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Published in:
Diversity

DOI:
[10.3390/d13110521](https://doi.org/10.3390/d13110521)

Published: 01/11/2021

Document Version
Publisher's PDF, also known as Version of record

[Link to publication](#)

Citation for published version (APA):

Olah, G., Smith, B. T., Joseph, L., Banks, S. C., & Heinsohn, R. (2021). Advancing genetic methods in the study of parrot biology and conservation. *Diversity*, 13(11), 1-22. [521]. <https://doi.org/10.3390/d13110521>

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Review

Advancing Genetic Methods in the Study of Parrot Biology and Conservation

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Abstract: Parrots (Psittaciformes) are a well-studied, diverse group of birds distributed mainly in tropical and subtropical regions. Today, one-third of their species face extinction, mainly due to anthropogenic threats. Emerging tools in genetics have made major contributions to understanding basic and applied aspects of parrot biology in the wild and in captivity. In this review, we show how genetic methods have transformed the study of parrots by summarising important milestones in the advances of genetics and their implementations in research on parrots. We describe how genetics helped to further knowledge in specific research fields with a wide array of examples from the literature that address the conservation significance of (1) deeper phylogeny and historical biogeography; (2) species- and genus-level systematics and taxonomy; (3) conservation genetics and genomics; (4) behavioural ecology; (5) molecular ecology and landscape genetics; and (6) museomics and historical DNA. Finally, we highlight knowledge gaps to inform future genomic research on parrots. Our review shows that the application of genetic techniques to the study of parrot biology has far-reaching implications for addressing diverse research aims in a highly threatened and charismatic clade of birds.

Keywords: Psittaciformes; conservation genetics; ecology; evolution; genomics; museomics



Citation: Olah, G.; Smith, B.T.; Joseph, L.; Banks, S.C.; Heinsohn, R. Advancing Genetic Methods in the Study of Parrot Biology and Conservation. *Diversity* **2021**, *13*, 521. <https://doi.org/10.3390/d13110521>

Academic Editors: José L. Tella, Guillermo Blanco and Martina Carrete

Received: 23 July 2021

Accepted: 9 October 2021

Published: 23 October 2021

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1. Introduction

The order of parrots (Psittaciformes) contains a diverse group of species distributed mainly in tropical and subtropical regions [1,2]. Around one third of the nearly 400 parrot species are threatened, and they are declining faster than other comparable groups of birds, making them one of the bird orders of greatest concern [3]. The most important threats affecting parrots are anthropogenic and include agricultural expansion, the wildlife trade, logging, climate change, and invasive alien species [3,4]. However, the relative importance of these threats differs geographically. In the Neotropics, agriculture is the greatest threat followed by the illegal pet trade and logging [5]. In the Afrotropics, the illicit wildlife trade has the biggest impact followed by agriculture and logging [3,6,7], and in the regions of Oceania and Indomalaya, logging and invasive species are the most critical threats to the survival of the endemic parrot species [8]. Some species have been introduced to regions outside their natural ranges, including cities worldwide [9], where they may be perceived as pests [10].

The discipline of genetics (using it in this review for all methods that include molecular analysis of DNA) has made a major contribution to understanding the natural world. With the advancement of new DNA sequencing technologies in the past two decades, genetic

research has been revolutionised and now has a wide range of applications to the field of biology and beyond. Genetics has contributed to the study of parrots in the wild and in captivity by helping to construct precise phylogenies [11,12], tracking the history of their early diversification [13], contributing important information at the population and individual levels to help conservation efforts [14–16], and revealing insights into their ecology and health [17,18]. Molecular genetic approaches have even been also used to further our understanding of long extinct parrot species [19–21]. Here, we review what has been learned through the use of different genetic methods applied to parrot studies in past decades and in the current era of genomics. The aim of this review is to provide a comprehensive overview of this field and highlight knowledge gaps to inform future genomic research on parrots.

2. Short History of Advances in Genetic Studies of Parrots

The word “genetic” was used for the first time in 1819 by Hungarian nobleman Imre Fesetics who formulated a number of rules of heredity [22], laying the groundwork for the discovery of Mendelian genetics in the mid-19th century [23]. However, the molecular background of these ground-breaking theories was unknown until the determination of the structure of the DNA molecule in 1953 [24], leading to deciphering of the genetic code and the central tenets of molecular biology [25]. The invention of the polymerase chain reaction (PCR; see Glossary) in 1983 enabled the amplification of DNA and revolutionised genetic research. Even though many bird studies made use of DNA fingerprinting from the late 1980s, molecular studies of wild parrots started more slowly.

The first scientific publications on parrot genetics used karyotypes and allozymes to study the chromosomal and protein evolution of parrots at the taxonomic levels of species, family, and order [26–29]. These were followed by molecular sexing with gel electrophoresis [30]. Then came the advent of mitochondrial DNA (mtDNA) analysis initially studied by enrichment and cloning, and later by sequencing of individual mitochondrial and nuclear genes (Sanger sequencing) eased by PCR technology. The initial research focus on parrots with these methods was on phylogeny and systematics [12,31,32] and then work increased on species-level taxonomy and phylogeographic scales [33–36].

Studies of detailed population structure and individual-based behaviour in wild populations of parrots began with the advent of DNA fingerprinting by **minisatellites**. Minisatellites (complex tandem repeat regions of DNA) were used, for instance, on the Burrowing Parrot *Cyanoliseus patagonus* [17], some macaw species [37–39], and in the Palm Cockatoo *Probosciger aterrimus* [40]. Later, the discovery of **microsatellite** genetic markers (simple sequence repeat) transformed the application of genetics to many biological research projects including parrot studies. The length of these markers can be measured precisely by capillary electrophoresis, providing a great advantage over the original fingerprinting methods of minisatellites visualised by gel electrophoresis. Various studies have identified and published species-specific microsatellites for parrots [41–47]. This advance resulted in important tools for a wide variety of genetic research via cross-species amplification to other parrot species. Microsatellites were mainly used for fine-scale studies of individuals including family relationships. For example, Klauke et al. [48,49] used these markers to report a cooperative breeding system, not widely known in parrots (e.g., [50]), and estimated fine-scale population structure in the recently discovered El Oro Parakeet *Pyrrhura orcesi*.

