1 The IUCN Red List is not sufficient to protect genetic diversity

2 Chloé Schmidt^{*1,2,3}, Sean Hoban⁴, Margaret Hunter⁵, Ivan Paz-Vinas⁶, Colin J Garroway³

3

4 Affiliations

- ¹ Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT, USA
- ⁶ ² Center for Biodiversity and Global Change, Yale University, New Haven, CT, USA
- ³ Department of Biological Sciences, University of Manitoba, Winnipeg, Manitoba, Canada
- 8 ⁴ The Center for Tree Science, The Morton Arboretum, Lisle, IL, USA
- ⁵ U.S. Geological Survey, Wetland and Aquatic Research Center, Gainesville, Florida, USA
- ⁶ Laboratoire Evolution et Diversité Biologique (EDB), UMR5174, Université Toulouse 3 Paul
 Sabatier, CNRS, IRD, Toulouse, France
- 12

ORCIDs: CS: 0000-0003-2572-4200; MH: 0000-0002-4760-9302; IPV: 0000-0002-0043-9289;
 CJG: 0000-0001-8010-9388

15

16 **Correspondence**:

- 17 Chloé Schmidt
- 18 Department of Biological Sciences
- 19 50 Sifton Road
- 20 University of Manitoba
- 21 Winnipeg, MB R3T 2N2
- 22 email: schmid46@myumanitoba.ca
- 23
- 24 Word count: 5,504

25 Abstract

26 The International Union for Conservation of Nature (IUCN) Red List is an important and widely used conservation prioritization tool. It uses information about species range size, habitat quality 27 28 and fragmentation levels, and trends in abundance to assess species extinction risk. Genetic 29 erosion is an additional key factor determining extinction risk, but the Red List was not designed 30 to assess genetic diversity. Declining populations experience stronger effects of genetic drift and higher rates of inbreeding, which can reduce the efficiency of selection, lead to fitness 31 declines, and hinder species' capacities to adapt to environmental change. Given the 32 33 importance of conserving genetic diversity, several studies have attempted to find relationships between Red List status and genetic diversity. Yet, there is still no general consensus on 34 whether genetic diversity is captured by the current Red List categories in a way that is 35 36 informative for conservation, likely partly due to assessments using different molecular markers and taxa. Here, we synthesize previous work and re-analyze three datasets using different 37 38 marker types (mitochondrial DNA, microsatellites, and whole genomes) to assess whether genetic diversity accurately predicts Red List threat status. Consistent with previous work we 39 found that on average, species with higher threat status tended to have lower genetic diversity 40 for all marker types, but the strength of these relationships varied across taxa. However, genetic 41 diversity did not predict threat status well for any taxon or marker type. Our analyses indicate 42 43 that Red List status is not a useful metric for informing species-specific decisions about the 44 protection of genetic diversity. This is unsurprising because the Red List was not designed for conservation at the genetic level. Our findings clearly indicate a need to develop and 45 46 incorporate metrics specifically developed to assess genetic diversity into our conservation policy frameworks. 47 48

49 **Keywords:** conservation policy, vertebrates, heterozygosity, genetic drift, molecular markers,

- data synthesis, mitochondrial DNA, nuclear DNA 50
- 51

52

53

55 Main text

56 Background

57 The International Union for Conservation of Nature (IUCN) Red List is a criterion-based

evaluation of species extinction risk that is widely used to prioritize species for conservation.

59 Specifically, the Red List evaluates demographic threats to species persistence. Species are 60 placed into one of several categories of extinction risk based on assessments of species-wide

61 declines in the number of adult individuals (Criterion A); small range sizes, very high levels of

habitat fragmentation, or few populations (Criterion B); a declining population (Criterion C); or a

very small number of individuals (Criterion D). The IUCN also classifies species abundance

64 trends as *decreasing*, *stable*, or *increasing*. Genetic diversity is not directly incorporated in risk

assessments; however, fragmented, small, and declining populations are susceptible to the

erosion of genetic diversity due to heightened levels of genetic drift. Low genetic diversity can

also lead to reduced population sizes and inbreeding, ultimately resulting in population declines
 via an extinction vortex. This has led to an ongoing conversation about the extent to which Red

List risk statuses might also be useful for guiding the protection of genetic diversity (e.g.,

70 (Garner et al. 2020; Canteri et al. 2021; Petit-Marty et al. 2021). Resolving this question is

important because genetic diversity is not well-integrated into global conservation policy (Hoban

et al. 2020). If Red List status sufficiently captures processes that reduce genetic diversity via

73 demographic changes in populations, there would be no need to add direct indicators of genetic

74 diversity to an already complex conservation policy toolbox.

