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Applications of Primate Genetics for Conservation and Management

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Keywords

nonhuman primates, genetic variation, conservation status, forensic analyses, in situ and ex situ management

Abstract

Conservation genetics is the use of genetics to understand and mitigate the threats caused by anthropogenic activities, including habitat loss and fragmentation, wildlife trafficking, and emerging diseases. In this review, we discuss the role of primate conservation genetics in the development of effective conservation strategies, emphasizing the importance of maintaining genetic diversity to enhance adaptive potential and prevent extinction. First, we discuss studies of various primate species that exemplify how genetic data have been instrumental in accurately assessing threat levels, identifying trafficked animals and tracing their geographic origin, and studying how habitat loss affects primate populations. Subsequently, we describe the various molecular tools and analytical approaches employed in these studies. Lastly, we provide a bibliographic review of research in conservation genetics over the last 20 years. We conclude with a brief discussion of the limitations and challenges in this field in developing countries and recommendations for future research.

1. INTRODUCTION

Effective population size (N_e): number of individuals that effectively breed and contribute offspring to the next generation; usually smaller than the census size

Phylogeography: integrative discipline that investigates relationships among individual genotypes within a species or a group of closely related species, correlating those relationships with their spatial distribution

Primates are increasingly threatened with extinction due to numerous anthropogenic activities that directly (e.g., pet trade) or indirectly (e.g., deforestation and fragmentation) affect their populations and habitats and, as such, are of great conservation concern (Estrada et al. 2017). In turn, these activities influence the demography and genetic diversity of primate populations, thereby limiting the viability of species and ecosystems and leading to the so-called sixth extinction (Ceballos et al. 2015). The first of the four long-term goals of sustainable development formulated by the Kunming–Montreal Global Biodiversity Framework (Conv. Biol. Diver. 2022) states that "the genetic diversity within populations of wild and domesticated species is maintained safeguarding their adaptive potential," highlighting the importance of genetic diversity for guaranteeing the evolutionary potential of populations and species as well as their ability to face environmental challenges.

Conservation genetics, although rather underutilized, is a discipline with nearly a half-century of history (Frankham 2019) that aims to preserve the genetic diversity of populations and species. This discipline has therefore become extremely valuable in addressing problems in primate conservation at both the population and species levels. Many factors, such as habitat degradation and fragmentation, act synergistically to threaten primates, leading to decreases in resource availability, restricting dispersion, and increasing exposure to pathogens from domestic animals. These consequences, in turn, result in a decrease in the effective population size (N_e), a decline in the genetic variability of populations, increased inbreeding, limited adaptive ability, and eventually higher mortality rates. Finally, this vicious cycle causes local extinction, likely taking place at various points within a species' range.

Genetics is also a valuable tool in addressing problems in taxonomy and systematics of primates, specifically in cases where morphological or chromosomal traits are ambiguous. Moreover, at the population scale, concrete and quantifiable genetic data can rapidly provide insights into the historical and contemporary processes shaping population structure and can aid our understanding of current and future adaptive challenges (Zhou et al. 2016, Teixeira & Huber 2021). Therefore, genetic analyses can be an effective approach to establishing and enforcing adequate management and legislation to better conserve primate species and populations. In this article, we summarize research in this discipline as applied to primates in three main sections: the purposes of conservation genetics, its analysis, and what has been accomplished so far. We conclude with a short discussion.

2. WHAT IS PRIMATE CONSERVATION GENETICS FOR?

2.1. Systematics and Taxonomy

Over the last few decades, molecular phylogenetics and phylogeography have been tremendously useful in elucidating the colonization, diversification processes, and current patterns of geographical distribution of a variety of primate taxa at the family, genus, and species levels, with significant ramifications for taxonomy and systematics. A better understanding of the underlying historical processes that shape the current patterns of geographical distribution of primate species and taxa is relevant to conservation because changes in the geographic distribution of major taxonomic groups and species affect estimates of phylogenetic diversity (the number of taxa for a given region) and help define critical areas for conservation.

The genus *Saguinus*, for instance, is widely distributed in northern South America and Panama, but a recent molecular phylogeny led to its redefinition as four monophyletic genera: *Saguinus*, *Leontocebus*, *Tamarinus*, and *Oedipomidas* (Carvalho Brcko et al. 2022, Lopes et al. 2023). While *Oedipomidas* occurs exclusively to the west of the Andes Mountains (*trans*-Andean) in Colombia and

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Panama, *Saguinus*, *Leontocebus*, and *Tamarinus* are *cis*-Andean. Like *Saguinus*, the genus *Callicebus* was split into three (*Callicebus*, *Plecturocebus*, and *Cheracebus*) on the basis of the deep phylogenomic divergence that originated in the Miocene (Byrne et al. 2016). All these taxonomical changes imply reductions in the geographic distribution ranges of the target genera, intensifying the need for conservation efforts in larger areas to preserve them. In the case of tamarins, these efforts mean conservation in both *cis*- and *trans*-Andean regions to preserve all four genera.

Molecular phylogenies have also been used to test the principle of monophyly, in which all the members of a single species are expected to correspond to a well-differentiated clade sharing a common ancestor in a reference phylogeny. In some cases where the boundaries between species violate this principle, redefinition of a species has been justified, but whether nonmonophyletic species should be accepted as valid taxa is controversial (for details, see Gutiérrez & Garbino 2018, Zachos 2018, Gippoliti 2019). Such is the case for five subspecies of *Cebus albifrons* sensu lato (i.e., *C. albifrons*, *C. cesarae*, *C. malitiosus*, *C. unicolor*, *C. versicolor*) that do not share a common ancestor according to phylogenetic analyses of mitochondrial lineages and, therefore, were elevated to species level (Boubli et al. 2012, Lima et al. 2017, Ruiz-García et al. 2019). Nevertheless, the taxonomic status of some other subspecies of *C. albifrons* is still a matter of discussion or contingent on future genetic evidence. Traditional phylogenetic methods assume that diversification processes are dichotomous and that genetic exchange between genetically differentiated taxa does not occur. However, many cases of incomplete reproductive isolation between species have been described in primates, resulting in numerous cases of genetic introgression. As a result, the evolutionary histories of hybrid species are particularly complex.

Incomplete lineage sorting is another factor that complicates the phylogenetic reconstructions and is frequent in cases of recent speciation events where genetic differentiation of two given species is incomplete. However, recent advances in genomic sequencing and phylogenetic methods have been useful in overcoming the challenges posed by genetic introgression and ILS for the understanding of evolutionary processes. In addition, efficient forensic methods, advanced sequencing technologies, and rigorous coalescence-based phylogenetic approaches have created new opportunities in conservation genetics to generate high-quality DNA sequences from degraded samples and specimens preserved in museums, as well as to recognize well-differentiated lineages and species (Leaché et al. 2014, Barido-Sottani et al. 2018).