Early, or first-generation, sequencing technologies (e.g., Sanger sequencing) made it possible to read the genetic code of specific DNA sequences. Later, molecular genetic technology advanced and phased into the second- or **next-generation sequencing (NGS)** or genomics era. The massively parallel high-throughput feature (i.e., sequencing multiple fragments and individuals at once) of these new sequencing platforms pushed down the price of sequencing and sped up the process of whole **genome** sequencing. The first complete mitochondrial genome (mitogenome) of a parrot was published in 2004 for the Kākāpō *Strigops habroptila* [51], followed by many more (e.g., [52,53]). The first draft of a full parrot genome,

the Budgerigar *Melopsittacus undulatus*, was uploaded to the National Center for Biotechnology Information (NCBI) database in 2011 (www.ncbi.nlm.nih.gov/genome/10765; accessed on 16 October 2021). This was followed by the Puerto Rican Amazon *Amazona vittata* in 2012 [54], and the Scarlet Macaw *Ara macao* in 2013 [55]. Whole genome sequencing aided the discovery of new microsatellite markers, for example the Orange-bellied Parrot *Neophema chrysogaster* [56] and the Scarlet Macaw [44]. At the time of this publication, there are whole genomes available from second-generation technologies for 36 parrot species and complete mitochondrial genomes for 69 parrot species in the NCBI genome database (www.ncbi.nlm.nih.gov/genome; accessed on 19 July 2021). This is approximately 10% and 20% of parrot species for nuclear and mitochondrial genomes, respectively. Currently, the best available parrot genomes assembled at the chromosome level belong to the Budgerigar (61x coverage, scaffold N50 size of 104 Mb, annotated with 16,458 protein-coding genes; GenBank assembly accession: GCA_012275295.1), Kākāpō (76x, scaffold N50 = 83 Mb, 16,053 protein-coding genes; GCF_004027225.2), Blue-fronted Amazon *Amazona aestiva* (60x, scaffold N50 = 89 Mb; GCA_017639355.1), and Monk Parakeet *Myiopsitta monachus* (67x, scaffold N50 = 76 Mb; GCA_017639245.1). However, international consortia of scientists continue to sequence the genomes of many more species. The Genome 10K project aims to sequence the genomes of representatives from all genera of vertebrates [57]. The B10K project [58,59] and OpenWings Project (openwings.org) aim to sequence all extant bird species and understand their evolutionary histories and relationships.

NGS opened new research pathways to genome-wide association studies aimed at understanding the underlying genetic variants determining traits [60]. Microsatellite, mitochondrial, and multi-locus studies have transitioned into analyses of many more (sometimes thousands) polymorphic sites of **single nucleotide polymorphisms (SNPs)**, which are found throughout the coding- and non-coding parts of the genome, giving them a further advantage over microsatellites. SNPs can be generated in several ways. In restriction-site-associated DNA sequencing (RAD-seq), one or two restriction enzymes cut the genome at enzyme-specific restriction sites, and these fragments are then barcoded, filtered, and sequenced [61,62]. In sequence capture methods, oligonucleotide probes (baits) are designed to hybridise with specific regions of interest. These are then captured, barcoded, and enriched before sequencing [63]. For this technique, the sequences of interest need to be known (e.g., from a complete genome of the same or related species), or the baits can be generated by other techniques such as double-digest RAD-seq [64]. The sequencer generated data can then be analysed in different bioinformatic pipelines [65]. This more comprehensive sampling of the genome has enabled more detailed examination of signatures of selection and local adaptation on the genome [66]. Sequencing RNA shows which genes are being expressed (transcriptomics) and can have an important role in reintroductions by predicting the potential for local adaptation and tolerance capacity in the source population [67].

In the past decade, further advancements in genome sequencing technology have pushed the boundaries of data collection. For example, nanopore technology has enabled portable sequencers as small as a USB drive [68,69]. Of great help to parrot biologists interested in conducting genetic research in the field, these sequencers were shown to work even in harsh environments [70]. Parrots are notoriously hard to capture in the wild, so making use of non-invasive sampling methods (e.g., feathers, eggshells, faeces, or even residual saliva) with the new technologies will provide further advances [71–73]. Metagenomic and metabarcoding applications, where all DNA materials are extracted from environmental samples, allow bioinformatic pipelines to be used to find and match sequenced DNA of species with reference to online databases (e.g., NCBI GenBank, European Variation Archive). This way, the presence or absence of species can be detected in the environment, and abundance estimates might be derived in some cases [74,75], although this technique needs further development. One of the major limitations of current parrot genomes is that they were produced with short-read sequencing. These short-reads make genome assembly more challenging by causing genomes to be more fragmented (with smaller scaffold sizes)

and incomplete, and limit the accuracy of some downstream uses of genomic data (e.g., studying structural variants). The advent of long-read or third-generation sequencing technologies can produce reads greater than 10 Kb in length, which allow for the assembly of chromosomal-level genomes [76]. These advances still present challenges including high-cost, specialised bioinformatic expertise, and access to high-quality genetic samples (i.e., DNA samples with high molecular weight), but these limitations are likely to be overcome in the near future.

3. Research Fields

3.1. Deeper Phylogeny and Historical Biogeography

An obvious contribution of genetics to parrot research is the construction of an accurate molecular phylogeny of the group. The first compendium of DNA-based molecular systematics for all birds was published in 1990 and was based on DNA–DNA hybridization of the whole genome [77]. Early sequencing studies used only a handful of genes mainly from mtDNA to study the phylogenetic relationship among some species [78]. Later studies included DNA sequences of both mitochondrial and nuclear origin to gain better resolution within certain taxa, like the genera *Amazona* [79], *Forpus* [36], or the broad-tailed (platycercine) parrots [80–82] and cockatoos (Cacatuidae) [83]. Using more genes and eventually whole genome resequencing [84], phylogenomics helped to resolve previously conflicting relationships on the phylogenetic tree. A surprising higher level result showed that parrots are the sister group of passerines (Passeriformes) and that falcons (Falconidae) are the sister group of both [85]. This was later robustly confirmed by other studies [86–88]. One of the most complete recent phylogenies for parrots was published in 2018 using a 30-gene supermatrix (12 mitochondrial and 18 nuclear genes) and included 307 species [11]. This study highlighted that phylogeographic or population genetic studies were only available for about a third of the extant parrot species [11].

