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REVIEW ARTICLE

Mapping our knowledge on birds of prey population genetics

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Abstract

The current and rapid anthropogenic environmental changes could disproportionately impact ecosystems, particularly when they affect species with critical roles in ecosystem integrity. As top predators, raptors provide critical top-down ecosystem services and structure food webs. Yet, many avian predators are currently experiencing global population declines and some are threatened with extinction. The dire conservation status of numerous raptor species warrants urgent action, and detailed ecological data are needed to guide management strategy, including empirical knowledge regarding genetic structure. To that end, we compiled published studies investigating population genetic structure in raptors. Out of a total of 83 publications on 50 raptors species published, we identified a lack of empirical genetic studies for species from the Southern Hemisphere and species with a high level of extinction risk according to IUCN Red List criteria. Only 24% of the species studied are considered "threatened" (*i.e.*, with the "*Vulnerable*", "*Endangered*", or "*Critically Endangered*" status). We found a significant signal of genetic differentiation in 41 species (82%) at the study-specific population. Isolation-by-Distance is a common pattern of genetic differentiation in raptors. Future steps in raptor conservation could prioritize facilitating genetic studies on species located in the Southern Hemisphere and on species with a conservation status. A better inclusion of some key genetic metrics (*e.g., Ne*, *Ne/Nc*, genetic diversity) in published studies will further help management and conservation across various species and ecosystems.

Keywords Conservation · Raptors · Genetic structure · Genetic diversity · IUCN Red List

Introduction

Around the world, birds of prey characterize ecosystems hosting a high level of biodiversity (Sergio et al. 2006; Tinajero et al. 2017) where they structure biological communities (Sergio et al. 2007), and act as indicators of environmental health (Donázar et al. 2016). Indeed, raptors can play regulatory roles in several ecosystems as they exert top-down pressures on prey communities (Therrien et al. 2014; O'Bryan et al. 2018; Terraube and Bretagnolle 2018). In addition, a diverse suite of scavenging raptors consumes considerable amounts of biomass, limiting outbreaks of disease-carrying organisms (García-Alfonso et al. 2019). Global anthropogenic activities, however, currently have profound negative impacts on biodiversity (Johnson et al. 2017) and species abundance (*e.g.,* Rosenberg et al. 2019), leading to known disruption in ecosystem services and alterations in human well-being (Sekercioglu et al. 2004; Balmford and Bond 2005; Haines-Young and Potschin 2010; Kremen 2018), underlining the dramatic consequences of key species loss on ecosystems functioning. For example, in India catastrophic economic and public health issues have arisen due to massive decline in vulture populations which has allowed feral dogs, carrying rabies, to fill the scavenging niche in the ecosystem (Markandya et al. 2008). As the natural environment continues to be altered, raptor populations have become fragmented and have decreased often to the point of endangerment (Sarasola et al. 2019). In a recent review, McClure et al. (2018) reported that 18% of all 557 raptor species are now considered threatened with extinction and 52% of them are exhibiting global population declines. In

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such a context, there is a critical need to improve and refine the current toolbox for the conservation of birds of prey worldwide (*e.g.,* McClure et al. 2018; Buechley et al. 2019).

Over the last two decades, population genetics has emerged as an important tool for wildlife conservation (see Martínez-Cruz and Méndez Camarena 2019 for a description and examples of application). Indeed, population genetic assessments (*e.g.,* genetic diversity, demographic history, or spatial population genetic structure) on a species or populations became central in, for instance, the designation of evolutionarily significant (ESUs; Crandall et al. 2000; Fraser and Bernatchez 2001) and management units (MUs; Frankham et al. 2002; Palsboll et al. 2007). Estimating genetic diversity allows researchers to evaluate population viability, which is essential for understanding and predicting genetic drift and inbreeding depression while safeguarding the evolutionary potential to adapt to a changing environment (Bruford et al. 2010; Allendorf et al. 2012). Conserving and monitoring genetic diversity within species is now one of the priorities in conservation programs (Hoban et al. 2013, 2020), and implemented strategies should aim to halt genetic erosion and preserve the adaptive potential of populations (Laikre et al. 2020).

In conservation biology, the effective population size (*Ne*) is an important key element (*e.g.,* Rieman and Allendorf 2001; Kamath et al. 2015; Markov et al. 2016), because it informs on the demographic trend of populations and species. *Ne* quantifies the impact of genetic drift in depleting genetic diversity by fixing and eliminating alleles in natural populations (Frankham 1995; Gilbert and Whitlock 2015). It also provides the prospects for the sustainability of the population if the current effective size is maintained into the future (Frankham et al. 2002, 2014; Allendorf et al. 2012). It can be used to assess the effectiveness of genetic management (*e.g.,* human-aided migration/relocation, habitat protection, or modification; Wang et al. 2016). A second complementary variable in a conservation context is the adult census size (*Nc*; Frankham 1995; Waples 2005; Waples et al. 2014). In particular, knowledge on the ratio of *Ne/Nc* is important for disentangling the relative importance of demography and genetic factors on the fate and persistence of species (Frankham 1995; Palstra and Ruzzante 2008). A population with a small *Ne/Nc* ratio will have a higher rate of gene diversity loss than a population with the same *Ne* but with a higher *Ne/Nc* ratio (*e.g.,* Ferchaud et al. 2016).

After more than two decades of use and democratization of population genetics in theoretical and applied ecology, we considered a review of literature timely to assess the current state of knowledge (and gaps within) on population genetics for birds of prey, and suggesting where future research should focus. Reviews on population genetics exist for several taxonomic groups (*e.g.,* fishes, Waples et al. 2020; tropical amphibians, Monteiro et al. 2019; seabirds, Friesen et al. 2007; Lombal et al. 2020) but none targeted raptors thus far. Systematic reviews of specific taxa provide a general portrait and can identify conservation priorities, *e.g.,* habitat protection and improvement in the management of land for bird species (Azpiroz et al. 2012) or prioritize conservation of shark and ray species with narrow geographic distributions and subjected to overexploitation (Domingues et al. 2018).

Here, we specifically (1) assess trends in scientific publications on population genetic structure for raptors over time, including the type of genetic markers used; (2) report and summarize the analytical methods commonly used to elucidate population genetic structure; (3) identify which raptor species are being studied in concerning the species-specific conservation status and population trends. Based on some key findings following our first three objectives, we are also (4) mapping the current knowledge gaps in population genetics in raptors and suggesting specific recommendations to overcome them.

Materials and methods

Studied species

Raptors are mobile species with broad distributions (Sarasola et al. 2019). Of the 557 extant species worldwide, about 202 are migratory (Bildstein 2006; Del Hoyo et al. 2019). Raptors are paraphyletic and belong to five families: Accipitridae (eagles, kites, hawks and Old World vultures), Strigidae (owls), Falconidae (falcons, kestrels, caracaras), Cathartidae (New World vultures), Sagittariidae (secretarybirds), and Pandionidae (ospreys; McClure et al. 2019).

