, can help to inform within-species variability in conservation strategies and ecological models; hence, this approach ensures that both ecological and evolutionary considerations are addressed when assessing the conservation status of elusive mammals suffering demographic declines and fragmented distribution area as a result of habitat destruction and overexploitation (Ducatez &

Shine, 2017). To our knowledge, little is known about whether decreasing PD may lead to lower GD across mammalian species, or whether there is a general pattern that can be broadly observed at a larger geographical scale. Previous studies have examined this hypothesis in a small number of non-mammal species at small scales, yielding contrasting results. Gram and Sork (1999) examined this relationship in three common and long-lived woody plant species (*Quercus alba*, *Carya tomentosa* and *Sassafras albidum*) in Missouri Ozark forests and found that PD had no effect on GD. On the contrary, Hague and Routman (2016) found that sympatric populations of four related lizard species in habitats with high PD had high levels of haplotype diversity.

Theory suggests that the interaction between demographic and genetic threats will push the population into a positive feedback loop, ultimately driving it towards extinction at an accelerating rate, which surpasses the time required for the population to recover. This phenomenon is called an extinction vortex by inbreeding depression (Tanaka, 2000), and is likely occurring in felids due to their intrinsic traits, such as low PD, slow reproductive rate and large home range (Macdonald & Loveridge, 2010). Furthermore, more than 60% of felids are already in poor conservation status, overall being at least Near Threatened in 2020 (IUCN, 2020). Many conservation efforts have targeted felids globally due to their charismatic nature (Macdonald et al., 2015) and inherent conflicts with humans (Inskip & Zimmermann, 2009), rendering abundant population-level data related to genetic variation and density across the species ranges. However, GD and PD data are rarely combined given the challenges associated with studying wild felids, such as low detectability and remote habitats (Anile et al., 2014). Another major drawback is that ecologists and conservation biologists do not employ the same methods when assessing conservation risk.

In this study, we repurposed data from independent studies of genetic variation assessment and camera-trapping surveys of felids to examine whether within-population GD estimates derived from presumably neutral nuclear microsatellite markers are associated with PD across species. Our response variables were the three most often reported measures of GD in population genetic studies: (1) observed heterozygosity (H_o), (2) expected heterozygosity (H_e) and (3) allelic richness (AR; or the mean number of alleles across loci examined within a population). We used PD data (i.e., number of individuals per 100 km²) estimated using spatially explicit capture–recapture (SECR) approach, with some exceptions to the lion's (*Panthera leo*) PD estimates because there were fewer lion studies using this approach (Braczkowski et al., 2020). We developed a method to scale estimates from capture–recapture records to SECR estimates. Because both GD and PD data were not provided to all sampled populations, we paired both estimates according to their spatial proximity across studies at local scale and country scale. The data set at local scale

was based on the spatial proximity of the populations within the species' dispersal distance range, whereas for the country-scale data set, we simply grouped the estimates within a country. These two data sets, hereby referred to as cluster and country data sets, respectively, were analysed separately using linear mixed-effects (LME) models to estimate a common slope for the PD effect on GD and to fit species as a random intercept. Because generation length (days), the mean number of individuals sampled for GD estimates (sample size) and body mass (kg) are critical variables in determining GD (Azizan & Paradis, 2021) and PD (Anile & Devillard, 2018, 2020), we examined whether these covariates affect the GD and PD relationship and could increase the predictive ability of our models.

2 | METHODS

2.1 | Data building

2.1.1 | GD data

We used within-population GD data collected and as presented elsewhere (Azizan & Paradis, 2021), including 10 additional studies published since 2020 found in Web of Science and Google Scholar ($n=175$). These additional studies provided data for Geoffroy's cat (*Leopardus geoffroyi*) (Bou et al., 2021), puma (Gallo et al., 2020; Zanin et al., 2021), European lynx (Herrero et al., 2021), jaguars (Kantek et al., 2021; Zanin et al., 2021), snow leopard (Korablev et al., 2021; Singh, Singh, Joshi, Chandra, et al., 2022), bobcat (Cancellare et al., 2021; Miller-Butterworth et al., 2021) and leopard (Singh, Singh, Joshi, Singh, et al., 2022). Detailed methods for assembling this data set can be found elsewhere (Azizan & Paradis, 2021). Briefly, we selected GD estimates within a population with at least five individuals, more than 70% of polymorphic loci and measured with a minimum of five presumably neutral and autosomal loci derived from a single set of microsatellite markers. In some cases, we recalculated the average GD estimates across loci developed from a single species genome which gave the greatest number of loci, using either the raw genotype data or the reported loci-specific GD estimates to prevent ascertainment bias. Where this was not possible, the data were excluded from the analyses. Since 93% of the GD estimates were derived from domestic cat microsatellite markers and given the highly conserved genomic architecture of Felidae (Cho et al., 2013), we assumed the effect of microsatellite marker choices to be similar across all studies in our data set. The distributions of sample size and number of loci per species are shown in Figure S5. Wild-born captive populations outside of their natural distribution, captive-bred individuals and any data beyond the "country" scale were excluded. Where GD estimates from different populations were reported, we treated the records individually. We did not conduct additional population structure analyses across the species' distribution to identify independent populations, and follow the designated localities by the authors of the study usually based

on population genetic structure analyses, subjectively where samples were retrieved or a priori grouping assumptions.