Phylogenetic data indicate that parrots originated from the southern supercontinent Gondwana [32,89–91], while the fossil record has been interpreted to indicate a northern origin [92]. Similarly, the time of the origin of parrots is under debate, where molecular dating is used in addition to the fossil record and biogeographic distributions [93]. Cretaceous origin, before the Cretaceous–Paleogene extinction event 66 million years ago (Mya), was proposed by an early study based on multilocus phylogeny and a splitting of New Zealand from Gondwana calibration [12]. Other studies based on three nuclear genes coupled with divergence dates from non-parrot bird fossil evidence also suggested dispersal from Australasia and Antarctica, but later in the Paleogene (66–23 Mya) period [13]; initial vicariance events (i.e., continental breakups) were followed by local radiations and crown group diversification around 58 Mya [94]. Taking into consideration the split between falcons and parrots/passerines (57–62 Mya), and between parrots and passerines (51.8–66.5 Mya), we note that current data suggest that parrot crown-group diversification probably happened in the early Oligocene, around 28–34 Mya [95].

There is consensus that the Strigopoidea superfamily (containing the New Zealand Kākā *Nestor meridionalis*, Kea *Nestor notabilis*, and Kākāpō) is sister to all other parrots, i.e., the clade containing Psittacoidea and Cacatuoidea [96]. Rheindt et al. [97] argued that within Strigopoidea the *Strigops* and *Nestor* lineages diverged probably ca. 28–29 Mya. This would have coincided with the potential Oligocene submergence of Zealandia when much of its landmass may have been fragmented into smaller islands, providing a setting for allopatric diversification [98]. Since their origination in the Neotropics, the Arini tribe diversified by early adaptive radiation, the rate of which has remained constant [99]. Constant diversification was also shown at a shallower phylogenetic scale in the Neotropical parrotlet genus *Forpus* over the past 5 Myr [36] but the pattern was dependent on how species were delimited. Also in the Neotropics, most of the speciation events in the genus *Aratinga* (*sensu lato*) occurred during the Pliocene (5.3–2.5 Mya) and Pleistocene (2.5–0.01 Mya), possibly related to climatic oscillations [100]. In what now comprises the genera *Pionopsitta* and *Pyrilia*, however, diversification was attributed more to geotectonic

events and river dynamics between 8.7 and 0.6 Mya than to glacial cycles [101,102]. A study on *Pionus* spp. (a genus occurring both in the Andes and the lowland Amazonian rainforest) showed that the elevation of mountains explained their disjunct diversification, while subsequent speciation within the mountains was linked to climatic oscillations and their effects on habitat change [103]. This was also confirmed with the other parrot species, implying a dynamic climatic history for South American biomes since the Pliocene [104]. With the increased availability of genetic datasets of parrots and other taxa with which they co-occur, it will be possible to directly test these proposed speciation hypotheses. Without genetics, it would have been impossible to reconstruct the historical biogeography of parrots. However, there are still many questions left about the exact routes and time of their early diversification, and the incongruency regarding the fossil record. With expanding detailed genomic data of parrot species, these questions might be better answered soon.

3.2. Species- and Genus-Level Systematics and Taxonomy

The species is the widely accepted default unit used for evaluating conservation status (e.g., in the IUCN Red List), hence defining species and resolving taxonomic uncertainties by genetic techniques is important for conservation [105]. Active speciation of parrots on islands is most readily evident in Australasia, as shown by the *Electus roratus* and *Trichoglossus haematodus* complexes [106]. In such cases of dynamic evolution, wider sampling and genetic data of finer resolution are often needed to resolve phylogenetic relationships [107]. The extinction of island-endemic parrot species and replacement by invasive alien species led to loss of phylogenetic diversity, but understanding these frameworks can aid conservation strategies to restore island ecosystem function [108].

In some parrots, the traditional taxonomy based on plumage might need some revision, as shown with a genetic study on amazon parrots in the Neotropics [109]. **Cryptic species** of parrots were suggested by genetic studies for various taxa, including the mealy amazons *Amazona* spp. (*A. farinosa*, *A. guatemalae*) in the Neotropics [110] and the ground parrots *Pezoporus* spp. (*P. wallicus*, *P. flaviventris*) in Australia [111]. The need to recognize subspecies within the Mulga Parrot *Psephotellus varius*, generally considered monotypic, was also evident from phylogeographic structure either side of a well-known biogeographic barrier in southern Australia in their mitogenomic diversity and genome-wide nuclear markers [112]. Notably in contrast, recognition of *Amazona gomezgarzai* by Silva et al. [113] has been roundly debunked by Escalante et al. [114].

Defining **management units (MUs)** within species also holds important merits for conservation [115], however a refinement to the original definition, which was framed in terms of allele frequency differentiation, would be to define MUs with reference to the management issue in question, such as identifying demographically independent units for population monitoring, or genetically differentiated units for mixed-source introductions. For example, a genetic study revealed cryptic diversity within the Bahama Amazon *Amazona leucocephala bahamensis* between populations living on two remote islands [116]. A study on the Blue-fronted Amazon suggested treating its two subspecies as separate MUs [33], and a recent study argued for MU consideration for the Atlantic Forest population of the Southern Mealy Amazon *Amazona farinosa farinosa* [117]. Similarly, another study on Military Macaws *Ara militaris* in Mexico proposed two MUs in the country based on genetic data [118]. In Africa, a study warned that a population of Grey Parrot *Psittacus erithacus* living on Príncipe Island, São Tome and Príncipe, should be treated as an independent MU from the continental African populations, given their evolutionary dynamics and heavy local poaching pressure [119]. The Cape Parrot *Poicephalus robustus* was previously considered to comprise three subspecies until a study using multilocus DNA analyses concluded that *P. r. robustus* diverged from *P. r. suahelicus* and *P. r. fuscicollis* around 2.4 Mya [120]. Accordingly, it is now usually treated as a monotypic species *P. robustus* and has been uplisted to Vulnerable by the IUCN Red List, while the other two subspecies now form the Brown-necked Parrot *P. fuscicollis* complex of Least Concern (e.g., [121–123]).