Literature survey

We conducted a literature survey through *Scopus* and *ISI Web of Science* databases, using the following combinations of keywords: "population genetic*" or "population structure" or "population genomic*" and "raptor*" or "bird of prey" or "eagle" or "hawk" or "falcon" or "owl" or "harrier" or "vulture" or "buzzard" or "kestrel" or "osprey" or "kite" or "caracara" or "secretarybird". We deliberately added the common genetic markers used in ecology (Allendorf et al. 2012) as keywords: "SNP*", "microsatellite*" or "mtDNA" or "mitochondria" or "allozyme*" to restrict the search. We did not consider "nuclear sequence" as a keyword. While we recognize the utility of nuclear amplicon sequencing (*e.g.,* MHC; Alcaide et al. 2007; Minias et al. 2019), to infer phylogenetic relationship among species or to investigate genome evolution (*e.g.,* Mahmood et al. 2014), nuclear sequences are rarely used in population genetics study to infer neutral population structure and gene flow, except to characterize SNP or microsatellite loci (Zhang and Hewitt

2003). This searching step generated a total of 331 articles. We excluded the articles common to both databases, for a total of 203 unique papers. We narrowed down our selection of studies by excluding off-topic research fields (See Fig. 1 for a summary of study refinement). Here, we only focused on studies that had inferred contemporary genetic structure at the intraspecific level. We also screened the references of each selected article to retrieve studies that might be relevant and that we could have missed in the literature survey. We additionally found some references in Sarasola et al. (2019).

Data collection

Information collected from each study

We recorded the following information for each article: genus, species, main study objective (as reported by the authors), hypothesis, location of the study, type of genetic markers used, number of markers, fragment size for mtDNA markers (in base pairs), DNA source (*e.g.,* non-destructive: buccal swab, blood, feathers *vs*. destructive: tissue/muscle), state of the sampled bird (*i.e.*, dead, alive or museum specimen), number of populations sampled and sample size (n), software used for genetic analysis, genetic differentiation observed (yes/no), number of genetic clusters inferred, and effective population size (*Ne*). We also reported the isolation-by-distance (IBD) analysis pattern (*i.e.*, a decrease of genetic similarity with an increase of geographic distance; Wright 1943), the number of alleles or allelic richness, summary genetic statistics used (*i.e., Fst*, *Rst*, *or Gst*, the most common indices of genetic structure; Meirmans and Hedrick 2011), observed and expected heterozygosity (*He*, *Ho*; average, maximum and minimum), and haplotype diversity for DNA sequences. Heterozygosity and haplotype diversity are used as a measure of genetic diversity (Allendorf et al. 2012). We also recorded the scale of the study: low < 599 km, medium: 600–1099 km, large: 1100–4000 km, very large: > 4000 km. To do so, we recorded the two most

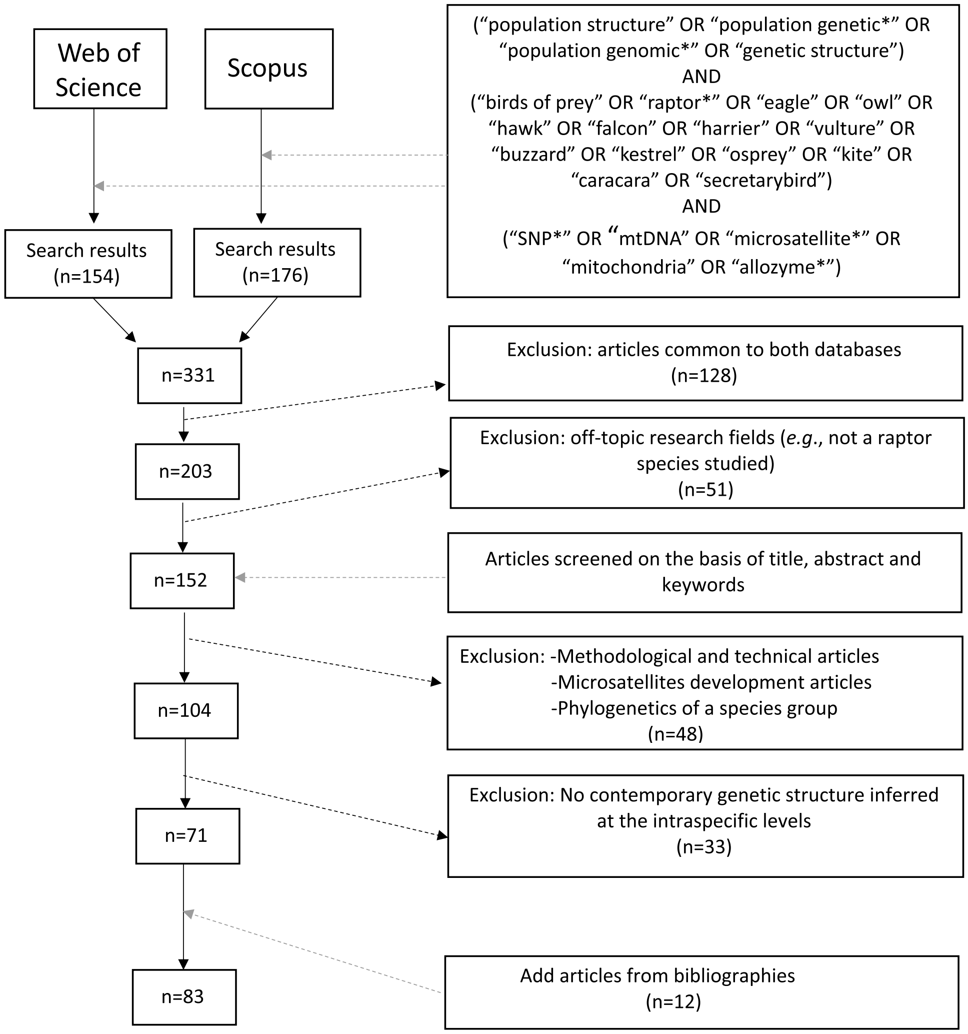


Fig. 1 Stages of selection and exclusion of scientific articles in our review on population genetic in birds of prey. The search engines used were Web of Science and Scopus. The number of articles (n) is indicated for each stage

distant sampling locations in the study using the available figures or the geographic coordinates. After, we grouped the study in the four arbitrary categories of scales listed above.