The large mitochondrial genetic distances between Sumatran (*Pongo abelii*) and Bornean (*Pongo pygmaeus*) orangutans were initially used as evidence to justify their designation as two separate taxa (Xu & Arnason 1996). Subsequently, analyses of complete genome sequences, in part from museum skins, unveiled profound genetic differences between two groups of Sumatran orangutans, including one more closely related to the Bornean orangutan (Nater et al. 2017). These findings led to the recognition of another Sumatran species of orangutan (*Pongo tupanuliensis*) currently categorized as critically endangered (Nowak et al. 2023). In Platyrrhini, similar cases of species newly described through the combined use of genomic, morphological, and geographic data are the marmosets *Mico schneideri* and *Mico munduruku* (Costa-Araújo et al. 2019, 2021), the uakaris *Cacajao ayresi* and *Cacajao hosomi* (Boubli et al. 2008), the titi monkey *Plecturocebus grovesi* (Boubli et al. 2019), the muriquis *Brachyteles hypoxanthus* and *Brachyteles arachnoides* (Chaves et al. 2019) and the tamarin *Tamarinus kulina* (Lopes et al. 2023).

Monophyly: clade in a phylogeny that includes all the descendants of a common ancestor; may be applied to the species level or higher hierarchical levels

Genetic introgression: integration of genes from one species into the gene pool of another because of hybridization

Incomplete lineage sorting: ancestral genetic polymorphisms shared by closely related taxa, primarily during rapid speciation events, that cause the species phylogeny to differ from gene trees

Coalescence-based phylogenetic approaches: genealogical methods intended to trace gene copies from offspring to the common ancestor in a population or group of taxa

2.2. Assessment of Conservation Status

Primates are a group of great conservation concern. According to the International Union for Conservation of Nature (IUCN) Primate Specialist Group, more than 62% of the 539 currently recognized species are included in one of the threatened categories of the IUCN Red List, with 16% considered critically endangered. Maintaining the genetic diversity of a species is essential

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so that the species can respond to future environmental challenges. The disappearance of local populations can quickly lead to more wide-spread regional extinctions if populations are separated by distances large enough to prevent recolonization of empty habitats or if there are physical or anthropogenic barriers that reduce both movement and survivorship of dispersing individuals (Allendorf et al. 2010).

Short tandem repeats (STRs): tandem repeats of short sequences (2–6 bp) of genomic DNA dispersed throughout the genome and highly polymorphic in repeat number; also known as microsatellites

Genetic parameters can be used to support recommendations regarding international conservation rankings. The genetic structure of many primate groups has been explored; however, these data have seldom been used in the development of management and preservation plans or in public policy (Blair et al. 2013; Moraes et al. 2017; Frandsen et al. 2020; Oklander et al. 2020, 2022). For example, despite the recognized importance of genetic diversity as one of the three basic components of biodiversity (Hoban et al. 2020), it is not yet considered as a criterion to evaluate conservation status in the IUCN Red List. The actual five different criteria (A–E) used to determine whether a taxon belongs in an IUCN Red List estimate of population size (N) or population decline mainly by species range extent and the number of mature individuals (IUCN 2012). However, N_e can differ from N as a result of variables like sex ratio, mating patterns, and generation time, among others (Frankham et al. 2014). To date, genetic data have only rarely been considered in one criterion (E) involving quantitative analyses.

Genetic studies provide insights into the historical and contemporary processes that shape the structure of populations. Moreover, concrete and measurable genetic data can be very effective tools in establishing and enforcing adequate legislation to diminish biodiversity loss. Gathering and publishing demographic and environmental data prior to management actions can be a lengthy process; in contrast, genetic tools provide a faster alternative to generate information about populations and species so as to design conservation actions. It is also important to recognize that laboratories equipped and available for wildlife genetic analyses are still relatively scarce in habitat countries, and the costs of maintaining these labs and performing such analyses are high. For these reasons, analyses are often conducted in nonhabitat countries, sometimes by foreign researchers or researchers from habitat countries who, being abroad, have access to international resources that would not be available for researchers at universities in primate habitat countries. As a general result, genetic data are still poorly represented in management and conservation plans.

Genetic data can be useful for categorizing the degree of threat to a species by IUCN because this categorization is often one of the few tools commonly used by governments and decision-makers when implementing management and conservation programs. Willoughby et al. (2015) analyzed the relationship between genetic diversity and IUCN conservation status across vertebrates and proposed incorporating the estimation of the expected loss of genetic diversity as another criterion for identifying species of conservation need. They found that the IUCN's existing criteria failed to identify populations with low genetic diversity and proposed estimating and using the number of generations (t) that it would take for the current genetic variability of a population to decline below a certain threshold (on the basis of its current genetic variability) as an additional criterion in the assessment of a taxon's conservation rank. Subsequently, Oklander et al. (2021) reviewed published studies that collected short tandem repeat (STR) data for Neotropical primates and used the methods employed by Willoughby et al. (2015) to analyze the relationship between the estimated loss of genetic diversity and the IUCN Red List conservation status. Their results suggest that several species and subspecies could be more at risk than suggested by their current classification on the Red List, a trend that may hold true in other regions as well. They also found that many publications containing genetic data applied to studies of kinship or mate choice, for example, did not present the basic heterozygosity or N_e parameters of the studied populations that could be estimated with the same database. For these reasons, we encourage researchers to publish, when available, observed heterozygosity, N_e, and N in genetic studies of wild primate

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populations, especially for the least-studied families, to provide a more accurate categorization of the conservation status and threat level for these species.

2.3. Forensic Analyses, Identification of Species, and Inference of Geographic Origins

Molecular techniques can be applied to criminal investigations such as illegal trafficking or hunting of primates, detection of hot spots of illegal animal extraction, and identification of individuals or samples of species.

2.3.1. Molecular identification of primate species. An analysis of 20 years of internationally legally traded wildlife (1997–2016) revealed that primates were the second most traded (22%) source of commodities; international trade in primates for "exhibition" represented US$3 billion (Andersson et al. 2021). These legal trade data make it easy to understand how the illegal wildlife trade can be a highly lucrative business, in contravention of national and international laws and treaties (Zimmerman 2003).

Molecular identification of species is particularly useful in law enforcement to assign species using animal derivatives including hair, fecal samples, museum skins, bushmeat, or processed items (Guschanski et al. 2013, Rashid et al. 2015, Smart et al. 2021). It can also be used to identify species when the reliability of morphological traits is dubious (Maldonado et al. 2023). Highlighting the importance of using molecular tools to correctly identify heavily traded primate species for both medical and bushmeat purposes, Rönn et al. (2009) developed a microarray system that allowed the identification of 45 out of the 65 primate genera recognized at that time of the study.