Evolutionarily significant units (ESUs) are independently evolving units of genetic variation [115]. These units were proposed for the two subspecies of the Orange-fronted Parakeet *Eupsittula canicularis* in Mexico [124]. A comprehensive genetic analysis (using genome-wide SNPs and mitochondrial data) of the Red-tailed Black-Cockatoo *Calyptrorhynchus banksii* identified five ESUs over their large distribution, and advised taxonomic reassessments including recognition of a new subspecies [125]. Distinctions between ESUs and MUs were made during a genetic assessment of Major Mitchell's Cockatoo *Lophochroa leadbeateri* [126]. An analysis employing mtDNA and microsatellite data failed to detect genetic evidence for the two subspecies of Kākā in New Zealand, instead it is hypothesised that phenotypic diversity was due to an adaptive latitudinal size cline consistent with Bergmann's rule [127], an important consideration for possible translocation attempts. In contrast, another study using similar genetic evidence argued that the current genetic clusters of Kea should not be considered as independent conservation units because the structure evolved through very recent postglacial recolonisation processes [128]. In these and similar cases, appropriate taxonomic rank is debatable, but conservation and management units can be assigned where appropriate. Again, as shown with the example studies, these units of conservation can only be revealed with the help of genetic studies, which also have an ever-growing role in defining taxonomic units.

3.3. Conservation Genetics and Genomics

Conservation genetics is an interdisciplinary science dealing with the genetic factors affecting extinction risk of species and how to minimise these risks [129]. It is transitioning into using genomic techniques [66]. In the previous section, we discussed the importance of phylogeny to conservation. Here, we provide an overview of other major areas where the transition to genomics has contributed to the conservation of parrots.

Preventing the loss of **genetic diversity** is an essential aim of any conservation project. Genetic monitoring can provide important tools to quantify this diversity before, during, or after management efforts on threatened parrot species or populations [130,131]. In small remaining populations of species, diversity can be lost due to **genetic drift**, which can override natural selection [132]. Intensive management restored the Echo Parakeet *Psittacula echo* population from 20 remaining individuals in 1987. Genetic research showed that re-distribution of genetic material among its populations has reduced the likelihood of losing private alleles that could otherwise be lost due to the random effect of genetic drift in small, isolated populations [16]. On the island of Tasmania and its own offshore islands, a study of the migratory Swift Parrot *Lathamus discolor* could not detect genetic differentiation among breeding populations in consecutive years and across multiple islands [133]. Genetic estimations were used to calculate the **effective population size** of their single, panmictic population, and after combining it with demographic data, the study calculated a potential contemporary population size as low as 300 individuals [134].

Contemporary population fragmentation due to anthropogenic factors can lead to reduction in **gene flow** among the fragments resulting in genetic structure detectable via genetic testing. It is important to detect early signs of genetic fragmentation as it could lead to loss of genetic diversity and eventually to inbreeding. However, these effects take time, depending on habitat corridors, migration rates, and the mobility, dispersal, and lifespan of the species. For instance, at least a 35-year-long lag was shown between deforestation in the Brazilian Cerrado biome and changes in the genetic structure of Goias Parakeet *Pyrrhura pyrrhura* populations [135], corresponding to about five generations of the species. Genetic structure was also found in the Scarlet Macaw in the highly fragmented landscape of Costa Rica [136]. Historical population structure can also have important implications for present day conservation efforts. A broader genetic analysis of the Scarlet Macaw for instance suggested a distinct conservation unit for its Central American subspecies *A. m. cyanoptera* [137]. A population genetic study on the Palm Cockatoo on Cape York Peninsula, Australia found genetic differences among the studied populations, probably due to a mountain barrier [138]. Incorporating this population genetic data, especially

the connectivity between populations, into a **population viability analysis (PVA)** model predicted that dispersal between populations is not enough to buffer decline given their extremely low breeding success. The study concluded that Palm Cockatoos in Australia should be uplisted from Vulnerable to Endangered [139].

Genetic studies can have an important role in *ex situ* conservation management of threatened species to avoid **inbreeding** and to maintain maximum genetic diversity among captive individuals. Genetic testing can accurately identify relatedness among birds, which can be useful for the mixing of breeding pairs as demonstrated by *Amazona* parrots [140]. However, in socially monogamous species like parrots, natural mate choice can result in higher reproductive success than forced choice based solely on genetics [141], as shown for Cockatiels *Nymphicus hollandicus* [142], where pairs with higher behavioural compatibility were better parents [143]. The effect of **inbreeding depression** was first explicitly studied in parrots with respect to clutch size of captive budgerigars in the 1980s [144]. It has been used to guide the Puerto Rican Amazon recovery program through genetic fingerprinting since the 1990s [14]. Low levels of inbreeding were detected for the Red-tailed Amazon *Amazona brasiliensis*, indicating that more direct threats, like habitat destruction and illegal wildlife trade, should be the focus of conservation efforts [145]. Genetics has also helped to identify the pedigrees of the remaining Kākāpō population *in situ* [15] and inform conservation strategies [146]. It can also detect signs of genetic adaptation to captivity, which can have negative effects on reintroduction success. A recent genetic study on wild and captive populations of Blue-throated Macaws *Ara glaucogularis* and Thick-billed Parrots *Rhynchopsitta pachyrhyncha* highlighted the need for both *in situ* and *ex situ* conservation strategies [147].