Species traits

To better described the diversity of species traits covered by population genetics studies in the literature, for each species studied, we assigned its migration strategies as being either resident (non-migrant), facultative (include partial, *i.e.,* irregular migration), or obligate (include complete; Dingle and Drake 2007; Newton 2008) and taxonomic family. When such information was not in the original article, we used the following resources: *The Birds of North America* (Rodewald 2015); *Eagle, hawks and falcons of the world* (Brown and Amadon 1968); and *Migrating raptors of the world* (Bildstein 2006). We also recorded the average body mass for each species using the *Handbook of the Birds of the World* (Del Hoyo et al. 2019). For each species, we used the IUCN Red List (International Union for Conservation of Nature) of threatened species to include the status and the population trends of the species in the database. The IUCN Red List classified species into categories of extinction risk (*Least Concern*, *Near Threatened*, *Vulnerable*, *Endangered*, *Critically Endangered*, *Extinct in the Wild*, and *Extinct*) based on quantitative criteria on the up-to-date size and trends of species populations and species distribution ranges (IUCN Standards and Petitions Subcommittee 2017).

Phylogenetics of the studied species

To illustrate what proportion of raptor phylogenetic diversity our literature survey covered, we inferred the phylogenetic relationship among most species listed in our database. To do so, we retrieved from Genbank the *cytochrome b* mitochondrial DNA (*cyt b*) sequences available for raptors, totaling 48 species out of 50 species included in the review (Table S1). The tree was rooted with the Hoatzin, *Opisthocomus hoazin* as an outgroup (GenBank Acc. number: AF168119; see Supplementary for method). The gene phylogeny presented here is not intended to replace species phylogeny but to illustrate the diversity of raptor species and families studied so far without pretending to resolve the phylogenetic links between them. For a large-scale phylogeny of birds, including few raptor species, the readers may, however, refer to Jarvis et al. (2014) and Kimball et al. (2019).

Results

Raptor data set

Our search resulted in a total of 83 peer-reviewed scientific journal articles assessing population genetics in raptors. Among these, 50 species from 23 genera were studied (Table S1). More than 50% of the studied populations were located in Europe (n = 33) or North America (n = 26; Fig. 2a). Seven studies were performed in Asia, three in Africa, one in Oceania, six in South America, and seven studies were located at the scale of the species distribution, encompassing more than one continent. Overall, the main research objectives (but not exclusive) were population genetic structure (n = 26 studies), conservation (n = 14), genetic diversity (n = 13), phylogeography (n = 9), gene flow (n = 6), connectivity (n = 5), and others (n = 10). Twenty-three studied species were characterized as residents (non-migrants), 17 as facultative migrants, and 10 species as obligate migrants (Table S1). The phylogenetic tree (Fig. 2b and Table S1) illustrated that there is no obligate migrant in the Strigidae family investigated so far. Indeed, the studied Strigidae had 67% resident species, which is more than any other family. Twenty-one studies (25%) had a low scale (LO: < 599 km), eleven studies (13%) had a medium scale (M: 600–1099 km), 23 studies (28%) had a large scale (L: 1100–4000 km), and 28 studies (34%) had a very large scale (VL: > 4000 km; Table S1). The mean sample size of individuals studied per study was 223 with a standard deviation of 223 and a median of 172. The maximum sample size was 1671 and the minimum was 40 individuals. The mean number of individuals sampled per population was 38 with a maximum of 244 individuals/population and a minimum of 5 individuals/population. Isolation-by-distance (IBD) was tested in 34 studies (41%; Table S1). Among them, 21 studies (62%) showed a significant IBD pattern: 70% for LO study scale (7 on 10), 60% for M (3 on 5), 50% for L (4 on 8), and 63% for VL study scale (7 on 11). A total of 23% of the studies (n = 19) provided online access to their data on one or more data deposits. Raw data were available in supplementary material (n = 5, 24%), on Dryad (n = 3, 14%), on Genbank (n = 12, 57%), or on Figshare (n = 1, 5%).

Prevalence of genetic markers in use over time in raptors research

Overall, nuclear microsatellite markers (n = 40 studies) were the most widely used genetic markers, with more than half of these studies (n = 21) using both microsatellites and mitochondrial DNA (mtDNA), and 14 studies used only