The idea of using a DNA sequence as a molecular barcode to recognize species is appealing because of its conceptual simplicity and application in forensic sciences (Hebert et al. 2003, Chapple & Ritchie 2013). DNA barcoding is based on the principle that a pair of universal primers (that recognize and amplify homologous sequences across multiple species) can be used after a validation process to obtain a nucleotide sequence of between 650 and 750 bases of the mitochondrial cytochrome *c* oxidase subunit I (CO-I) and then find potential matches in reference databases such as GenBank (see **https://blast.ncbi.nlm.nih.gov/Blast.cgi**) and the Barcode of Life Database (BOLD; see **https://www.boldsystems.org/index.php**) (Hajibabaei et al. 2006, Ratnasingham & Hebert 2007, Chac & Thinh 2023). BOLD includes 51,015 records for primates, representing 327 species. Minhós et al. (2013), who surveyed primate species traded in two urban markets in Guinea-Bissau using DNA barcoding, distinguished between species with similar body size and demonstrated that misidentification bias can result in inadequate conservation policies by neglecting some of the most affected species. More recently, Gaubert et al. (2015) developed a multilocus approach amplifying fragments of four mitochondrial genes (cytochrome *b*, CO-I, and ribosomal subunits 12S and 16S) to establish a framework for DNA typing of African bushmeat. They provided an amplification protocol and a DNA-typing decision pipeline through the database DNAbushmeat (see **http://mbb.univ-montp2.fr/MBB/DNAbushmeat**), enabling automated taxonomic identification of bushmeat items from African forests using the GenBank database. Using these methods, Dipita et al. (2022) assessed the taxonomic identification of traded bushmeat in Cameroon and one seizure from a French airport, successfully identifying 12 species of primates. They also found that primate species were inaccurately identified by customs (in France) and by market-recruited assistants (in Cameroon), demonstrating that accurate species identification is fundamental for effective conservation strategies.

A more sophisticated version of the molecular barcoding approach, known as metabarcoding (Quéméré et al. 2013), relies on the same principle of barcoding but couples high-throughput sequencing (HTS) methods with bioinformatics to simultaneously coamplify and recognize DNA

Molecular barcode (DNA barcode): analogous to supermarket barcodes, a species identification system that uses a short DNA sequence from an individual sample

Metabarcoding: simultaneous identification of species through sequencing of a specific DNA marker from a mixed sample

High-throughput sequencing (HTS): refers to sequencing technologies that generate extensive amounts of genetic data relatively faster and more cost-effectively than traditional sequencing; also known as next-generation sequencing (NGS)

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from mixed sources (e.g., feces, water, soil, or even air). This method has been widely used in the last decade to make inventories of gastrointestinal parasites, microbiomes, and diet components from primate fecal samples (Quéméré et al. 2013, Lan et al. 2023, Schneider et al. 2023). It is also an effective method for forensic wildlife species identification in complex samples containing a mixture of different species, such as manufactured products or dietary supplements (Arulandhu et al. 2017).

Nuclear copies of mitochondrial DNA (numts): originate from the transposition of mitochondrial DNA fragments into the nuclear genome or from duplication of another numt

Genotype reference database (GRDB): species-specific database of genetic variants of individuals throughout species distribution; allows origin identification of unknown samples by comparing them with the database

2.3.2. Care in the use of molecular barcodes. Despite the tremendous impact of molecular barcoding and metabarcoding in molecular taxonomy and forensics, these methods are a double-edged sword, since universal primers may unintentionally amplify nuclear mitochondrial DNA (numt) and hinder the identification process. Among mammals, numts are particularly prevalent in the genome of primates (Mundy et al. 2000, Soto-Calderón et al. 2012, Dayama et al. 2020). Also, given the rapid degradation rate of mitochondrial DNA in comparison to its nuclear counterpart in hair, feces, and preserved skins (Berger et al. 2001, Foran 2006, Soto-Calderón et al. 2009), these DNA sources are more prone to amplification of numts in primates than blood or soft tissues (Clifford et al. 2004, Soto-Calderón et al. 2012), thus requiring the implementation of protocols to either prevent or discern the amplification of numts. Several strategies encompass careful design of primers and identification of nonsense or frameshift mutations in presumed mitochondrial coding sequences or unexpectedly long branches in a mitochondrial phylogeny (Anthony et al. 2007, Song et al. 2008).

2.3.3. Inference of geographic origins. Unlike species identification, tracing the geographic origin of a sample or individual requires the construction of a genetic/genotype reference database (GRDB) of the species in question across its distribution range, with sufficient representativity and power to discriminate among geographic regions. By analyzing the DNA sequences of the mitochondrial control region, Gani et al. (2021) determined the subspecies and origin of 12 captive specimens of *Hylobates lar* and Clifford et al. (2004) discriminated between northern and southern populations of lowland gorillas. However, to date the most widely used markers for genetic assignment are STRs, which have been applied to numerous taxa such as macaws (Presti et al. 2015), African elephants (Wasser et al. 2022), chimpanzees (Ghobrial et al. 2010), and howler monkeys (Oklander et al. 2020).

Although recent advances in HTS have allowed STR markers to be identified relatively quickly and cost efficiently (De Barba et al. 2017, Roy et al. 2021, Alves et al. 2022), they were traditionally developed by constructing expensive and time-consuming enriched genomic libraries (Muniz & Vigilant 2008), which represent a limitation for most primate habitat countries (Di Rocco & Anello 2021). Once a panel of STRs is isolated for one primate species, polymorphisms can be tested for use in closely related species (Arandjelovic & Vigilant 2018). Reference databases have been constructed, for example, for *Pan* (Gonder et al. 2011), *Oedipomidas* (Acevedo-Garcés et al. 2021), *Gorilla* (Arandjelovic et al. 2010), macaques (Zhou et al. 2023), and gibbons (Kheng et al. 2018). In several cases, they have been used to assign the geographic origin of specimens either trafficked or internationally traded before the CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) was adopted in 1975 (Hvilsom et al. 2013, Soto-Calderón et al. 2015, Oklander et al. 2020, McDonald et al. 2023). One example is the use of a reference STR database to discern different management units and estimate the origin of 22 confiscated specimens of the South American howler monkey *Alouatta caraya*, the most commonly trafficked primate species in Argentina (Oklander et al. 2020). The authors of this study found that the assigned origins of most confiscated individuals were primarily areas around the Argentina–Paraguay border (near northeastern Argentina's largest cities, Chaco and Corrientes) and National Highway 12, which ends in Buenos Aires, where most confiscations

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occur. The illegal sale of *A. caraya* had previously been reported at several locations along this highway. This example illustrates how genetic analysis helps trace wildlife trafficking routes and hot spots, thus aiding in the planning and implementation of more effective control measures.

All of the above underscores the applications of genetic markers and databases as tools for detecting and combating the illegal trade in primates. Genetic analyses in forensic cases can reliably assess the effects of exploitation and the conservation needs of species, which would be otherwise impossible to determine. We encourage the production of high-quality genetic databases for all primate species to apply forensic DNA analysis in judicial cases in order to contribute to their conservation.