Establishing captive populations of endangered species is often used by conservation management programmes. However, rapid genetic adaptation to captivity (within a few generations), low founder diversity, and potential inbreeding are of concern for future recovery goals, but these have been rarely studied in parrots. A captive population of Orange-bellied Parrots was founded in 1985 and later supplemented with wild individuals. A recent study found low diversity in their toll-like receptors (TLR), partially responsible for the innate immune response and so the first line of defence against pathogens, highlighting that they might be unable to adapt to novel disease outbreaks [148]. For instance, a spillover of beak and feather disease virus (BFDV) to the remaining wild population almost wiped out the entire species [149]. The psittacine beak and feather disease (PBFD) was first reported on Red-rumped Parrots *Psephotus haematonotus* in 1907 near Adelaide, Australia [150]. BFDV was isolated and characterised much later from cockatoos [151]. PCR tests were developed for the detection of BFDV [152,153], helping to identify cases in psittacines. A recent study provides an excellent overview of the ecology of PBFD in parrots and highlights the importance of mitigating its effects on threatened parrot species [18]. BFDV is also an ongoing threat to many other Australian parrot species [154]. Another study, using SNP data of the wild and captive populations of the Orange-bellied Parrot, showed that their genetic diversity could be retained in the captive population [155], possibly improving their health for future reintroductions. Retaining diversity at the major histocompatibility complex (MHC) is also important, as it is responsible for the adaptive immune response in birds and other vertebrates [156]. However, the MHC has been studied in only a handful of parrot species, including the Budgerigar [157], the Green-rumped Parrotlet *Forpus passerinus* [158], and the Red-crowned Parakeet *Cyanoramphus novaezelandiae* [159].

Outbreeding depression occurs when distinct species hybridise or isolated populations of the same species are mixed and the results are adverse [160]. One proposed underlying mechanism is that species have coadapted gene complexes nearby on the same chromosomes and that recombination during hybridization disrupts their adaptive functions [161]. Alternatively, outbreeding depression is likely to be rare and its effects restricted to the first few generations of crossing among evolutionarily diverged lineages [162]. Around 8% of parrot species have been recorded to hybridise in the wild [163]

and almost half of all parrot species have been reported to hybridise in captivity [164]. Genetic screening of the last remaining population of the Critically Endangered Forbes' Parakeet *Cyanoramphus forbesi* helped to determine the magnitude of hybridisation with the Chatham Island Red-crowned Parakeet *C. novaezelandiae chathamensis* and to identify cryptic hybrids [165]. A complex hybrid zone was studied involving the phenotypically distinct non-sister species Pale-headed Rosella *Platycercus adscitus* and Eastern Rosella *P. eximius*, and showed a lack of post-zygotic barriers to gene flow between these species [166]. The last remaining male individual of the Spix's Macaw *Cyanopsitta spixii* was breeding with a Blue-winged Macaw *Primolius maracana* and genetic sequencing showed that the resultant embryo was indeed a hybrid of the two species, but it never hatched [167].

Molecular genetic techniques can be applied in **wildlife forensic** investigations. Molecular genotyping helped Australian authorities to match DNA extracted from eggshells found in the wild to a nestling of Red-tailed Black-Cockatoo at a nearby property [168]. During the investigation, forensic scientists concluded that the nestling was hatched from the eggshell recovered from a tree hollow and this led to a criminal conviction. In another case, eggs were seized from an alleged trafficker arriving in Australia. Comparing the extracted mtDNA to the genetic database of the NCBI, researchers identified several threatened parrot and cockatoo species, and the smuggler was prosecuted [169]. Poachers were also arrested in Brazil intending to fly to Europe, one in 2003 with avian eggs later identified by molecular genetic techniques as of parrots and owls [170], and another in 2018 with eggs identified as of Short-tailed Parrot *Graydidascalus brachyurus* [171]. Ewart et al. [126] developed a forensic test with 20 nuclear SNPs for the Major Mitchell's Cockatoo and demonstrated its application for subspecies identification. A similar toolkit combining various forensic techniques was developed earlier for the Glossy Black-Cockatoo *Calyptorhynchus lathami* [172]. A set of microsatellites were developed in the Cape Parrot with sufficient discriminatory power to distinguish captive versus wild birds via parentage analyses [173], and similar markers proved to be successful in determining the geographic origin of a captive individual of Military Macaw [174]. The control regions of mtDNA of Blue-and-yellow Macaws *Ara ararauna* confiscated from the illegal wildlife trade in Brazil were sequenced and compared to reference sequences of the species, in order to find their provenance and advise on reintroduction planning [175].

3.4. Behavioural Ecology

Genetic techniques have revealed many interesting aspects of behaviour in parrots. Wirthlin et al. [176] looked at the genomic basis of high cognitive abilities, vocal communication, and longevity in parrots by generating an annotated genome for the Blue-fronted Amazon and comparing it to 30 other bird species. They discovered new lifespan-influencing genes, parrot-specific genes critical for brain function, and even indications of convergent evolution of cognition relative to changes in the human genome. Phylogenetic analysis was used to study another cognitive function of parrots, cerebral lateralisation, which is also closely linked to the development of human language [177]. This underpins the well-established behaviour in many parrot species of using the left foot for holding food [178,179], and which may have a fitness benefit deeply rooted in their evolutionary history. Similarly, Benavidez et al. [180] applied phylogenetic analyses to look at diet and range size of Neotropical parrots. They found that diet was independent of phylogenetic history and that range and body size explained diet composition.

Genetic evidence has been often used to reveal an unexpected diversity of breeding systems and individual dispersal patterns in parrots. Using DNA fingerprinting for paternity testing on parrots, Masello et al. [17] found that the Burrowing Parrot is an example of both social and genetic monogamy. This social structure was also shown to be the case for Palm Cockatoos reusing nests in Australia [40] and Blue-and-yellow Macaws in Brazil [181]. When mtDNA and nuclear microsatellite genetic markers were compared for the same species, the observed patterns were best explained by male-biased dispersal and female philopatry [182]. Through application of microsatellite genetic markers, Heinsohn

et al. [183] revealed cooperative polyandry and polygynandry in Eclectus Parrots *Eclectus roratus* in northern Australia. Another study showed remarkably similar cooperative polyandry in the Greater Vasa Parrot *Coracopsis vasa* in Madagascar [184].