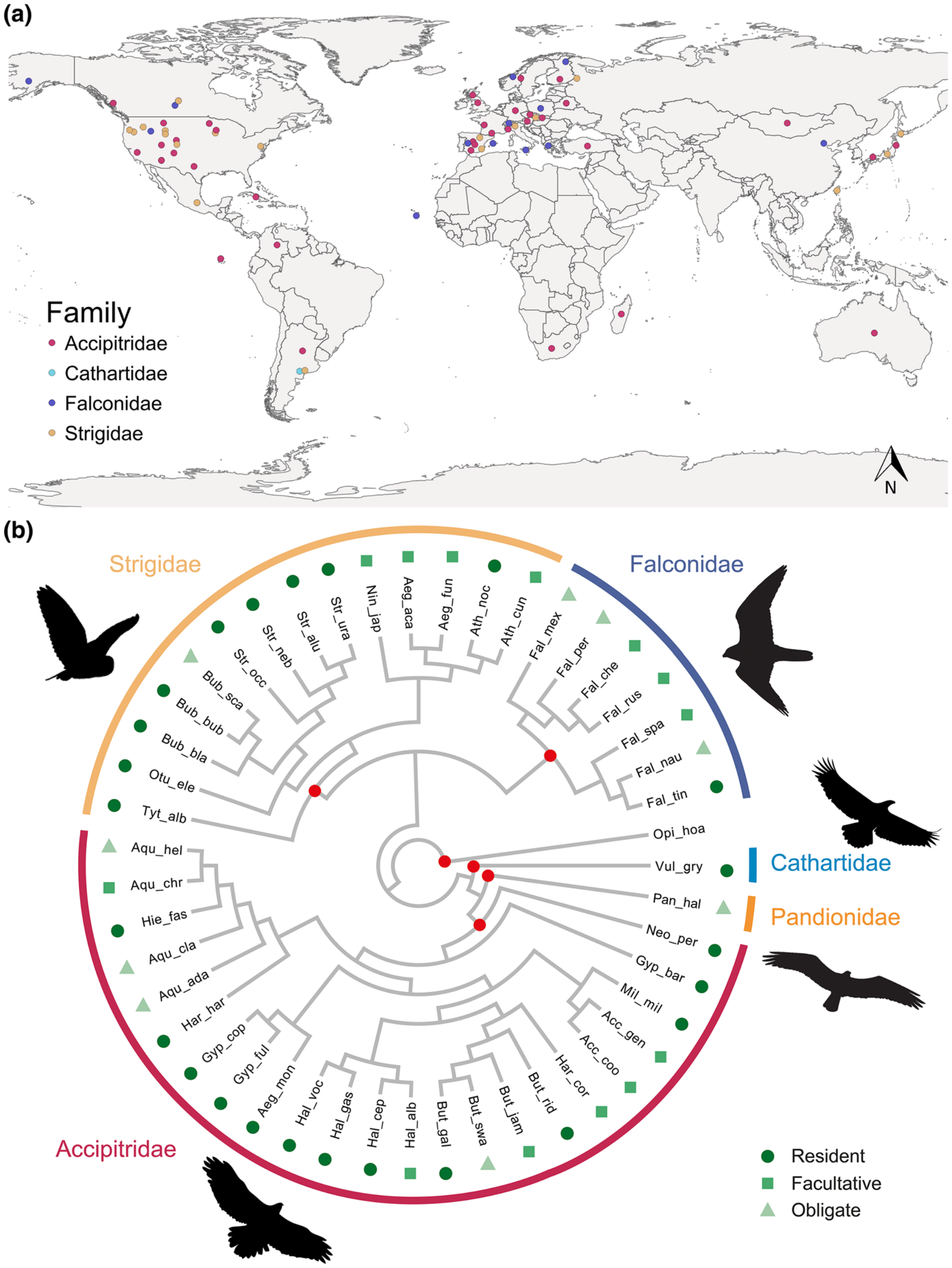


Fig. 2 **a** Sampling locations of the surveyed studies published between 2000 and 2020. Family groups are indicated by colors (Dark pink = Accipitridae [n = 41], Light blue = Cathartidae [n = 1], Dark blue = Falconidae [n = 14] and Light orange = Strigidae [n = 20]). Seven studies (Accipitridae = 3, Falconidae = 2, Pandionidae = 1 and Strigidae = 1) based on multiple continents are not represented on the map. **b** Illustrative phylogenetic tree of raptor species studied with population genetics. Tree was obtained using a maximum likelihood approach based on cytochrome b sequences retrieved from Genbank and was rooted with the Hoatzin, *Opisthocomus hoazin* as an outgroup (GenBank Acc. number: AF168119)

mtDNA (Fig. 3a). The mean number of microsatellites used was 13 ± 6, with a maximum of 36 and a minimum of 3. For mtDNA markers, the control region was the sequence used in 92% of the 53 studies. Mean fragment size was 686 ± 469 base pairs (interval = 345–2300 bp). In the early 2000s, other types of markers were also used in two articles (*i.e.,* variable number tandem repeat [VNTR] and random amplified polymorphic DNAs [RAPDs]). Six studies used SNPs (Single Nucleotide Polymorphisms; Fig. 3a), with the first such study published in 2016. The most published articles in a single year happened in 2018 (n = 10, Fig. 3b).

Raptor conservation status and species studied

Among the 50 studied species, 12 of them (24%) were considered threatened (*i.e.,* IUCN status *Vulnerable*, *Endangered* or *Critically Endangered*) with a further nine species (18%) classified as *Near Threatened* (Fig. 5d). The 29 other species (58%) were classified as of *Least Concern*. The Accipitridae had the highest proportion of threatened species which has been studied, with nine threatened (36%) out of 25 species. The Accipitridae also had population genetic studies on two *Critically Endangered* species, the highest level of threat (Fig. 5a): the Madagascar fish-eagle

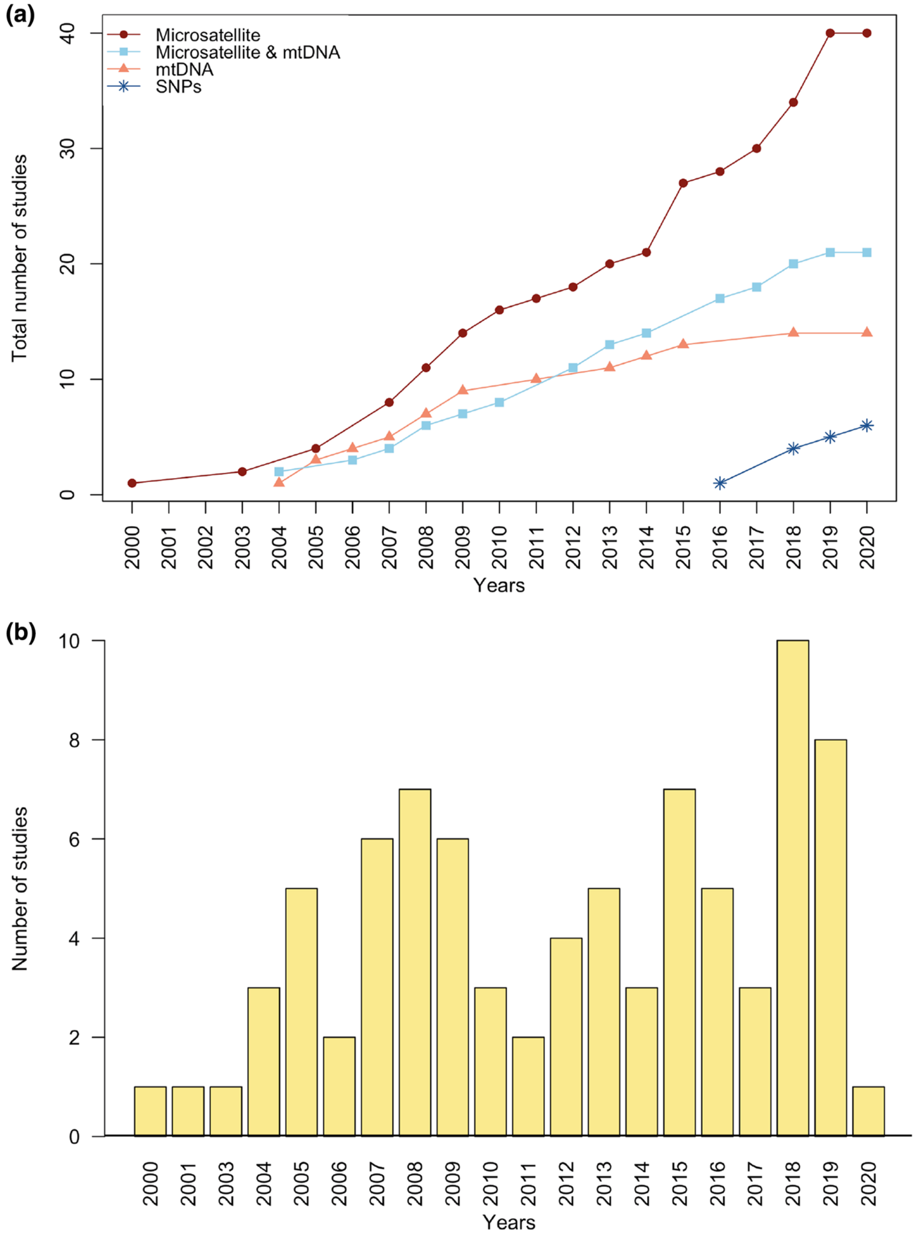


Fig. 3 **a** Cumulative number of raptor studies (n = 81) sorted by the type of genetic markers used, published between 2000 and 2020. **b** Number of raptor studies produced per year