75 Resolving the question of whether Red List status captures genetic diversity in a way that is

vseful for species assessments is timely for conservation policy given recent and upcoming

77 Convention on Biological Diversity post-2020 Global Biodiversity Framework talks (Xu et al.

- 2021). Several studies have addressed the question of whether the Red List is suitable for
- assessing extinction risk due to low genetic diversity (Nabholz et al. 2008; Rivers et al. 2014;

80 Doyle et al. 2015; Willoughby et al. 2015; Li et al. 2016; Brüniche-Olsen et al. 2018, 2021;

81 Garner et al. 2020; Buffalo 2021; Canteri et al. 2021; Petit-Marty et al. 2021). Relationships

82 between Red List risk status and genetic diversity are generally-but not consistently-detectable,

- and it is often argued that these associations are informative for conservation and management
 decisions related to genetic diversity (e.g., Canteri et al. 2021; Petit-Marty et al. 2021). However,
- it remains unclear whether these general associative trends between species' Red List risk
- status and genetic diversity are useful for identifying species exhibiting genetic erosion (Fig. 1).

87 Models that capture general trends in data often perform poorly when the goal is prediction.

688 General trends between Red List status and genetic diversity (e.g., Li et al. 2016; Brüniche-

Olsen et al. 2021; Canteri et al. 2021; Petit-Marty et al. 2021) suggest that, on average,

90 threatened species tend to have lower genetic diversity than non-threatened species. However,

91 if the models detecting these general relationships have low predictive accuracy, then they will

not be informative for identifying whether individual species in a given threat category are at risk

of genetic erosion (Fig. 1). Thus, our ability to use Red List status as a proxy for genetic

94 diversity status for specific species hinges on the strength of this relationship and model

95 predictive accuracy. If the general trends detected to date are deemed useful for conservation

96 policy, then policymakers could use Red List status to assess genetic diversity in the absence of

97 genetic data, which is still not available for most species. Additional metrics developed

specifically for assessing genetic diversity status and trends would not be needed (Laikre et al.

2020; Hoban et al. 2020, 2021). However, if the relationship between Red List status and

100 genetic diversity is weak and has poor predictive accuracy, relying solely on Red List status

- 101 would result in a lack of formal and sufficient protection for genetic diversity in natural
- 102 populations. To evaluate the extent to which species' genetic diversity is predictive of Red List
- risk status, we reanalyzed three genetic datasets (two previously used for this purpose)
- 104 containing estimates of genetic diversity obtained from different markers (mitochondrial gene
- sequences, microsatellites, and whole-genome sequences).

106 Our first dataset contained estimates of mtDNA *cytochrome B* diversity from 1036 bird species.

- 107 This dataset was compiled by Canteri et al. (2021), who used it to assess the relationship
- 108 between Red List risk (threatened or not) and genetic diversity. They concluded that the Red
- 109 List species-level conservation criteria capture low levels of genetic diversity. Canteri et al.
- obtained *cytochrome B* sequences from GenBank, a genetic sequence database, and
- 111 measured genetic diversity at the species level using nucleotide diversity for species with 5
- sequences minimum (median = 11 sequences across the data set). Species' Red List statuses were included with the posted data, and we added population trend classifications for species
- using the 'rredlist' package in R (Chamberlain 2020). IUCN population trend assessments were
- 115 available for 984 species.
- 116 Our second dataset consisted of genetic diversity estimates from whole genome sequences
- 117 (WGS) for 68 bird species from a dataset compiled by Brüniche-Olsen et al. (2021) from two
- sequence databases, EMBL-EBI and NCBI. Genetic diversity was measured with genome-wide
- observed heterozygosity estimated from the site frequency spectrum for 1 sequence per
- species. With these data, Brüniche-Olsen et al. found that threatened species (Endangered and
- 121 Critically Endangered) had lower observed genomic heterozygosity than non-threatened
- 122 species. Species Red List categories and population trends were included in this dataset.
- 123 Finally, our third dataset was the MacroPopGen database (Lawrence et al. 2018, 2019). This database contains site-level estimates of genetic diversity from microsatellite markers for 124 vertebrate species (terrestrial vertebrates and freshwater fish) across North and South America 125 harvested from the literature. We assigned Red List categories and IUCN population trend 126 classifications to species with rredlist. We were able to assign Red List status to 693 species 127 128 (80 amphibians; 215 birds; 143 mammals; 120 reptiles; 134 ray-finned fishes; 1 lamprey). We chose to use gene diversity (reported as expected heterozygosity in MacroPopGen) as our 129 130 metric of genetic diversity because it does not depend strongly on sample size (Charlesworth and Charlesworth 2010). Gene diversity is the average probability that two randomly selected 131 alleles in a population are different (Nei 1973). We averaged gene diversity across sample sites 132 to obtain a species-level measure of genetic diversity comparable to the genetic diversity 133 estimates in the mtDNA and WGS datasets. Among bird species in our analyses, only 5 species 134 were present across all three datasets (54 species shared between mtDNA - microsatellite data 135 sets; 20 mtDNA - WGS; 9 WGS - microsatellite). 136
- 137 We modeled general relationships between our measures of genetic diversity (nucleotide 138 diversity for mtDNA data, observed genome-wide heterozygosity for WGS data, and gene 139 diversity for microsatellite data) and Red List categories with the same two models fit to each 140 dataset. The first model type was an ordinal logistic regression implemented in the MASS library (Venables and Ripley 2002). The dependent variable was threat status ordered by risk (least 141 concern – LC; near-threatened – NT; vulnerable – VU; endangered – EN; and critically 142 143 endangered – CR). Then, to more closely resemble previous work (Brüniche-Olsen et al. 2021; Canteri et al. 2021), we also tested how well genetic diversity classified broader binary Red List 144