A 6-year-long study incorporating genetic sampling of nestlings, eggshells, and adults of the Swift Parrot proved that their clutches had high levels (50%) of multiple paternity of the nestlings although the birds remained socially monogamous [185]. Molecular sexing showed that Swift Parrots have adaptive sex allocation with mothers biasing their early hatched nestlings towards males. This is interpreted to allow the males to get extra food and gain greater fitness when they later compete for rare females [186]. The study used population viability analysis to predict a dramatic decline in population size due to an introduced predator to Tasmania. Extra pair paternity was also confirmed in the Echo Parakeet in Mauritius [187]. In the Monk Parakeet, sexual monogamy was shown in their native and invasive sites [188], while a later study found evidence for extra pair paternity in their native range in Argentina and intra-brood parasitism at invasive sites [189]. A recent study on their breeding colonies showed fine-scale genetic structure, high breeding site fidelity, absence of inbreeding, and female-biased natal dispersal by genotyping individuals [190].

In Ecuador, breeding pairs of El Oro Parakeets have been shown to have helpers, whose genetic quality (measured as heterozygosity by microsatellite markers) increased reproductive success of the breeding pairs [49]. The above studies all questioned the widely held notion that parrots are monogamous, and instead showed that parrots have flexible mating systems. In both Eclectus Parrots and Swift Parrots, polyandry is believed to be a result of strong, male-biased adult sex ratios [183,185]. Conversely, it is unknown whether the similarly biased sex ratio in Glossy Black-Cockatoos on Kangaroo Island [191] is associated with polyandry.

A study examined the association between genetic structure and song culture in the Yellow-naped Amazon *Amazona auropalliata*. It found that the factors are not closely associated and that there is high, possibly female-biased gene flow across dialect boundaries [192,193]. There is little evidence that dialects in *Amazona* parrots would isolate populations, which would eventually generate genetic differences among the populations [194]. A recent study on these species showed that their call and genetic divergence did not correspond, which indicated that vocal dialects are not the best surrogates for genetic structure in lifelong local learners like *Amazona* parrots [117]. A study using SNP data of Palm Cockatoos found an association between the nuclear genomic structure of the populations and vocal dialect boundaries, however, these possibly originated from the separation of populations by mountains in the late-Quaternary [138]. In Budgerigars, their life-long vocal learning was found to be associated with the expression levels of specific transcription factors, hence their regulation seems to be essential for vocal mimicry [195,196]. Genetics will further our understanding of the mating system, song culture, and even cognitive abilities of parrots. So far only a handful of genetic studies have focused on these topics and implementing them to other parrot species could reveal important insights into the behavioural ecology of this diverse group.

3.5. Molecular Ecology and Landscape Genetics

Molecular ecology has illuminated the origin of some introduced parrot species, which has been recently reviewed [197]. For instance, Russello et al. [198] sequenced the mtDNA control regions of Monk Parakeet museum specimens from the species' native range and of individuals from their naturalised range in the United States. Their results confirmed that the geographic origins of the U.S. populations overlapped with past trapping records, so the naturalised populations possibly originated from the international pet trade whether from accidental or purposeful releases. A global study of their invasive populations also supported the pet trade hypothesis and observed low genetic diversity, indicating that invasiveness might not be linked to high genetic variation and the role of selection should be further investigated in allowing the birds to adapt to novel urban settings [199]. The

success of the Ring-necked Parakeet *Psittacula krameri* as an invasive species to Europe was also studied by determining the genetic origin of the invasive populations [200]. The study showed admixture between individuals from different origins and argued that morphological changes in the introduced parrots might be attributed to their rapid adaptation to European environments over the past 50 years.

Molecular techniques can be used to track individuals in the landscape using their genotype, analogous to telemetry studies. Termed genetic tagging, this technique has been applied to macaws in Peru using shed feathers in the landscape as the source of genetic material [201]. The study revealed how macaws used clay licks and it enabled group size estimates based on genetic capture-mark-recapture analysis [72]. Such non-invasive genetic sampling provides an important tool for studying wild parrot populations, negating the need to capture the birds [202].

Landscape ecology is an interdisciplinary science focusing on the ecological understanding of spatial heterogeneity. Incorporating genetic studies into landscape ecology can reveal the complexity of genetic structure compared to the simpler approach using comparisons of populations selected *a priori*. A landscape genetic study, applying the theory of electrical circuits and resistance surfaces, on Scarlet Macaw populations in Peru showed that outlying ridges of the Andes mountains can limit gene flow between populations [203]. Similar findings were made on the same species in Costa Rica [136]. In the Ecuadorian Andes, limited dispersal was found in the El Oro Parakeet in a fine-scale landscape genetic study [48]. The genetic divergence between populations was again attributed to geographic barriers. The authors argued that climate change might explain upslope movement of this already endangered species eventually leading to isolation of populations. Another study also used a landscape genetics approach to look at climatic and geographic effects on the genetic structure of the Burrowing Parrot in the Southern Andes [204], and revealed that climate (precipitation and temperature) indeed drove changes in their genetic structure.

In Australia, dispersal of Palm Cockatoos is inhibited by narrow corridors of rainforest habitat, the two major populations being poorly connected due to a mountain barrier [205]. In contrast, no geographical or ecological barriers were found for the Red-fronted Macaw *Ara rubrogenys* across inter-Andean valleys in Bolivia. This suggests that social factors might reinforce their philopatry-related genetic structure, as cliffs with nest sites are not continuously distributed across the landscape [206]. Landscape genetics was also used to study the historical and current distributions of the Crimson Rosella *Platycercus elegans* complex, showing that population expansion followed by secondary contact and hybridization might be responsible for their present genetic structure [207]. A recent study looked at functional genomic differences between the alpine Kea and the forest adapted Kākā in New Zealand, and showed that these adaptations are not driving the ecological differentiation between the two species [208].

Understanding the drivers of genetic structure of parrots in the natural environment can be important for understanding the impacts of anthropogenic and natural dispersal barriers and help guide decisions about important corridors for maintaining population connectivity and gene flow. Genetics at the landscape level also helps us to understand the environmental correlates of population boundaries, assign MUs, and inform better decisions on connectivity plans.