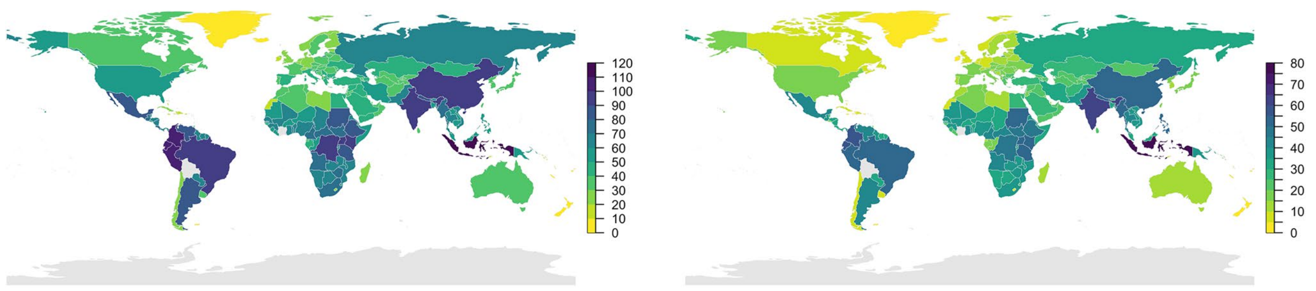
Haliaeetus vociferoides (Johnson et al. 2008) and the Ridgway's hawk *Buteo ridgwagi* (Woolaver et al. 2013). Most studies were focused on species exhibiting decreasing population trends (53%, Fig. 5d). Species with stable population trends were addressed in 31% of all cases. Decreasing trends were observed more prominently in Strigidae (9 species, 60%) and in Accipitridae (13 species, 54%). The Strigidae had the lowest percentage of studied species (n = 16 out of 236 species or 7%, Fig. 5b). By increasing order, we then have the Accipitridae (25 out of a total of 234 species; 11%), the Falconidae (7 out of 64 species; 11%), the Cathartidae (a single species among a total of 7; 14%, Fig. 4b). Finally, the only species of the Pandionidae has been studied (Fig. 4b). Between 2000 and 2020, only 9% of all raptor species have been studied (50 out of 557 species Fig. 4c). Overall, there is information on population genetics for less than 30% of all raptor species, but for Strigidae, Falconidae, and Accipitridae, this value is less than 15% (Fig. 5b).

Detecting population genetic structure in raptors

Most of the studies (76%, n = 63) detected significant genetic differentiation at the scale of the studies with an average number of genetic clusters of 2.29 ± 1.11 and a maximum of six. Significant genetic structure was detected in 25 studies (86%) of residents, 25 studies (71%)

(a) All raptors

(b) Threatened and declining raptors



(c) Percentage of raptors investigated

(d) Percentage of threatened and declining raptors investigated

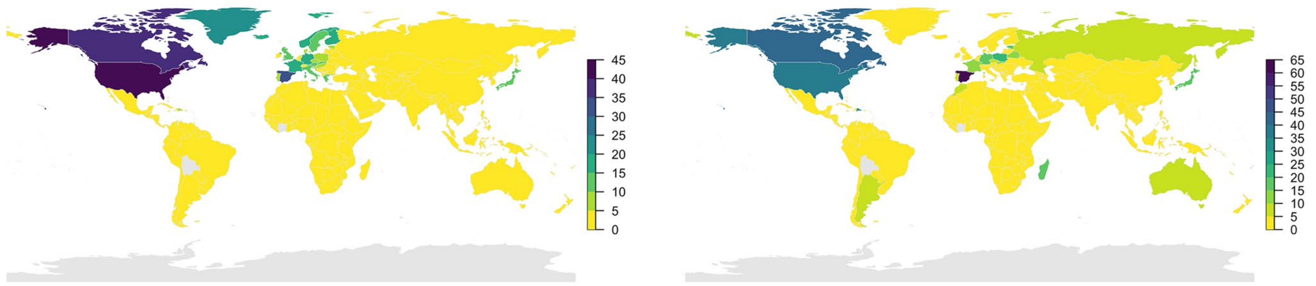


Fig. 4 Maps showing the number of **a** total **b** threatened and declining **c** percentage of genetically investigated **d** percentage of genetically investigated threatened and declining extant raptors per country. The scale represents the number of raptor species and ranges from purple, indicating many species, to yellow, indicating few species. Data from **a** and **b** came from McClure et al. (2018). Original data came from BirdLife International (2017) downloaded in April 2019

of facultative migrants, and 13 (76%) studies of obligate migrants. A total of 41 species (82%) had at least one study that revealed population structure. Sixty-nine percent of the studies used the software Structure (Pritchard et al. 2000) for inferring the number of clusters and the presence of genetic structure. Eighty-six percent also published the software settings to allow reproducibility of analyses. This software was often used in combination with other software like Arlequin (Excoffier et al. 2005), Genepop (Rousset 2008), or genalex (Peakall and Smouse 2012). One study used Beast (Drummond and Rambaut 2007), two studies used Geneland for complementary clustering results (Guillot et al. 2005), and two studies with SNPs based their results on Admixture (Alexander et al. 2009) for assessing population structure. A total of 15 articles (18%) presented effective population size (*Ne*) estimations (Table S1). The most commonly used software to estimate effective population size (*Ne*) was NeEstimator v2 with the linkage disequilibrium (LD) method (Do et al. 2014). Only one article reported the ratio of the effective size and census size (*Ne/Nc*), with a value of 0.044 for the Africain cape vulture *Gyps coprotheres* (Kleinhans and Willows-Munro 2019). Mean expected heterozygosity (*He*) seemed similar across conservation status (Fig. 6a) and per families (Fig. 6b). The low sample sizes for some categories preclude statistically test differences in family or IUCN Red List levels.

Discussion

While population genetics is a key component of any conservation and management program (Allendorf et al. 2012), our results highlight the fact that a very small percentage of raptors have been investigated so far (*i.e.,* 9%; Fig. 5a), and most of these studies are geographically biased towards North America (n = 26, 31%) and Europe (n = 33, 40%; Fig. 4c). Following our investigation, we can conclude that species considered "threatened" (*i.e.*, with the "*Vulnerable*", "*Endangered*", or "*Critically Endangered*" status; Fig. 4a) are underrepresented in the raptor genetics' literature. That means that species of conservation importance are those for which we have little or no genetic information. Strigidae was the family with the lower percentage of investigated species. That could be related to the fact that these species are mostly nocturnal and may be more difficult to monitor. Genetic diversity (*He*), a key component of conservation practice (Hoban et al. 2013, 2020) was available in many