2.1.2 | PD data

PD data were based on those collected elsewhere (Anile & Devillard, 2018, 2020), including 168 studies published since 2018 ($n=479$). We scaled capture-recapture (CR) estimates to SECR estimates (either via maximum likelihood or Bayesian) in a single relationship with body mass (or density-mass allometry, DMA) under the assumption that estimates from the two methods are correlated (Jędrzejewski et al., 2018; Luskin et al., 2017). We initially selected PD records estimated using the CR method ($n=41$ for 5 species and 19 study sites) and with full mean maximum distance moved (CR-FMMDM) and half mean maximum distance moved (CR-HMMDM) approaches.

We first scaled CR-FMMDM estimates to CR-HMMDM, which was the most-used approach for estimating PD before the advent of SECR. We hence built a global linear mixed-model-relating density based on CR-FMMDM ($D.f$) to density based on CR-HMMDM ($D.h$), to predict $D.h$ estimates when only $D.f$ is available.

$$D.h \sim SD + TN + NC + PS + D.f + \text{species as random error} \quad (1)$$

This Equation (1) was performed on a restricted data set which included only records ($n=41$) where potential uncorrelated confounding factors such as study length in days (SD), number of trap nights (TN), number of cameras (NC) and camera polygon size (PS) were available. From this global model, we selected the most supported models among this set of candidate models using the function *dredge* in the package "MuMIn" for R software (Bartoń, 2020). Results from this first model selection indicated only two models were supported ($\Delta AICc < 2$) and we conducted model averaging for parameter estimation accordingly (Table S6).

After model averaging, NC, which was retained in the second-most supported model, was no longer considered a significant variable (Table S7). Therefore, a simple model $D.h \sim D.f + \text{random (Species)}$ was ran on a larger data set ($n=68$ for 9 species from 42 study sites), in which records without the confounding factors were included. This model explained 97% of the variation observed between CR-FMMDM and CR-HMMDM estimates leading to robust $D.h$ estimates from $D.f$ estimates (Figure S4). The scaling equation for fixed effects was $D.h \sim 1.912421 * D.f + 0.268856$. We then used this equation to predict $D.h$ when only $D.f$ is available.

Following the same logic and approach as above, we then scaled CR-HMMDM estimates to SECR records ($D.secr$). For the 30 records (4 species and 18 study sites) where both approaches (ML and BA) were used to estimate PD, we averaged the estimates. The global model is as followed:

$$D.secr \sim SD + TN + NC + PS + D.h + \text{species as random error} \quad (2)$$

Results from the model selection indicated only the model without any potential confounding factors was supported (Table S8). Therefore, the simple model $D.secr \sim D.h + random$ (Species) was run on a larger data set ($n=63$ for 6 species from 42 study sites), which included records missing the potential confounding factors. This latter model explained 93% of the variation observed between CR-HMMDM and SECR estimates leading to robust $D.secr$ estimates from $D.h$ estimates (Figure S4b).

The scaling equation for fixed effects was $D.secr \sim 0.3672654 * D.h + 0.8616620$. We then used this equation to predict $D.secr$ when only $D.h$ is available.

2.2 | Data merging

Although molecular tools and non-invasive sampling methods have been deployed to estimate the number of individuals, we did not find any camera-trap study that reported both PD estimates calculated using SECR models and GD estimates derived from microsatellite markers within the same area. Most of our data were not collected at the same sites, that is, a precise overlap between the geographic coordinates of the populations whenever provided or extracted by ourselves. Thus, clustering was necessary in order to spatially match estimates of GD and PD at local and country scales. Since GD or PD estimates from the same population have been reported in different studies by the same or different authors, we refer to each individual estimate which may originate from the same population but published in a separate study, as a “record” of GD or PD throughout this study.