3.6. Museomics and Historical DNA

Museum collections are becoming increasingly important in genomic studies as they are repositories of genetic material from the past [209,210]. Using historical DNA (hDNA) of birds can be challenging but nevertheless offers important insights into their evolution, ecology, and conservation [211]. Museum samples have been used to study the subspecies- [212] and population-level structures [138] of the Palm Cockatoo in New Guinea and Australia, of the *Pezoporus* ground parrots [111], and of Red-tailed Black-Cockatoos and Major Mitchell's Cockatoos in Australia [125,126,213]. Jackson et al. [108] extracted mtDNA from toepad samples of three extinct *Psittacula* parrots (*P. exsul*, *P. eques*,

P. wardi). They resolved the species' taxonomic placement and quantified how their replacement on Indian Ocean islands by the invasive Ring-necked Parakeet led to the loss of endemic phylogenetic diversity. Conversely, another study of Indian Ocean parrots [214] involving the extinct Mascarene Parrot *Mascarinus mascarin* was misled by technical errors, which led to generation of a false hypothesis about its taxonomic placement [215].

Several hDNA studies have recently used genome-scale data to look at whether now extinct or endangered species were declining prior to the Anthropocene. The first mtDNA sequences from the extinct Carolina Parakeet *Conuropsis carolinensis* museum specimens were obtained in 2012 [216], and their analysis found robust support for placing the species in a clade of long-tailed parrots, including the genus *Aratinga*. Gelabert et al. [19] generated the whole genome of this species and found no evidence of a dramatic demographic decline in the past or of excess homozygosity, reinforcing anthropogenic causes of the species' extinction. Another study looking at the extinction of eastern North American birds found lower genetic diversity in Carolina Parakeets and a lower effective population size, but a similar demographic history compared to species that persisted; this study also suggested their disappearance was due to anthropogenic factors [21]. In addition, the western subspecies *C. c. ludovicianus* went extinct about 30 years earlier than the eastern *C. c. carolinensis* possibly driven by different pressures [217].

The first whole mitochondrial genome of an extinct parrot species was published by Anmarkrud and Lifjeld [218] for the Paradise Parrot *Psephotellus pulcherrimus*, a species of central eastern Australia that went extinct in about 1928; the sequenced museum specimen was collected in 1881. A whole genome resequencing study used another museum specimen collected during the period when the species started to decline (in the second half of the 19th century). It argued that the species had relatively high effective population size and had not declined before the major expansion of pastoral settlements in its range. That expansion led to destruction of the parrots' nesting habitat and subsequent trapping for the avicultural trade, so excluding causes of extinction related to genetics [84]. The mitogenome of the extinct Cuban Macaw *Ara tricolor* was published in 2018 and showed that the species was closely related to the extant Military Macaw and the Great Green Macaw *Ara ambiguus*, possibly diverging from them around 4 Mya [20].

Museum and contemporary specimens were used to study the underlying processes leading to the collapse of the historically widespread and abundant Kākāpō in New Zealand. A study analysing mtDNA, microsatellites, and models of their demographic history concluded that a population bottleneck linked to the European colonisation ruled out earlier Polynesian settlement as a cause of the species' decline [219]. Another study sequenced full mitogenomes of the species and confirmed the previous study's conclusions, and found no evidence for fixation of deleterious mutations [220]. However, it argued that despite high pre-decline genetic diversity, a rapid decline combined with the species' lek mating system and its life-history traits contributed to a rapid loss of genetic diversity. By sequencing historical and modern genomes of the Kākāpō, a recent study showed that the remaining island population has a reduced number of harmful mutations compared to the extinct mainland individuals, providing key insights into their recovery [146].

Parrots have been appreciated and traded since historic times [221]. For instance, Scarlet Macaw bones were recovered from archaeological sites in northern Mexico and the southern United States, over a thousand kilometres outside their endemic range [222]. Low genetic diversity found after sequencing the mitochondrial genomes of the macaw remains pointed towards a macaw breeding colony translocated by humans possibly from Mexico or Guatemala [223]. The first study relying solely on ancient parrot feathers, recovered from a pre-Hispanic religious site in the Atacama Desert in Peru, has successfully obtained and sequenced hDNA and identified various parrot species native to the Amazonian region of the country [224]. Captive rearing of macaws and amazon parrots was also shown to have occurred in the Atacama Desert in Chile around the years 1100–1450, at least 500 km outside their present-day native range [225].

Capitalising on less destructive sampling methods, trace DNA, and technological advances in museomics, genome-wide markers can now be generated from old museum specimens. A study generated thousands of SNP markers from museum (up to 123 years old) and contemporary specimens by a RAD approach and highlighted higher error rates and missing data in SNPs from the museum samples of Red-tailed Black-Cockatoos [213]. Another study used a hybridisation RAD (hyRAD) technique where probes generated from fresh samples were used to hybridise to fragmented museum hDNA (up to 140 years old), and similarly indicated lower diversity of SNPs in older samples of a songbird [226]. Hence, studies using low-quality museum samples to generate phylogenomic data must be careful and follow best practices for assembling, processing, and analysing such data to avoid misinterpretations [107].

4. Conclusions

Our overview has shown wide application of molecular genetic- and genomic techniques for studies of parrots in their global distribution. There is increasing interest by field biologists studying parrots in incorporating genetics as part of their research agenda. Given the high proportion of threatened species in the group, and the extraordinarily high level of interest in parrots among humans (including the wildlife trade and captive breeding), one or more centralised parrot genetics laboratories, perhaps on different continents, might be advantageous for future collaborative research. This could also consolidate expertise and boost efficacy in sample collection, DNA extraction, sequencing, and genomic analysis. It would be important to include genetics as a component of studies on parrot species with high conservation concern, as this could help to find populations with low genetic diversity and the most appropriate source populations to “rescue” them.