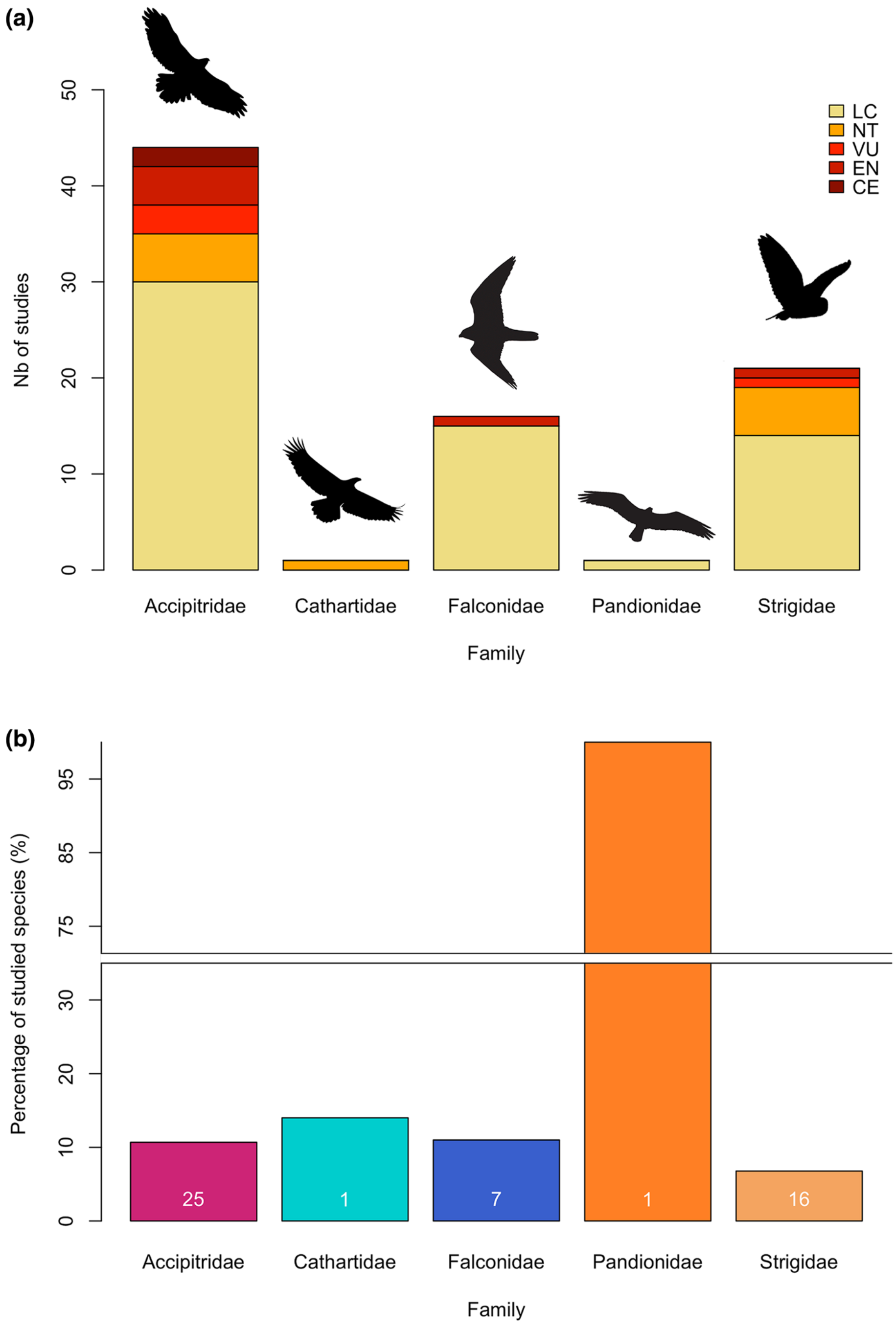


Fig. 5 **a** Number of species studied for each raptor family within each IUCN Red List category (*Critically Endangered* [CE], *Endangered* [EN], *Vulnerable* [VU], *Near Threatened* [NT] and *Least Concern* [LC]). **b** Proportion (in percentage) of the studied species on the total number of species comprising the family (n represents the number of species studied included in this review)

species, but at a different level, *i.e.*, *He* at the sample (*e.g.*, individual, or population) or at the locus levels. This makes any comparison between family, conservation level, or migration behavior almost impossible.

With the available studies and data, we were also unable to perform any kind of meta-analysis. We were limited by the number of papers available in the literature that performed similar analyses or reported the same metrics when analyzing population genetic structure. Indeed, some authors reported global *F*-statistics or pairwise *Fst* while others only presented results of bayesian or multivariate clustering. This heterogeneity in reported metrics prevented us to perform a strict meta-analysis; it was indeed difficult to find a standardized effect size for *e.g.*, *Fst* = 0.001 *vs.* K = 5 obtained with the software Structure. This situation prevented us from finding potential common patterns (*e.g.*, environmental, demographic, *e.g.*, De Kort et al. (2021)) in the genetic structure studies of raptors. Such limitations could negatively affect the effective conservation of raptors.