2.2.1 | Cluster data set

The first approach used K-means clustering algorithms to assign GD and PD estimates based on spatial proximity and similarities following these steps:

1. Each population was geo-referenced with coordinates in decimal degrees, as provided in the studies or approximated from Google Maps and GeoNames (<https://www.geonames.org>) based on the given sample localities, sampling areas or study maps. Where studies only reported the country name as the locality of the population, we used the country's centroid geocoordinates; populations at country scale were not common (<7% of all data). Because the majority of felid species are solitary, and their continuous distribution over a landscape given their long-distance movement, we believe that spatially defining the population with a spatial approach is meaningful.
2. To ensure greater ecological similarities between data points, we overlaid biogeographic regions obtained from Olson et al. (2001) over our data points (both GD and PD) so the K-means clustering can be applied within each region for each species.
3. Since we were interested in maximizing the number of groups, we specified in each run either GD or PD population coordinates

as initial centroids in the *kmeans* function as implemented in the “stats” R package, with a maximum of 10 iterations. Then, we visually evaluated the clustering results between separate runs and chose the approach (either GD or PD population coordinates as initial group centroids, Figure S5a,b) which yielded the greatest number of resultant clusters with both GD and PD data points in place (Figure S5c).

4. We masked all the points retrieved in (3) and inspected the unassigned points which did not capture a different type of data point (i.e., only GD or PD points in the clusters). Then we identified the nearest cluster by calculating the minimum distance between points among the rest. If the nearest cluster corresponded to a different type of data point and if the distances between GD and PD points were smaller than the mean distances of the points obtained in the optimal clusters in (3), these were pooled in an additional cluster.
5. Finally, we only considered clusters with PD and GD data that fell within each species' dispersal distances in km. Distances between data points were calculated using the *pointDistance* function in the “raster” R package. Average species' dispersal distances were estimated following Macdonald et al. (2018) and we used the spatial parameter, σ , computed in SECR, which is a proxy of home range size under the assumption of a circular area. After this step, three species, *Felis chaus* in India, *Leopardus geoffroyi* in Argentina, Brazil and Bolivia, and *Leopardus tigrinus* in Brazil were excluded from the cluster data set.

2.2.2 | Country data set

To test whether the clustering approach had any influence on the relationship between GD and PD, we also grouped GD and PD estimates to the country reported. We also assumed species populations within a country were more continuous than those in the cluster data.

PD estimates fluctuated more frequently than GD as camera-trapping surveys at a given location occurred during multiple periods (e.g., winter/summer, wet/dry and annual records). Therefore, for each cluster or country within a species, we took an average of PD across all estimates as an approximate value. Furthermore, since most GD estimates pooled samples from multiple years and there were few raw genotype data available, we could not accurately match PD and GD estimates based on sampling years. Thus, we assumed the temporal GD variation to be negligible. Occasionally, some groups (either from the cluster or country data set) had several GD estimates, leading to unbalanced data, thus we considered these multiple response values as repeated observations (i.e., same PD value for all GD observations in a specific cluster, instead of using an averaged GD estimate per group). The number of clusters and countries per species is given in Table S1.

The map of the population locations in Figure 1 was generated using *ggmap* package in R.