Evolutionarily significant unit (ESU): set of one or more populations of a given species with substantial genetic and adaptive differences that are considered a unique component of the species, usually for conservation purposes

2.4. Neutral Versus Adaptive Genetic Variation

Population genetic studies have historically relied on neutral or quasi-neutral molecular markers to estimate population parameters and understand demographic processes. The level of genetic differentiation and the shared demographic history between populations have been key in delimiting so-called evolutionarily significant units (ESUs) and prioritizing populations for conservation purposes (Moritz 1994, Crandall et al. 2000). However, more recent points of view highlight the importance of involving adaptive variation and functional genetics in the definition of ESUs, management units (MUs), and conservation units (CUs) (De Guia & Saitoh 2007, Palsbøll et al. 2007, Casacci et al. 2014). Even though the clear connections between functional genetic diversity and adaptation of wild populations to local environments (e.g., habitat type or infectious diseases) are only now being recognized, rapid advances in gene mapping and association studies in genetically distinct populations seem to finally be overcoming these obstacles. An interesting example is the recent genome scan of two subspecies of *Macaca mulatta* adapted to contrasting environments, which showed evidence of positive selection in genes involved in gluconeogenesis and response to starvation, as well as other genes related to cardiovascular function and response to environmental temperature (Liu et al. 2018). Likewise, polymorphisms in genes responsible for local adaptation to altitude have been found in several species of snub-nosed monkeys (*Rhinopithecus*) (Yu et al. 2016). Also, positive selection in cytokine receptors as a response to the simian immunodeficiency virus explains differences among chimpanzee subspecies distributed in contrasting environments (Schmidt et al. 2019).

Recent advances in genomics have allowed a better understanding of the connections between genotypes and phenotypes and of adaptive genetic processes overall, since neutral genetic diversity may not be always an accurate indicator of such phenomena (Kuang et al. 2023). These developments present a remarkable opportunity for future analyses of functional genetic variations associated with diseases and environmental changes, considering that adaptive challenges may also originate from recent effects of increased interaction with populations of humans and their pets, habitat disturbance, pollution, and climate change, affecting the types and quantity of available resources and the spatial patterns of parasite species (Graham et al. 2016, Estrada et al. 2017). Some pioneering studies in this area warn, for example, of a range expansion of parasites affecting lemurs in Madagascar (Barrett et al. 2013, De Winter et al. 2020, Marquès Gomila et al. 2023), including helminths (*Hymenolepis* spp. and *Trichuris* spp.), mites (*Schoutedenichia microcebi*), lice (*Lemurpediculus* spp.), and ticks (*Haemaphysalis lemuris*), highlighting both the importance of studying new interactions and the role of immunogenetics in the response of primate species to anthropogenic changes (Bradley & Lawler 2011, Larsen et al. 2014).

2.5. Life History Traits

Classic life history traits represent properties of organisms that are directly related to the two major components of fitness: survival and reproduction. In the literature, the term "life history

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trait" is often used interchangeably with fitness components; as a result, many phenotypic characters such as morphological, physiological, and behavioral traits with major effects on reproduction and survival have been called life history traits (Flatt & Heyland 2011).

Until recently, all existing knowledge about the life history traits and dispersal patterns of primates came from long-term observational studies. These studies offered insights into maternal kinship, reproductive success of females, and dispersal patterns by recording the entry or exit of individuals from groups in some species. However, these studies became possible only after years of continuous monitoring (Ross 1998, Strier 2008). Genetic analyses have only recently become feasible and can help confirm previously gathered observational data, in addition to providing information on male reproductive success, paternity, and paternal relatedness that is impossible to obtain through observation alone.

Since the early use of STRs, there has been a boom in studies on reproductive skew and extragroup mating. Initially, STRs developed for humans were used for phylogenetically close species, but as access to these markers improved, studies expanded to include a wide range of other species. Several authors have tested hypotheses on reproductive skew that, in general, demonstrated a positive correlation between high male rank and siring success [e.g., *Papio cynocephalus* (Altmann et al. 1996), *Pan troglodytes* (Constable et al. 2001), *Pan paniscus* (Gerloff et al. 1999), *Cercocebus torquatus* (Gust et al. 1998), *Semnopithecus entellus* (Launhardt et al. 2001), *Cebus capucinus* (Muniz et al. 2010), *A. caraya* (Oklander et al. 2014)], even in bonobos [*P. paniscus* (Mouginot et al. 2023)] and sifakas [*Propithecus verreauxi* (Kappeler & Schäffler 2008)]. Moreover, a recent reanalysis of male reproductive skew in 31 primate species (Ross et al. 2020) showed that a previously reported negative effect of group size on mating skew was an artifact (Kutsukake & Nunn 2006). However, a few studies suggest that reproductive skew may be greatly diminished in egalitarian species or those with weak hierarchies (Paul & Kuester 2004, Strier et al. 2011).

There are excellent reviews on the effect of kinship in primates and the application of molecular tools to study dispersal and kinship in primates (Strier 2008, Di Fiore 2009) highlighting the features of primate social systems that are intractable for researchers to study in the field. Patterns of dispersal and kinship among individuals in groups are intimately linked. If both females and males disperse when reaching sexual maturity (unbiased dispersal), then the groups will be composed of adults of both sexes who are not related to one another. If the males are the ones who disperse and the females have philopatric behavior (male-biased dispersal), when analyzing kinship relations, we find that females are related (mothers/daughters, sisters, half-sisters), because they have stayed in the group. In contrast, if the females are the dispersers (female-biased dispersal), then the males in the group will be related. Therefore, depending on dispersal, individuals are likely to spend a large portion of their adult lives in groups with or without close kin.

As mentioned above, the application of molecular studies is indispensable only for the estimation of male reproductive success and paternal relatedness, but it can also be a shortcut to deciphering these same traits in females, allowing much faster insights into genetic relatedness within and between groups and populations in comparison to long-term, multigenerational observational studies. However, when mapping behavior onto genetics, as in the influence of kin relationships in cooperative, affiliative, competitive, and/or aggressive behaviors, it is still necessary to carry out observational studies to recognize individuals and register behaviors (Chapais 2001, Smith 2014). Kin selection model studies have been tested in several primate species, showing notably mixed results (Grebe et al. 2022). This variation in results is often discussed on the basis of whether kin discrimination is possible, which is necessary for kin selection and inbreeding avoidance (Widdig 2007).

Life history traits and dispersal patterns are influenced by environmental changes, such as habitat loss and fragmentation (Boyle & Smith 2010, Carretero-Pinzón et al. 2016). Genetic

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studies are increasingly being used to register variation in these traits and the resulting inbreeding/outbreeding, comparing conserved and disturbed environments.