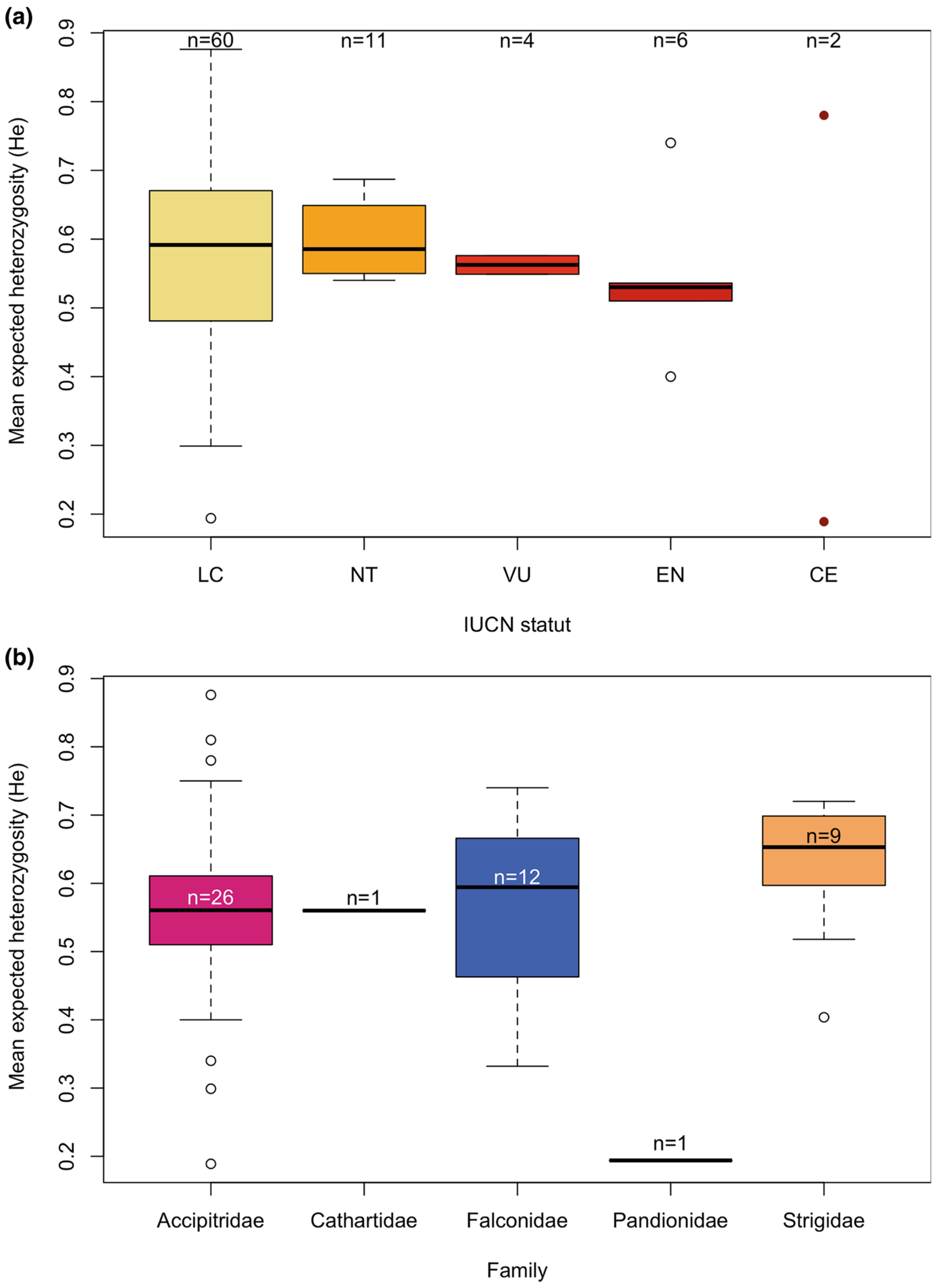


Fig. 6 **a** Boxplot of mean expected heterozygosity within each IUCN Red List category (*Critically Endangered* [CE], *Endangered* [EN], *Vulnerable* [VU], *Near Threatened* [NT] and *Least Concern* [LC]). **b** Boxplot of mean expected heterozygosity within each raptor families

Prevalence of genetic markers in use over time in raptors research

Microsatellite markers have been the most commonly used type of genetic marker in raptor population genetics so far (See Supplementary for a summary of advantages and inconvenience of using genetic markers; Fig. 3a). In the overall conservation genetics realm, Single Nucleotide Polymorphism (SNPs) has been increasingly used since 2004 (Morin et al. 2004) and became the go-to marker in many taxa because of its potential for higher genotyping efficiency, data quality, resolution, genome-wide coverage, and high variability (Morin et al. 2009). Yet, these biallelic makers only recently began to be used as genetic markers for birds of prey. With the recent development in genomic techniques (*e.g.*, next-generation sequencing, whole-genome scans), it is becoming possible to apply SNPs to non–model species of ecological and conservation relevance (Martinez-Cruz 2011; Hendricks et al. 2018). For example, with these data, it is possible to understand patterns of adaptive variation in endangered species where traditional approaches had previously failed (Manel et al. 2010; Nielsen et al. 2012) with direct application to defining conservation units (Funk et al. 2012). Indeed, only six studies (7%; Fig. 3a) used SNPs, and increasing the number of studies with this type of marker could be advantageous in the conservation of threatened raptors. However, there are still some challenges (*e.g.*, software complexity, cost of sequencing a full genome) to overcome before genomic tools can be used to their full potential for conservation genomics (see Kraus and Wink (2015) for the application of genomics in birds; Shafer et al. 2015).

Detecting population genetic structure in raptors

The software Structure for clustering methods for population differentiation was the most widely used software according to a methodological review of Latch et al. (2006) and still returns 19,390 records on Web of Science-Core-Collection by 04/27/2020 and then the number of records per year is still increasing since the initial article that described the method was published in 2000 (Pritchard et al. 2000). According to our results, this trend also applies to studies on raptors. However, this software suffers some drawbacks discussed in depth in recent publications (Puechmaille 2016; Wang 2017), *e.g.,* when the sample size is uneven between subpopulations, or when sampling is not spatially balanced or discontinuous (Serre and Pääbo 2004; Lawson-Handley et al. 2007). More generally, reproducibility of results is a problem in ecology and population genetics is no exception. Several authors, therefore, argue for an in-depth reporting of settings and parameters used in the Structure (Gilbert et al. 2012) or in other population genetics software (*e.g.,* Miller et al. 2020) to allow better comparison among taxa. We argue here that raptor genetic studies are not immune to this issue.

Isolation-by-distance (IBD; Wright 1943) a decrease in genetic similarity among populations as the geographic distance between them increases (Rousset 1997) driven by migration-drift equilibrium, is often used in population genetic studies (Jenkins et al. 2010; Wang et al. 2013) to assess the effect of distance only on genetic differentiation, in conjunction for example with more meaningful landscape-related distances (*e.g.*, through an isolation-by-resistance, IBR; McRae and Beier 2007; isolation-by-environment, IBE; Wang and Bradburd 2014 approaches). Following our systematic review, IBD is a ubiquitous pattern in the genetic differentiation in raptors. Moreover, we identified that a significant IBD is more common at small (*i.e.*, < 599 km) or very large study (*i.e.*, > 4000 km) scales.

There are urgent need to link movement behavior and genetic studies as it can help characterize connectivity, migratory divide, and gene flow among populations (Agudo et al. 2011; Ruegg et al. 2014; Delmore and Irwin 2014; Shafer et al. 2016; Sherry 2018). Only a single publication on birds of prey, focusing on the Egyptian vulture *Neophron percnoterus,* used movement tracking data together with genetic data in the same study design (Agudo et al. 2011). Indeed, combining animal tracking technology (*i.e.,* allowing the fine study of individual movement) with genetic data could help elucidate many ecological and evolutionary processes (*e.g.,* migration, hibernation, responses to environmental changes; Shafer et al. 2016). Examples of such an approach combining movement data and genetics exist in mammals (*e.g.*, satellite telemetry with microsatellites for assessing responses to environmental changes in ringed seals *Pusa hispida*; Martinez-Bakker et al. 2013), and other bird taxa (*e.g.*, radio transmitters combined with genomic data to characterize migratory behavior of partial migration in blackbirds *Turdus merula*; Franchini et al. 2017; band recoveries and mtDNA to evaluate migratory divide in Swainson's trushes *Catharus ustulatus*; Delmore et al. 2012). Unfortunately, no such studies are available for raptors. In addition, stable isotopes (*e.g.*, carbon or nitrogen) are also being used in conjunction with genetic information to infer the origin of migratory species (*e.g.*, Clegg et al. 2003; Zimmo et al. 2012; Katzner et al. 2017; Pokrovsky 2018). Yet, we are not aware of any study that combined genetic data with tracking data and stable isotopes in raptors.