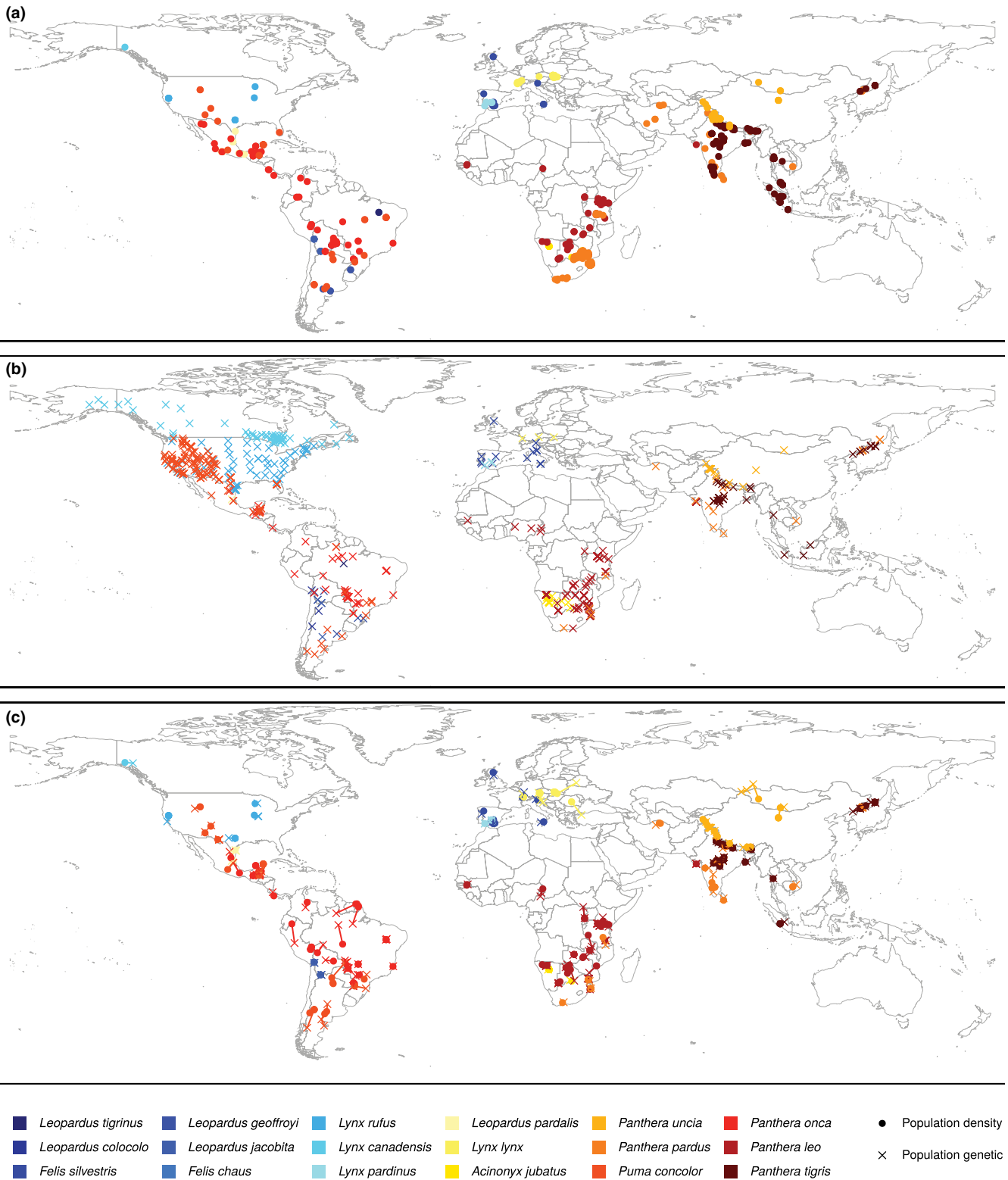


FIGURE 1 (a) Locations of the $n=683$ records of population density (●). (b) Locations of the $n=484$ records of population genetic diversity (X) across 18 felid species. (c) Only records from the cluster data set are shown with lines joining the data points indicating the clustering groups ($n=132$). Species are ranked by body mass, from small (blue) to large (dark red).

2.3 | Statistical analyses

To identify outliers in the response variables, we used boxplots on all three GD estimates and PD estimates per species (Figure S1). Any

data points that fell outside of the $1.5\times$ interquartile range (whiskers) were considered outliers. These outliers were hence labelled in both data sets and we assessed the GD–PD relationship with and without outliers (Table S2). We also inspected the relationship of PD

and GD within five species with the greatest number of clusters to check the subsequent effect of these outliers (Figure S3).

We performed linear mixed-effects (LME) modelling using the “lme4” package (Bates et al., 2015) with species set as random intercepts to capture between-species variability (i.e., the effect of explanatory variable was allowed to vary between species). Generation length data were extracted from Pacifici et al. (2013), and body mass data were obtained from Johnson et al. (2017). We assessed the predictive power of our models by comparing the marginal R^2 between simple and more complex models (Nakagawa et al., 2017). The best-fit models were chosen based on the lowest AIC. We used the *dredge* function in the “MuMin” package (Bartoń, 2020) to compare summary statistics of models containing every possible combination of the explanatory variables. In the final data sets, AR, PD, body mass and sample size were \log_{10} transformed prior to model fitting. All covariates were scaled to have mean=0 and standard deviation=1. The *p*-value for each covariate was computed using the “lmerTest” package (Kuznetsova et al., 2017), and the confidence intervals (95%) of the fixed-effect estimates were calculated using parametric bootstrapping ($n=100$). To assess the robustness of our findings, we performed sensitivity analyses to examine the impact of several factors by their removal from the data set. These factors were the outliers detected using the interquartile range method, species with less than 5 data points and country-scale populations that were included in the cluster data set. Assumptions of the LME models were checked visually using the relevant plots. All statistical analyses were performed using R software version 3.6.3.

3 | RESULTS

Of the 449 studies found during the literature search, we retrieved PD and GD data from a total of 330 studies that corresponded to our selection criteria. These studies were published between 1998 and 2022 and encompassed felid populations across 41 countries (Figure 1). We were able to group 38% of PD and GD records from all retrieved records using the K-means clustering method which resulted in 132 groups across 15 species in the cluster data set (Table S1). The joining of PD with GD populations according to the countries where the studies were conducted yielded 72 groups across 18 species, from 683 records of PD (76%) and 484 records of GD (84%; Table S1). A bias towards large-bodied species was evident and there were marked differences in the number of records according to the type of studies among species (Figure 1).