Inbreeding avoidance theory posits that relatives will avoid mating because inbreeding depression can reduce offspring fitness. Similar to other field studies on this topic, inbreeding avoidance research in primates has also yielded mixed results. Some studies claim that dispersion and death are sufficient mechanisms to prevent inbreeding. However, in cases where parents and their offspring live together for long periods of time, other mechanisms must be at play, as genetic studies in several species revealed avoidance of close kin in mate selection (Vigilant et al. 2015, Godoy et al. 2016, Chaves et al. 2023). Galezo et al. (2022) studied avoidance mechanisms in baboons and found strong evidence that mate choice promotes inbreeding avoidance in kin classes with relatedness greater than or equal to 0.25, with maternal kin being more effectively discriminative in undisturbed social groups. However, a social group living in anthropogenically disturbed habitat with reduced male dispersal exhibited inbreeding rates 10 times higher. In *A. caraya*, Oklander et al. (2010) found high genetic differentiation among groups in fragmented environments plus an incest event (a female mothered a son with her previous son), suggesting that increasing habitat fragmentation may have severely limited the group's dispersal ability. Together, these examples suggest that inbreeding avoidance mechanisms can be significantly affected by anthropogenic disturbance.

Outbreeding (exogamy): offspring of distantly related individuals such as those belonging to historically isolated populations, subspecies, or species

Inbreeding depression: reduced biological fitness resulting from inbreeding caused by a higher probability of homozygosity of heritable disease traits

Reviewing the bibliography for Platyrrhini, we found only 10 papers about variation in dispersal patterns between fragmented and continuous forests, and they covered only species exhibiting male-biased (*Cebus capucinus*; Fedigan & Jack 2001) and unbiased dispersal (*Alouatta* spp.; Van Belle & Estrada 2008, Oklander et al. 2010). These studies suggest that habitat fragmentation influences dispersal patterns. It seems that males continue to disperse regardless of habitat fragmentation while females modify their dispersal behavior. Further studies comparing populations in disturbed and undisturbed environments will shed light on the limits of plasticity and could be used to develop accurate management actions in disturbed primate populations.

With these examples, we aim to highlight the usefulness of molecular methods to detect inbreeding and dispersal history of groups and populations without long-term observations. Therefore, genetics can be more time efficient in some studies of life history traits than observational studies, although sampling logistics, the availability of laboratories for these analyses, and costs must always be taken into account.

2.6. In Situ and Ex Situ Management

Many primate populations worldwide are small and increasingly isolated in human-dominated landscapes. In this context, primate species may require management programs for their long-term conservation, which involve ex situ centers either for the rehabilitation of animals from trafficking or for reproduction programs (Gilbert & Soorae 2017, Pizzutto et al. 2021, Estrada & Garber 2022). This type of intensive management involves the joint work of rescue centers, scientists, and local or regional authorities and emphasizes the importance of a so-called one-plan approach conservation program linking in situ and ex situ efforts (Traylor-Holzer et al. 2019).

Ex situ populations of primates are small or dispersed in multiple facilities, making them prone to extinction due to demographic stochasticity and erosion of genetic diversity (Lande 1988, 1998). Given their small population sizes, the use of studbooks (family books) is key to recognizing family relationships (kinship), selecting potential breeders, and, in doing so, minimizing the probability of inbreeding depression and loss of genetic diversity (Ayala-Burbano et al. 2020, Muñoz-Lora et al. 2020). Molecular methods become essential to uncover the geographic origins of surrendered and confiscated animals that may increase the genetic diversity of ex situ populations (Witzenberger & Hochkirch 2011).

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Reintroduction: release of individuals inside their known or inferred historical distribution from which they have disappeared

Reinforcement: release of individuals into an existing population of conspecifics

Close proximity within and between species in animal enclosures, stress-induced immunosuppression, and introduction of specimens with genetic diseases may have serious epidemiological implications for ex situ populations, which demands the use of genetic and immunological methods for early diagnostics in primates and potential reservoirs, and decision making regarding the destination of affected animals. During the recent COVID-19 pandemic, molecular diagnosis revealed the transmission of the virus SARS-CoV-2 from humans to gorillas at the San Diego Zoo Safari Park (USDA APHIS 2021). Also, a recent analysis of gastrointestinal protists using a real-time polymerase chain reaction (quantitative PCR) approach in 10 species of nonhuman primates present at the Córdoba Zoo Conservation Centre in Spain revealed a wide variety of parasite species, in part due to the role of other reservoirs such as free-living rats (Köster et al. 2021). A notable case was the early detection of the callitrichid hepatitis virus in a group of tamarins held at the Smithsonian National Zoological Park in the United States that were to be released in Brazil, which halted the translocation and highlighted the potential pathogen spread following reintroduction programs (Anderson 1991).

Population reinforcement or reintroductions as conservation translocation practices are important strategies for threatened species but should require rigorous justification (Zlatanova 2015) and be part of a broader strategy that includes complementary efforts such as habitat restoration and education. In both types of translocations, conservation genetics can help identify the best release site on the basis of studies of previously assigned clusters or conservation units of the species in question.

The return of these animals to the wild has received strong support from the public. However, trafficked animals should ideally be reintroduced into the population they were extracted from or translocated to another suitable site within the species' original range. Detrimental consequences for the animal and/or the environment can result from returning individuals to natural habitats if decisions are not properly based on scientific evidence. Specifically with regard to genetics (without further elaboration into all the recommendations given by the IUCN for translocations), when significant genetic structure exists within a species, translocations of individuals to populations different from the population of origin may inadvertently lead to admixture of distinct evolutionary lineages and homogenize existing diversity and biogeographic patterns instead of protecting them.

For forensic studies, genetic assignment to a geographic area of origin is possible only when a suitable GRDB is available for a species with discrete clusters (e.g., ESUs, MUs, and CUs) identifiable by significant differences in allele frequency distributions and significant divergences in mitochondrial or nuclear loci (Moritz 1994). If a GRDB is available, analysis of individuals of unknown provenience can be performed to identify the probable locality or cluster to which they belong. If determined ahead of time, this identification would enable researchers to estimate the genetic diversity introduced into the environment before every translocation and/or reintroduction.

A recent study of *A. caraya* assigned its geographic origin after two translocation events (Oklander et al. 2020). The authors found that only 1 of the 12 individuals had been released into a site in its cluster of origin, resulting in the injection of genetic variation from animals belonging to different genetic clusters. In the second translocation, three out of five released individuals belonged to the same cluster; therefore, translocation of these animals also introduced nonlocal genetic variability, albeit in a lower proportion.

Furthermore, when reintroducing animals, it is crucial to know the genotypes of the founder individuals to monitor the success and long-term viability of the restored populations. Such studies have been carried out successfully in released apes (Goossens et al. 2002) as well as in a case of translocations and reintroductions of the lion tamarin *Leontopithecus rosalia* (Moraes

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et al. 2017) in the lowland Atlantic Forest. Moraes et al. (2017) recommend considering population genetic monitoring before and after management measures and maintaining population connectivity. These examples, and many others, show that genetic tools are necessary for in situ and ex situ programs in at least three settings: (*a*) identification of the most probable regions of origin of rescued individuals in order to determine the genetic suitability of potential populations to receive translocated individuals, (*b*) analyses of individuals in breeding programs to avoid reproduction between related animals, and (*c*) subsequent monitoring and evaluation of genetic parameters that guarantee a minimum population size and gene flow among the populations. With some exceptions (Strier et al. 2017), most biodiversity management and conservation plans and public policy have yet to incorporate genetic techniques into translocation policy and decisions (Torres-Florez et al. 2018). Genetics can provide valuable tools and the evidence-based science necessary for designing future conservation translocations.