Effective population size (*Ne*) in raptors

The most common research priorities for raptor species according to the IUCN Red List assessments are to measure the current and past population demographic trends (McClure et al. 2018). However, the lack of data is a common challenge for most species, and raptors are no exception (*i.e.*, population long-term monitoring or monitoring of many individuals over several generations is a long and often costly task). By using genetic information, it is possible to address these needs by assessing genetic drift and changes of *Ne* over time (Waples 2016). Estimation of *Ne* is crucial for the management of endangered species. In general, a minimum value of *Ne* of 100 individuals is advised to prevent loss of genetic diversity by genetic drift for five generations and *Ne* of 1000 individuals to maintain long-term evolutionary potential (Frankham et al. 2014). According to our systematic review, we retrieved *Ne/Nc* ratio for only one raptor species, *i.e.,* the Africain cape vulture *G. coprotheres* (Kleinhans and Willows-Munro 2019). This type of information is sorely lacking in our literature review and will need to be largely addressed in conservation programs.

Nevertheless, obstacles persist for the practical application of *Ne*, *e.g.,* the need to characterize the temporal and spatial scales of *Ne* estimations can render the results difficult to interpret (Hare et al. 2011). Also, there are numerous methods to compute *Ne* (Frankham 1995; Gilbert and Whitlock 2015; Greenbaum et al. 2018). Despite such shortcomings, many publications use *N*e estimates for the management of populations especially to infer population demographic trajectories (*e.g.,* Frankham 1995; Hare et al. 2011; Husemann et al. 2016). For comprehensive and detailed reviews on the application and utilization of *Ne,* see *e.g.,* (Wang et al. 2016; Waples 2016).

Raptor conservation status *vs.* studied species for population genetics

Of all 557 raptor species, 103 species (18%) are considered threatened (*Vulnerable*, *Endangered* or *Critically Endangered*), with a further 70 (13%) classified as *Near Threatened* (McClure et al. 2018). Although our review points to 25% of genetic studies targeting species with conservation priorities, only 12 of the 103 threatened species (12%) have been examined so far. Our results also show that there are more genetic studies on species with a lower level of threat (Fig. 5a). McClure et al. (2018) showed that Asia, Africa, and South America were the regions with the most threatened and declining raptor species (Fig. 4b), and yet, these same regions are also underrepresented in genetic studies conducted since 2000. The raptors located in South America, Africa, and Southeast Asia are also identified as a high priority for raptor research and conservation (Buechley et al. 2019). Knowledge of the population genetics of these species could be a great start and provide useful information for management and conservation actions.

Recommendations

We still know so little about migration and life history in raptors, more work is needed to resolve this, and population genetics approaches can be of great value. Following our systematic review, we can build recommendations to help maximize the comparability across studies and address the current gaps in ongoing research in raptor population genetics. First, our study highlights a gap in species of conservation concern status and on those located in the Southern Hemisphere; and increasing a focus there in future studies will be imperative for raptor conservation. This can help to enhance both our global understanding of population genetics and the impact of such data on management actions. Recent advances in the use and effectiveness of non-invasive sampling techniques (*e.g.,* feathers, swab) now allow much-reduced manipulation time and stress for the bird (Handel et al. 2006; Vilstrup et al. 2018). All sampling techniques have to remain within the ethical standard. For instance, we do not recommend an increase in sampling at the expense of the threatened species. One of the priorities in conservation programs is to conserve and monitor genetic diversity within all species (Hoban et al. 2013; Laikre et al. 2020). By systematically reported *He* per individual and per population, we can achieve this objective and have a standardized value to compare between species in raptors research. *Ne*—in conjunction with *Nc* and the *Ne/Nc* ratio—has, also, a great potential for managing populations as an indicator of genetic drift and inbreeding (Frankham 1995; Waples 2016; Wang et al. 2016), providing that it is estimated similarly across studies and that the limitations of this estimate (*e.g.,* restrictive assumptions to the computation) should be taken into account when interpreting data. In addition, detailed analytical procedures for assessing population genetic structure (*i.e.,* all parameters and software settings used; see Gilbert et al. (2012) or Miller et al. (2020)) should be included as well. Having access to the raw data (*e.g.,* genotypes and sequences) could also allow the computation of missing values, the estimation of *Ne* or *He* per individual and per population, if not already done in the original study. In fact, despite sustained calls for open access data (*e.g.,* Evans and Reimer 2009; Pasquetto et al. 2019) and the easy access to public data repositories (*e.g.,* Genbank (Benson et al. 2007) or Dryad (Vision 2010)), only a few studies (23%) provided online access to their data, with 35% in the last 5 years.

Conclusion

Overall, this study reveals important knowledge gaps regarding existing studies that have been conducted on raptor population genetics. We have assembled a list of recommendations that we feel could fill some of these gaps as follows: (1) increase the number of studies on threatened species or on species located in the Southern Hemisphere; (2) systematically reported genetic diversity (*He*); (3) increase the number of studies that estimate a demographic trend based on change of effective population size (*Ne*) and (4) provide open access data. Advances in population genetics have been rapid in recent decades (*e.g.,* development of new markers and new analyses), resulting in a proliferation of published studies, but there is a lack of continuity and standardization of methods, such that direct comparison of results of these studies is challenging. Understanding the connectivity and genetic structure of populations is important for establishing effective conservation plans, particularly for populations or species that are threatened and in urgent need of conservation actions (Cresswell 2014). We may be at the beginning of the genomic revolution in conservation genetics, since the technology for direct analysis of genomes of organisms, including non-model organisms, becomes increasingly available (*e.g.*, for birds the Bird 10,000 Genomes (B10K); https://b10k.genomics.cn/). In this context, detailed and informative population genetic structure data will be of prime importance in effective natural resource management. For the first time, we have all the elements needed at our fingertips to enable the application of population genetic studies to global raptor conservation, provided that these elements are considered in conservation programs.

A general gap happens between the scientific community that produces pure scientific knowledge and practitioners involved in conservation and management actions. This general observation is particularly true for the translation of genetic information to conservation (Arlettaz et al. 2010; Shafer et al. 2015; Haig et al. 2016; Domingues et al. 2018). This gap may stem from the lack of information transfer on methods, results, and interpretation from scientific to a larger audience (Arlettaz et al. 2010; Domingues et al. 2018). Better inclusion of genetic information in conservation and management policies would require, among others, an improvement in the communication between scientists and policymakers (Hoban et al. 2013; Haig et al. 2016). This is an ongoing work, for instance, the IUCN Conservation Genetics Specialist Group, whose active role is to facilitate collaboration and communication by promoting the use of genetics in conservation management, decision-making, and to help in applying genetics to species of concern (see Garner et al. 2020). Best conservation practices should then imply a standardized use of population genetic tools as well as a better transfer of knowledge to practitioners.

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Data availability Database used in the article can be found on Figshare: https://doi.org/10.6084/m9.figshare.12455732 and the R script for figures https://doi.org/10.6084/m9.figshare.12455759.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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