The LME models with a single fixed term revealed that the effect of PD was significant and positive on five out of six measures of GD across both data sets (Figure 2). The relationship between *He* and PD in the cluster data set was not statistically significant ($\beta_{PD}=0.02$ [−0.01–0.06]). Despite the significant effect of PD for all three GD measures in the country data set, the strength of the relationship was weak in *Ho* ($\beta_{PD}=0.03$ [0–0.06]) and *He* ($\beta_{PD}=0.04$, [0.01–0.07]) compared to in *AR* ($\beta_{PD}=0.09$, [0.04–0.14]). As shown in Figure 2,

we highlighted five populations with extremely low PD estimates in the cluster data set. These five populations were consistently identified for all three GD measures, but they may not necessarily have the lowest GD estimates in comparison to other populations of the same species.

Some species with a large number of clusters revealed a consistent relationship with a moderate index of Pearson's correlation, such as in leopard (*Panthera pardus*) ($r=0.48$ – 0.63) and tiger (*Panthera tigris*) ($r=0.5$ – 0.55); however, in other species the relationship was unclear and could be influenced by outliers (Figure S3). For instance, among the populations of leopards, those in Sri Lanka and South-Western Primorye stand out as outliers, exhibiting significant differences in their *He* (0.49 and 0.45, respectively) compared to the other populations. In Sri Lanka, the GD is accompanied by a very high PD estimate (10.6 ind/100km²). In contrast, the population in South-Western Primorye has up to 12 times lower PD (0.84 ind/100km²) than in Sri Lanka. The sensitivity analyses showed that despite these outliers, the general relationship between GD and PD remained consistent (Table S2). However, when we singularly removed the species with the largest number of records, this disproportionately affected the regression (Table S3).

All LME models indicated that generation length improved the prediction of GD consistently in both data sets (Tables S4 and S5). Moreover, sample size was also an important predictor for all three GD estimates, but the effect was more strongly pronounced in *AR*. In the models where PD was fitted as a single fixed effect, the proportion of variance explained by PD is small, ranging from 4 to 9% for *Ho*, 1 to 4% for *He* and 4 to 16% for *AR*, across the two data sets (Tables S4 and S5). The covariates in the best models chosen based on the AIC values increased the proportion of variation explained by the fixed terms in the data sets (marginal R^2), between 29% and 60%, in which PD remained a significant factor (Table 1).

4 | DISCUSSION

Our analyses provide compelling evidence that low-density populations harbour lower GD across felid species in agreement with the prediction of neutral theory (Figure 2). Our findings are in contrast to Gram and Sork (1999) but corroborate Hague and Routman (2016). Gram and Sork (1999) attribute the lack of relationship to the large population size of their studied species and the young age of the forest which may not have been at mutation–drift equilibrium at the time of the study.

Furthermore, the effect of PD on GD is slightly stronger in the country than in the cluster data set (Table 1), which could possibly be due to a larger sample size of GD records since the data set identified greater sampling effort across countries without the restriction of species' dispersal distance, compared to local and small populations as in the cluster data set (Figure S2). Additionally, these differences between the two data sets might arise as pooling PD data using socio-political or geographical boundaries could overestimate the effect (Vitkalova et al., 2018).