Recent breakthroughs in technology and consolidation of approaches will allow genetic techniques to be used more extensively in wildlife forensic investigations. The lack of validated DNA reference sequences is hindering our ability to accurately assign species identity. A focus on establishing DNA reference databases for the most traded wildlife species will assist in forensic casework. Building a baseline reference genomic database of wild parrot populations could help to determine the provenance of confiscated birds, aid rewilding and translocation projects, and resolve questions about captive or wild origins. As part of the licensing agreement to maintain some protected species in captivity, DNA samples could be taken with the explicit intention of using them to verify parentage and identity in the future [227,228]. Genetics has also been effective in disease testing. Studying the interactions between the TLR, MHC, and resistance to diseases would be important for both captive and wild parrot populations.

Choosing the correct markers for genetic analyses is very important as different conclusions might be reached without a genome-wide investigation. For instance, using RAD-seq data, Shipham et al. [229] confirmed a sister relationship between the Pale-headed Rosella and Northern Rosella *Platycercus venustus*, which was previously all but overlooked based purely on mtDNA sequences in which there had been a mtDNA capture event between non-sister taxa. However, the switch from solely sequencing mtDNA regions to relatively cheap and easy SNP genotyping methods has limited the capacity for comparative studies among species as different marker panels are used, optimised for each species. Absolute metrics of genetic structure and diversity are therefore not readily comparable, so approaches that produce DNA sequences may be preferable. For example, ultraconserved elements (UCEs) that target portions of the genome that remain similar across divergent clades but contain variable sequences in the flanking regions are a common approach used in avian phylogenomic studies [230]. UCEs have been used in studies on the phylogenomics of lorikeets [107] and historical demography of the Carolina Parakeet [21]. There is increasing interest in applying comparative genomic techniques to conservation studies [231,232]. These are limited with current data types but perhaps the increasing use of whole genome sequencing will make independent datasets more comparable among individuals, populations, and species. This would open up interesting opportunities for

questions from behavioural, conservation, and evolutionary perspectives. The field of genetics has always been at the forefront of data sharing through repositories such as GenBank, so the opportunities for comparative analyses and insights as data comparability increases are enormous. However, sequence data alone are not enough to understand genome evolution and function, and entirely new approaches, like chromosomics [233] with superior bioinformatics like pangenome models [234], are needed in the future.

In conclusion, genetics has aided parrot research substantially in the past and will continue to do so as exciting new applications emerge in the advancing genomic era. We certainly encourage parrot researchers to consider implementing genetics as part of their research agenda, given the wide array of questions genetics can help to answer as demonstrated in this review. We realise that these research projects often do not have the capacity, expertise, or funds to do genetic research. However, many commercial laboratories now provide sequencing services at ever-dropping costs, so researchers might consider using these services to generate data from their samples. For genomic data interpretation, we propose a consortium of scientists sharing their experience in conservation genomics, analysis pipelines, and mentorship of students in genetic research on parrots. This consortium could work as a specialist group within the well-established Parrot Researchers Group.

Author Contributions: Conceptualization, G.O., B.T.S., L.J. and R.H.; Investigation, G.O.; Data curation, L.J. and B.T.S.; Writing—original draft preparation, G.O., B.T.S., L.J. and R.H.; Writing—review and editing, G.O., B.T.S., L.J., S.C.B. and R.H.; Supervision, R.H.; Project administration, G.O.; Funding acquisition, G.O. and R.H. All authors have read and agreed to the published version of the manuscript.

Funding: B.T.S. was supported by awards from the National Science Foundation US (DEB-1655736; DBI-2029955). MDPI waived the publication fee of this publication.

Acknowledgments: We thank Jose L. Tella for inviting us to contribute this review paper to the special issue on parrots. We are grateful to Juan Masello for building a comprehensive online library on parrot research, which is available via membership of the Parrot Researchers Group. We thank Rod Peakall and four anonymous reviewers, whose comments largely helped to improve this manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

Glossary

Cryptic species	Morphologically often indistinguishable but genetically distinct species, following the evolutionary species concept.
Effective population size (N_e)	The size of the ideal, panmictic population that would experience the same loss of genetic variation, through genetic drift, as the observed population.
Gene flow	The exchange of genetic information between randomly mating populations through migration, measured in allele frequencies.
Genetic diversity	The extent of genetic variation in a population, species, or across species, measured in heterozygosity, allelic diversity, or heritability.
Genetic drift	Random changes in the genetic composition of a small population between generations. It results in loss of genetic diversity, random changes in allele frequencies, and diversification among populations.
Genome	The complete genetic material of an organism, including nuclear and mitochondrial DNA.
Inbreeding	The accumulation of deleterious mutations due to breeding among close relatives.
Inbreeding depression	Reduction in reproduction, survival, or related characters due to inbreeding
Management units (MUs)	Populations with significant divergence of allele frequencies at nuclear or mitochondrial loci, regardless of the phylogenetic distinctiveness of the alleles.
Microsatellite	A locus with a short tandem repeat DNA sequence, typically showing variable number of repeats across individuals. Consequently, they are highly informative genetic markers.

Minisatellite	Typically, between 6–100 bp section of DNA, repeated many times in a long string with no gaps between the repeats. These were the first type of DNA markers used in human identification and later in wildlife genetics.
Next generation sequencing (NGS)	Includes technologies that use short-read, massively parallel, high-throughput sequencing of the genetic material (e.g., Illumina, Ion Torrent).
Outbreeding depression	Reduction in reproductive fitness due to crossing of two populations, subspecies, or species.
Polymerase chain reaction (PCR)	A method to replicate copies (amplify) of specific segments of DNA, with thermostable Taq polymerase enzyme in a thermocycler.
Population viability analysis (PVA)	A model to predict the extinction risk of a population by using information about population size and structure, birth and death rates, risks and severity of catastrophes, levels of inbreeding depression, rate of habitat loss, etc. PVA can be used as a management tool to examine different management options to recover threatened species.
Single nucleotide polymorphism (SNP)	A nucleotide site (base pair) in a DNA sequence that is polymorphic in a population and can be used as a marker to assess genetic variation within and among populations.
Wildlife forensics	Application of science to the law, including detection of illegal wildlife trade with DNA-based methods.

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