Allelic dropout: biased amplification of one of the two alleles of a locus due to low DNA concentration, frequent in noninvasive samples

3. HOW DO WE ANALYZE PRIMATE CONSERVATION GENETICS?

Biologists, park rangers, and field naturalists should be encouraged to familiarize themselves with proper sample collection techniques, the potential scientific value of the samples, and the research opportunities they present, as well as to responsibly collect samples from their subjects in the field, whenever possible, in compliance with national law.

3.1. Sampling

Collection of tissue or blood that involves physical and/or chemical restraint is called invasive sampling. It usually causes stress to the animal and presents health risks, including injuries and zoonosis, and consequences for future behavior in the presence of humans (Pedersen & Davies 2009). Individuals can be captured with baited traps or darted with anesthetic or sedative drugs (Jolly et al. 2011). These procedures must be supervised by veterinary professionals, and personnel handling and sampling wildlife must comply with basic biosafety standards (Soto-Calderón et al. 2023). Ear tags, bracelets, or tattoos may be applied to the animals in order to recognize them for future studies and prevent resampling (Honess & Macdonald 2011).

Various types of samples that do not require animal restraint (noninvasive) have been explored for DNA analysis, including feces, hair, urine, and saliva (Constable et al. 2001, Inoue et al. 2007). Noninvasive approaches to sampling avoid capture of the animals, minimizing any undesirable behavioral or physical effect on both the animal and the collector. Feces are the most popular noninvasive sample type, and in some cases trained dogs can be used to locate them (Arandjelovic & Vigilant 2018). The advantage of fecal sampling is that it can generally be performed during monitoring, ensuring host identification and sample freshness. Gloves and a mask must always be worn when collecting samples in order to avoid contaminating them with the collector's DNA (humans are primates, and the sequences sought are very likely to also amplify our own DNA).

In recent decades, noninvasive genetic studies from feces have revolutionized our understanding of primate evolution, population structure, phylogeography, and behavior. Fecal samples contain low host DNA concentrations, which are mixed with other DNA sources (food, intestinal bacteria and parasites, environmental organisms) and therefore are prone to genotyping errors such as allelic dropout (i.e., random amplification of only one allele) that result in false homozygosity (Johnson & Haydon 2007). Pilot studies are recommended to estimate the error rate, and several amplifications are needed to obtain reliable genotypes (Taberlet et al. 1996, Arandjelovic et al. 2009) (**Table 1**).

Another source of noninvasive DNA is saliva, which has been collected from chewed plants dropped by mountain gorillas (Smiley et al. 2010). DNA has also been recovered from saliva

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Table 1 Blood and tissue versus fecal samples

Blood/tissue	Feces
Invasive	Noninvasive
Expensive and logistically complex	Opportunistic and inexpensive
Directly assigned to a specific animal	Assignment is possible during monitoring, but if feces are collected from the ground or with dogs, individual identification is not possible
No PCR inhibitors	Presence of PCR inhibitors in soil and diet content
High DNA integrity and concentration	Low DNA integrity and concentration; rapid degradation
High PCR success	Low PCR success, error-prone genotyping
Idoneous for genetic and genomic methods	Suitable for short sequences (e.g., STRs, COI, CytB, Sanger sequencing, metagenomics of microbiomes and diet content)

Abbreviations: CytB, cytochrome b; COI, cytochrome oxidase subunit I; PCR, polymerase chain reaction; STRs, short tandem repeats.

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in groups of habituated Tibetan macaques using devices specially designed for this purpose and placed in trees (Simons et al. 2012).

3.2. Preservation of Samples

Both quality samples (blood or tissue) and noninvasive samples (such as feces) undergo a degradation process in which enzymes called nucleases cut DNA into smaller fragments. Enzyme activity increases in humid and high-temperature environments. In fecal samples, the more time passes between defecation and collection of the material, the greater the degradation suffered by the sample will be. The sooner the sample is collected, the higher the quality of the DNA will be. There is substantial literature regarding storage methods, especially for noninvasive samples [cryopreservation (Mazur 1970), commercial kits (Graham et al. 2008, Duval et al. 2010), RNAlater (Michaud & Foran 2011, Camacho-Sanchez et al. 2013), and specifically for stool (Morin et al. 2001, Nsubuga et al. 2004, Oklander et al. 2004, Ramón-Laca et al. 2015)].

3.3. DNA Extraction

Extraction methods depend on the type of sample. Tissue and blood samples can be extracted with different combinations of solvents (Chelex, PK-SDS/phenol/chloroform, CTAB/chloroform; Green & Sambrook 2012), although commercial kits are also available. On the other hand, most studies using DNA from fecal samples employed mostly one kit: the QIAamp® DNA Stool Kit by Qiagen (Morin et al. 2001, Muniz & Vigilant 2008, Van Belle et al. 2012). These studies usually introduced minimal modifications to the kit's protocol to optimize the extraction.

The advantages of these kits are their rapid, high-quality purification of DNA and that they generally completely remove contaminants and inhibitors. The disadvantages are their high cost and the delays and complications that arise in the importation of these reagents to low- and middle-income countries. In all cases, it is important that DNA extraction reactions include negative controls and that appropriate precautions be taken to avoid contamination (or cross-contamination) of the samples.

3.4. Selection of Markers

Primates are diploid, meaning that they have two copies of each DNA segment (except sex chromosomes). As an analogy, consider the genome (complete collection of DNA) as a library, where the chromosomes are the books and the genes or loci are the phrases within the books. Until very recently, it was impossible to study the entire genome, and even today it is extremely expensive both financially and computationally. Therefore, most analyses consist of using PCR to

Table 2 Comparison of molecular markers and high-throughput sequencing

Mitochondrial DNA	Short tandem repeats	High-throughput sequencing
No need for previous knowledge of the genome sequence	Require isolation/characterization of locus-specific polymorphic sequences	Reference genomes may be necessary to assemble and facilitate resequencing
Requires training to read and edit sequence data	Allow individual identification (genetic fingerprint)	Chips are available for model species (e.g., apes and macaques)
Straightforward analysis methods	Require cross-laboratory standardization of allele sizes	Relatively few wet lab experiments
Suitable for small or large sample sizes	Require training to read and interpret raw data profiles	Bioinformatics knowledge is required to clean and consolidate data
Feasible with noninvasive samples	Straightforward analysis methods	Cost effective for large sample sizes
	High risk of allelic dropout in samples with low DNA quantity	Not easily achievable with noninvasive samples
	Suitable for small or large sample sizes	
	Feasible with noninvasive samples	

copy these "phrases" or markers of interest so many times that the rest of the DNA becomes negligible. This technique is performed similarly to DNA extraction with negative controls and requires extreme care to avoid contamination. To make these copies, it is necessary to know the flanking sequences of the locus of interest, known as initiators or primers. PCR products (either by size or by sequence variation) can then be determined using automated sequencers. Depending on the question we want to answer, we can select different polymorphic sites. Various techniques have evolved from cytogenetics to recent HTS to obtain information from the entire genome (**Table 2**). The best known are markers in the nuclear DNA (amplified fragment length polymorphism, STRs, single-nucleotide polymorphisms), mitochondrial DNA (maternal lineage tracing), Y chromosome (paternal lineage tracing), and genomic data (RADSeq, ultraconserved elements).