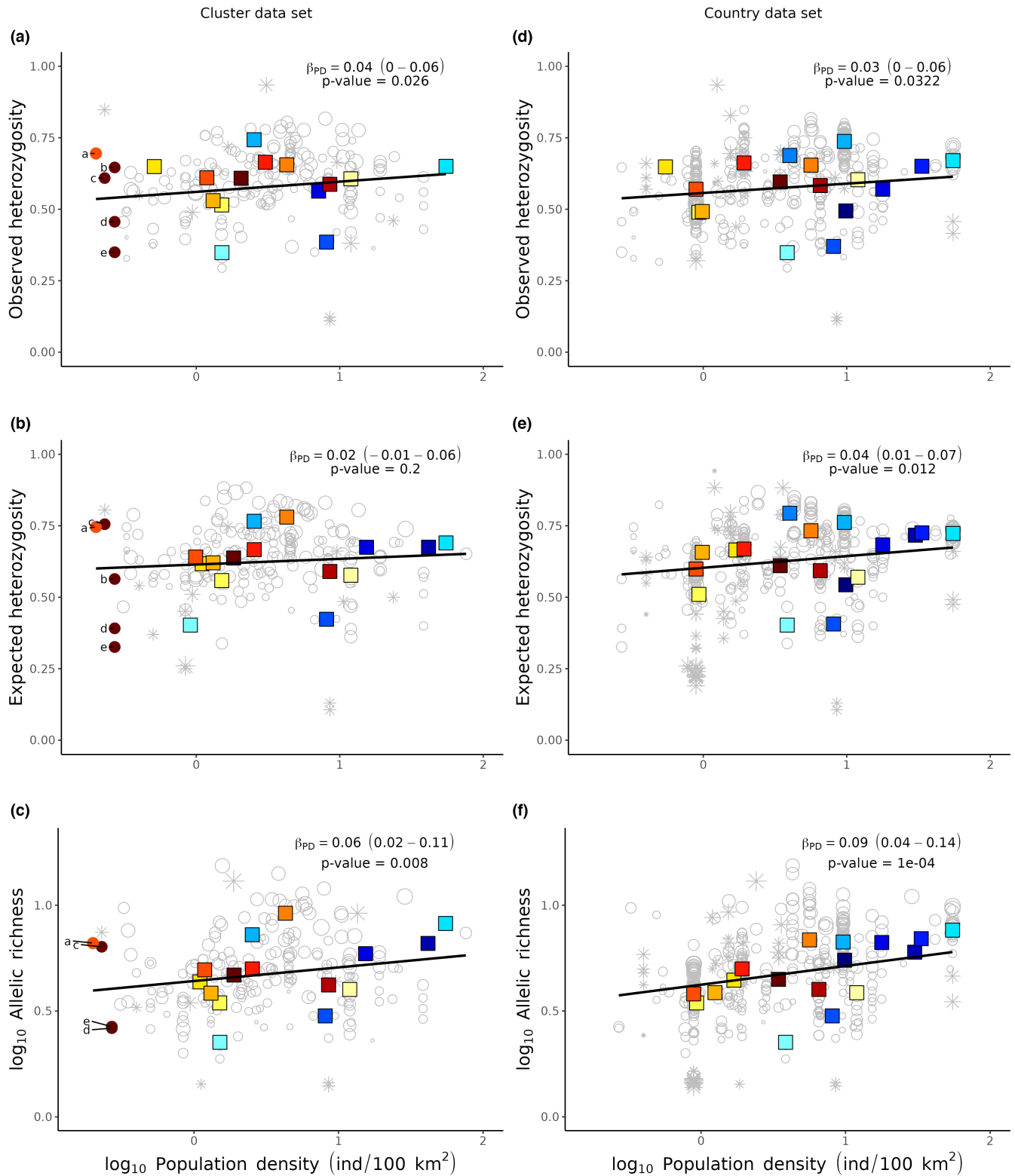


FIGURE 2 Positive relationship between within-population genetic diversity and population density from camera-trap surveys across wild felids using cluster (a–c) and country (d–f) data sets. Regression lines represent model predictions using population density as the only fixed effect, with the slope parameters (β_{PD}) and its 95% confidence interval (CI) computed using the bootstrap. The median GD and PD values for each species calculated from the data sets are represented by the square shape (see legend in Figure 1 for the corresponding names). Each observation is represented by a white circle which has a size proportional to the mean number of individuals sampled for the GD estimates. The star-shaped points represent the outliers detected using the boxplot method. Coloured circles are populations with extremely low PD values in the cluster data set: (a) jaguars in South Brazil and tigers in (b) Changbai mountains, (c) Bhutan, (d) North-East China and (e) Hunchun National Reserve.

TABLE 1 Summary statistics and parameters from the best-fit linear mixed models.

Data set	Observed heterozygosity		Expected heterozygosity		Allelic richness	
	Cluster	Country	Cluster	Country	Cluster	Country
No. of observations	192	369	195	403	197	391
<i>Parameter estimates</i>						
Intercept	0.594 [0.552–0.637]	0.593 [0.548–0.638]	0.635 [0.6–0.669]	0.649 [0.606–0.686]	0.676 [0.632–0.719]	0.689 [0.643–0.735]
Population density	0.024** [0.009–0.039]	0.039*** [0.021–0.057]	–	0.021* [0.002–0.039]	0.028* [0.008–0.049]	0.053*** [0.031–0.075]
Generation length	0.057** [0.028–0.087]	0.054** [0.019–0.089]	0.054** [0.024–0.083]	0.051** [0.019–0.084]	0.058* [0.018–0.098]	0.057** [0.015–0.098]
Sample size	0.015* [0.001–0.029]	–	0.026*** [0.013–0.041]	0.013** [0.005–0.021]	0.091*** [0.072–0.11]	0.075*** [0.063–0.086]
Body mass	0.020 [–0.008–0.048]	0.026 [–0.012–0.064]				
Variance of the random effects (Species)	0.002	0.004	0.002	0.006	0.003	0.006
No. of species	14	17	15	18	15	17
Residuals	0.008	0.007	0.008	0.006	0.015	0.012
Marginal R ²	0.31	0.29	0.29	0.29	0.43	0.6
Conditional R ²	0.39	0.47	0.41	0.6	0.51	0.63

Note: Values in the bracket are the bootstrapped 95% confidence intervals of the fixed-effect estimate (standardized). Outliers detected by interquartile range method were excluded. Allelic richness, population density, body mass and the mean number of individuals included for GD estimates (sample size) are in log₁₀ scale.