4. WHAT HAVE WE DONE SO FAR?

We searched Scopus to compile articles, reviews, and book chapters published between January 2001 and October 2023 to identify trends in the use of genetics and genomics to diagnose and solve problems directly or indirectly related to conservation or population management of primates. We restricted our search to the title, abstract, and keywords using the terms (conservation AND genetic*) OR (conservation AND genomic*) AND primate*. We excluded biomedical research and molecular and chromosomal evolutionary studies, unless applied to adaptation, conservation, or ecology; we included genetic and genomic studies at the population level in molecular taxonomy and systematics, parasite diagnosis, adaptation, design of molecular methods, and microbiome and diet with direct or indirect applications in conservation and management. Despite this systematic search, we may have missed publications lacking any of the keywords in the original search (e.g., primate*); therefore, our results represent a subset of genetic studies designed to address conservation questions. Genetic analyses of topics such as paternity, mate choice, or dispersal have direct implications for conservation and management but may not have been identified by our search criteria. The authors of the publications were identified by continent, defined as Africa, Asia, Europe, North America, and Neotropical America (South and Central America and Mexico). We classified Turkey as part of Europe.

The search yielded 1,406 documents, but only 395 of them met the search criteria (see the **Supplemental Material**). These studies were conducted on multiple genera (27%) or 1 of 56 different genera (73%). The most represented (>3%) were *Macaca*, from in situ and ex situ locations;

Supplemental Material >

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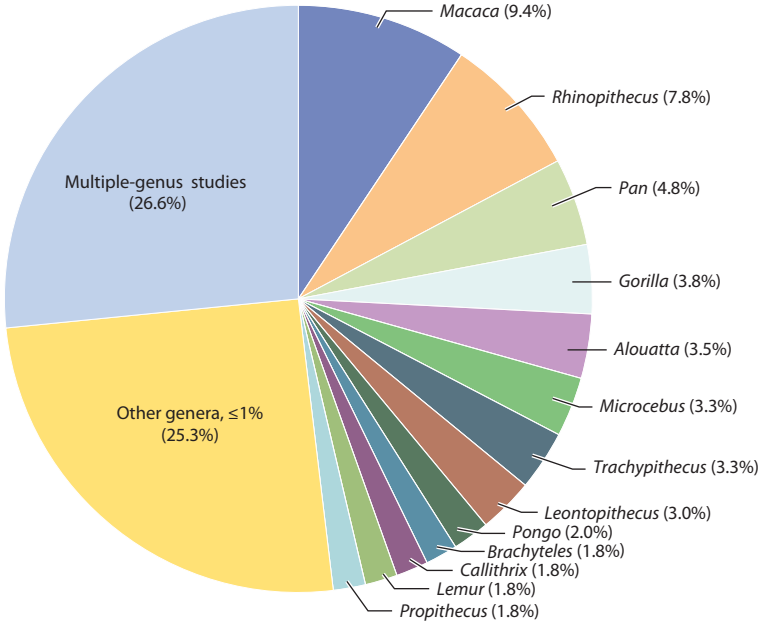

Figure 1

Proportion of 395 studies (articles, book chapters, and reviews) in primate conservation genetics retrieved from the SCOPUS database for the period January 2001 to October 2023, aimed at multiple or single genera. "Other genera" refers to genera covered by 1% or fewer of the total number of studies collapsed into one group.

Rhinopithecus and *Trachypithecus* from Southeast Asia; the great apes *Pan* and *Gorilla* from Central Africa; the South and Central American *Alouatta* and *Leontopithecus*; and the lemur *Microcebus* from Madagascar (**Figure 1**).

The authors of the studies were located in 76 countries. The most-represented habitat countries (>1%) were China (8.9%), Brazil (5.7%), Madagascar (2,5%), Argentina (1.5%), Uganda (1.3%), Colombia (1.3%), Malaysia (1.2%), Indonesia (1.2%), and South Africa (1.1%) (**Figure 2**). Authors from Europe and North America led or collaborated on most of the studies (67.1% and 56.7%, respectively), even though those regions are not within the original distribution range of extant nonhuman primates. These regions were followed by Asia, Africa, and Neotropical America (38.7%, 24.8%, and 23.8%, respectively). Only 3% of the studies had authors from Oceania or undefined regions. English was by far the dominant language (97.7%), followed by Chinese (2.0%) and Spanish (0.3%).

The 395 studies deal with nine different topics or combinations thereof:

- Genetic diversity and structure: variability in in situ and ex situ populations, delimitation of evolutionary and management units, parentage and relatedness, demographic processes (population sizes and migration), response to fragmentation and loss of habitats, and response to exploitation and hunting.
- Taxonomy and phylogenetics: identification and diagnosis of cryptic species, description of new genera, promotion of subspecies to species, and delimiting distribution ranges of taxa and species.
- Chromosome studies: recognition of sex determination systems, species identification, aneuploidy diagnosis and assessment of chromosomal signatures of hybridization.

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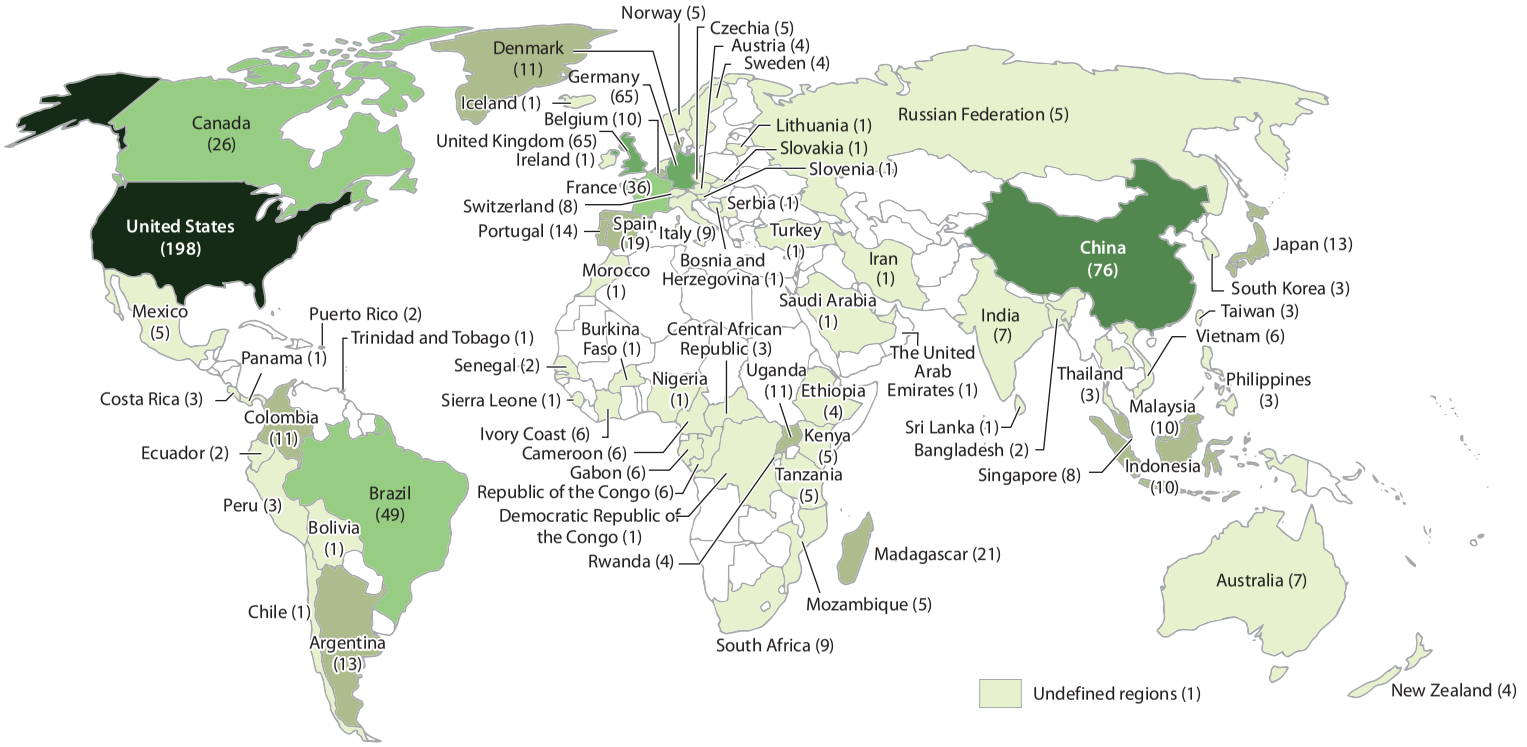

Figure 2

World map depicting the countries where 846 authors of 395 studies (articles, book chapters, and reviews) in primate conservation genetics and published between January 2001 and October 2023 are located.

- Microbiomes and diet: description of gastrointestinal microbiome communities mostly using genomic response to stress, diet, contact with humans and captivity, and feeding habits and their relationship to habitat disturbance. One study assessed the vaginal microbiome in relation to age and reproductive cycle.
- Functional genetics: local adaptation, response to climate change, *CD94* gene, major histocompatibility complex genes, epigenetics (methylation) of aging, expression of small interfering RNAs, regulation of gene expression, antimicrobial resistance genes, deleterious mutations (cystic fibrosis in orangutans, cardiomyopathy in bonobos, mitochondriopathies, cancer, and cases of inbreeding depression), and genetic implications of climate change.
- Tools: genetic databases, sampling methods (noninvasive samples, ancient DNA), types of genetic/genomic data (STRs, major histocompatibility complex, single-nucleotide polymorphisms), and analytical methods.
- Landscape genetics: addressing the problem of dispersal and functional connectivity in various habitats including flooded landscapes, fragmented forests, and agricultural land, and identification of priority areas for restoration or landscape features relevant for conservation.
- Parasite–primate interactions: Studies in primate virology represent approximately a third of all studies on this topic, followed by studies of unicellular or multicellular parasites. This area encompasses reports of molecular detection of parasite infections, genetic characterization of parasites, resistance genes in the host, and the impact of infections on the viability of the host.
- Hybridization: recognition of hybridization and genetic introgression. Several events correspond to historical natural hybridization, whereas others are recent and derive from anthropic factors.

5. FUTURE RESEARCH AND CHALLENGES

The last decade has witnessed a dramatic increase in the availability of genetic information (Bradley & Lawler 2011, Kuderna et al. 2023). Such information can help diagnose genetic diseases in wildlife, major challenges of which are identifying candidate genes under selection and understanding the impact of deleterious mutations on the viability of populations. Recent technological advances have even drawn attention to the ethical aspects of using cloning or genome-editing tools (such as CRISPR-Cas9) to fix deleterious mutations as a means to safeguard threatened species from extinction (Johnson et al. 2016, Desalle & Amato 2017).

The insights gained from future research in genetic diversity, genetic susceptibility to disease, and genetic response to climate change can be integrated into assessments of species' conservation status. A growing area of research is landscape genetics, which has been tremendously useful in understanding the impact of habitat loss and fragmentation (Montero et al. 2019, Westphal et al. 2021).

The recent development and adoption of HTS technologies have had a moderate impact on primatological studies as a result of the difficulty of obtaining high-quality samples that can only be obtained invasively. As discussed above, noninvasive samples represent a challenge not only for locus-specific analyses but also for genomic analyses with massively parallel sequencing. For example, fecal DNA would produce only a small proportion of reads that match the host genome, although it is possible to enrich host cells before sequencing (Chiou & Bergey 2018). Even though such analyses have been performed in some cases (Snyder-Mackler et al. 2016, Hernandez-Rodriguez et al. 2018), in order for them to be used systematically on a population scale, an improvement in technology and a substantial reduction in cost would be necessary (Arandjelovic & Vigilant 2018).

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Our literature review revealed that conservation genetics research on primates is geographically biased, with most studies conducted or led by institutions and researchers in nonhabitat countries, and that genetic data have not been fully integrated into conservation policies. These observations highlight the importance of transnational collaboration for capacity building, engaging in financial and human resources, creating and provisioning of research facilities in habitat countries, integrating the conservation of victims of international trafficking with ex situ populations in nonnative countries, and facilitating import/export permits of samples and research supplies (Muñoz-Lora et al. 2020).

The gap between conservation literature and practice has delayed the resolution of the pressing issues mentioned in the first section of this review. A possible explanation for this disconnect is that knowledge gained from scientific research is not often effectively communicated to those with the power to formulate and enact policies. We need greater knowledge of the usefulness of genetic tools to fight trafficking and the relevance of genetic attributes of populations in conservation and management decisions by governmental and nongovernmental stakeholders. Therefore, finding common ground between stakeholders and researchers is key to integrating scientific research into decision-making. Finally, more scientists must be trained in the use, interpretation, and integration of genetic/genomic research in the development of conservation strategies.

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