****p*-value < 0.001; ***p*-value < 0.01; **p*-value < 0.05.

We identified that Amur tiger populations in North-East China had both low GD and PD compared to other species (Figure 2A–C). The fitness of Amur tigers through their reproductive rate is much lower than those of Bengal tigers (Kerley et al., 2003). This could increase their risk of extinction and further monitoring is warranted. In contrast, tiger populations in Changbai Mountain and Bhutan, as well as a puma (*Puma concolor*) population in southern Brazil, had low PD, but these populations represent almost doubled GD estimates compared to the Amur tigers aforementioned (Figure 2). We hypothesized that these populations showing low PD represent remnants of past populations with high GD and have recently undergone bottlenecks, or that these areas cannot sustain high PD levels and individuals detected were transient from different populations. We recommend acquiring high-quality GD and PD data from these populations to closely inspect whether the relationship between the two variables is still present. This information can be crucial to identify candidate populations for genetic rescue (Whiteley et al., 2015), that is, by introducing individuals from populations with both high density and genetic diversity to restore population health, as demonstrated in the Florida panther (Johnson et al., 2010; Van de Kerk et al., 2019).

We cannot exclude the possibility that the generality of the relationship between PD and GD across species could be potentially influenced by outlier populations (Figure S3) and by particular species with the most data (Table S3), especially in the larger-sized felids. For

instance, our data showed that Sri Lanka had among the densest population of leopards but with a very low *He*, which could be considered an outlier. Subsequently, we observed a significant positive relationship between PD and *He* within this species only after excluding this population from the data set. However, the high PD and low GD observed in this case could also reflect a natural pattern, suggesting a recent population expansion from a founder population. Considering the population in Sri Lanka is isolated by water barriers, it is possible that the population density has recently increased due to the abundance of resources in this area (Kittle & Watson, 2018), as well as reduced competition from continental leopard populations. However, it is important to note that in crowded areas, increased contact within the same genetic pool and the absence of migration can contribute to a higher rate of inbreeding in this population. Another explanation for this discrepancy is that GD estimates for leopards in Sri Lanka were collected from one study (Uphyrkina et al., 2001), where the estimates were averaged across the country and may not accurately represent the true population status. Another outlier in the leopard's data is the population in East Asia, which had the lowest *He* among other populations of the same species. We do not believe these were inaccurate data points (sample size = 23, no. of loci = 12) and they might accurately represent the populations given that similar low GD can be observed in the populations of tigers at the same locality (Sikhote-Allin and South-Western Primorye, Figure S3II) where these habitats are almost at the limits of the species' distribution. In the lion data set, the Indian lions

in the Gir Forest were an outlier population with an extreme reduction in genetic diversity compared to African lions. Furthermore, since we included population density of lions estimated using non-SECR framework (e.g., distance sampling and track surveys) as there were very few PD data that reached our criteria (3 of 17 studies), these outliers might have arisen given the difference in methods used for the estimation of the PD. Additionally, we found that the significance of the relationship between H_o and PD diminished when we individually excluded the leopard and tiger populations, which represented a significant portion of our data set. This finding further emphasizes the importance of population assessments in least-studied species and areas, as well as the need to examine the general trend in the relationship between GD and PD using population-specific data instead of mean values per species. Given these results, we argued that the strength of the effect could indeed be specific to a given population or a few closely related species with similar historical, demographic and ecological influences.

Generation length can be considered a proxy to slow-fast life history continuum, given it is related to several demographic parameters (Gaillard et al., 2005). It is expected that species with short generation length have higher population turnover, resulting in large gains in genetic variability in comparison to slow breeders (Gaillard et al., 2005). As shown previously (Azizan & Paradis, 2021), species with short generation length had lower GD than species with long generation length, which is inconsistent with our prediction. Our findings suggested that when all species experience population decrease, those with short generation lengths are more sensitive to genetic erosion and inbreeding because their populations respond to ecological changes faster than those with long generation lengths (Daskalova et al., 2020).

We found body mass is not a significant factor driving GD variation in felids, which is most likely influenced by the strong taxonomic bias in research towards larger species (Brodie, 2009; Tensen, 2018), and as a result, the sample size of the small- to medium-sized felids was limited in our study. Furthermore, some medium-sized species had lower estimates compared to some small and large felids (Figure S1). Our results supported previous studies which have also found that GD does not vary with body mass across mammalian species (Doyle et al., 2015; Garner et al., 2005). Thus, body mass may not be an appropriate indicator of genetic vulnerability in felids, and our data suggest that both large and small felids may be experiencing similar genetic consequences due to population decline in their habitat.

4.1 | Limitations and uncertainties

Although we found strong evidence that PD was positively related to GD, the proportion of variance explained by PD was small (Tables S4 and S5). Much of the data variability, however, resided in the study design of GD (sample size), species-level trait (generation length) and the variation within species (random effect). In our study, we were primarily interested in the association between PD and GD, nevertheless, we also showed that PD alone cannot be predicted by GD with high certainty and precision, given the structure of our current data set. Future studies should include other ecological factors

that may affect PD and GD, such as habitat quality and connectivity (Gibbs, 2001), to increase the explanatory power of the model.

Merging independent microsatellite data sets within a species was challenging because allele sizes at a particular locus were obtained from different studies conducted at different locations. Source studies also varied in how loci were chosen, in reporting the GD measures and in providing the raw microsatellite data available. Unfortunately, we found very limited raw genotype data, measures of dispersion for each loci-specific GD estimate, as well as overlapping loci across studies and species. Thus, we were unable to account for the microsatellite and sample size effect in the GD data set beforehand. Nevertheless, in a previous study using the same genetic database (Azizan & Paradis, 2021), the effects of sample sizes and number of loci on heterozygosity and allelic richness were significant but weak. Despite the more recent and attractive tools to assess population genetics such as the single nucleotide polymorphism (SNP), microsatellite markers are still relevant and less costly and time-consuming to develop for conservation efforts.

Our study revealed that GD studies were less numerous than PD (116 vs. 214), and 60% of the retrieved records were excluded in the cluster data set due to insufficient overlap or distances between the GD and PD records exceeding species dispersal (Figure S5). The uneven assessment of GD and PD across species and distribution areas further complicated the pairing of these two records for analysis. For instance, while leopard PD has been extensively measured in Africa through 25 studies, only 4 studies have reported their GD using microsatellite markers. The leopard cat (*Prionailurus bengalensis*), which occurs through most of Asia, provides another example. Although PD records were available in five countries, GD has only been measured in South Korea, where PD data were not available. Conversely, puma GD records in North America ($n=120$) greatly exceeded the number of PD records ($n=26$) and population genetic studies on the Canada lynx (*Lynx canadensis*) provided 47 GD records, whereas there was only one PD study in the same area which corresponded to our criteria (Table S1). Although molecular tools are also used to estimate PD (e.g., Anile et al., 2014; Janečka et al., 2011), we found no direct comparisons with GD estimates in felids.

A recent debate about whether neutral GD metrics should be incorporated into conservation assessment has arisen (DeWoody et al., 2021; Teixeira & Huber, 2021). Although imperative conservation action often requires holistic solutions, genetic information is only rarely considered as part of the quantitative criteria for classifying the extinction risk of species within the IUCN Red List species assessments (Garner et al., 2020). Our data set highlights the value of measuring both GD and PD concomitantly at population level using non-invasive methods to better characterize species extinction risk.

5 | CONCLUSIONS

By identifying the positive relationship between population density and genetic diversity across felids, our study has considerable implications for conservation:

1. Population density can be used as a proxy of population size (N_c) when performing macroecological analyses involving GD, especially for widely distributed species with a large metapopulation structure.
2. Populations at risk of extinction vortex deserving quick conservation actions can be identified based on lower-than-expected GD for their PD.
3. Critical populations with very high PD but low GD, and vice versa, should be re-evaluated to understand the ecological and evolutionary processes leading to the observed discordant pattern.
4. The gold standard for assessing population status should involve the simultaneous sampling of both PD and GD data for a given species within its distribution area and ideally during the same time window. This can be achieved through collaborative efforts between conservationists, ecologists and geneticists, with a concerted planning a priori. Improving the standardization and integration of both GD and PD study designs, which can be conducted for multiple populations as well as related species, would represent a significant step forward.
5. Where collecting new data is not feasible, *K-means* clustering to join GD and PD from independent studies, as well as using regressions to scale the population density, were an easy and useful approach to repurpose existing data. Although it requires a strong assumption of the population structure and further testing to assess its scalability to a variety of other species, it has the potential to overcome the challenges of linking data from different studies.
6. Our data were largely skewed towards big cat species which could bias the relationship between PD and GD, hence research efforts towards small cat species are urgently needed.
7. Finally, in the spirit of improving both the methodological framework and the data sets, we provide an interactive map of PD and GD records and their associated studies, including those which were not used in our analyses such as the approximate locations of captive populations and large-scale studies, to identify where and which species have not been studied and to provide references at targeted priority areas more easily (<https://itsamira.github.io/GDfelids/>).

AUTHOR CONTRIBUTIONS

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CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

Code and data used for the statistical analyses are accessible at Figshare (DOI: [10.6084/m9.figshare.23047334](https://doi.org/10.6084/m9.figshare.23047334)). No new data were generated specifically for this study. These data were compiled from the following resources which can be located here (https://itsamira.github.io/GDfelids/interactive_map_GDfelids.html).

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SUPPORTING INFORMATION

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

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