- categories, threatened (comprised of CR, EN, and VU categories) vs. non-threatened (NT, LC),
 using logistic regressions. All analyses were repeated for mtDNA, microsatellite, and WGS
- diversity estimates separately. These models are similar to those used previously, thus we
 expected to find similar general trends of a decline in diversity with increasing threat status.
- We then took the important next step in assessing the policy relevance of these trends by
- 150 assessing the ability of our models to accurately categorize individual species' risk status using 151 genetic information alone. To do this we estimated the predictive accuracy (the proportion of
- 152 correctly classified observations) of models using confusion matrices calculated in the 'caret' R
- 153 package (Kuhn 2021).
- 154

155 Genetic diversity does not predict species Red List status

- 156 Consistent with previous analyses (Willoughby et al. 2015; Li et al. 2016; Brüniche-Olsen et al.
- 2021; Canteri et al. 2021; Petit-Marty et al. 2021), we found that the Red List status was
- associated with genetic diversity across marker types and all taxa examined except for fishes
- 159 (Table 1). Genetic diversity for all markers tended to decrease with higher threat statuses (Fig.
- 160 2). We also found general associations between genetic diversity and IUCN population size
- trends: microsatellite diversity for birds, mammals, and amphibians tended to increase for
- species with positive population size trends. However, diversity decreased for bird mtDNA and
- whole genome data, and reptile and fish microsatellite data with positive population trends as
- species-level population sizes moved from decreasing, to stable, to increasing (Table 2, Fig. 3).
 Our results therefore suggest that genetic diversity is generally statistically related to Red List
- 166 status and population trends, although directions of effect are not consistent across taxa.
- 167 While our models had good predictive accuracy (ordinal regressions: 57-84%; logistic
- regressions: 63-90%; Tables 1, 2), these levels of accuracy were achieved by classifying nearly
- all species as Least Concern or non-threatened (Figs. S1-S2). This is known as the accuracy
- 170 paradox (Fernandes et al. 2010), i.e. when models have low predictive power despite high
- accuracy. Most species across all datasets were listed as Least Concern (84% of mtDNA data,
- 65% of microsatellite data, 69% of whole genome sequences), and this category generally
- encapsulated variation in genetic diversity across all other Red List categories for all marker
- types. Our tests of predictive accuracy show there is no strong tendency for Critically
- 175 Endangered, Endangered, or Vulnerable species to have markedly low genetic diversity, and
- that Least Concern species are equally likely to have low genetic diversity (Figs. 1, 2). These
- results demonstrate that we cannot predict a species' Red List risk status from species-level
 genetic data, nor conversely can Red List status be used as a surrogate for species' risk of
- genetic erosion in the absence of genetic data. Therefore, Red List status alone is not useful for
- 180 decisions related to the conservation of genetic diversity of individual species.
- 181

182 Relationships across marker types

183 Although we tested 3 marker types, we note that biological differences among markers mean

- they are not all equally informative for conservation. Mitochondrial genomes are maternally
- inherited, behave as a single locus because they do not recombine, and have several protein-
- coding genes-meaning they most likely do not evolve neutrally (Galtier et al. 2009).

Mitochondrial DNA diversity is generally not correlated with genome-wide diversity or adaptive
potential, two core targets of conservation genetics (Kardos et al. 2021). It is also not strongly
related to population size (Bazin et al. 2006), which is a central component for Red List
assessment. Mitochondrial markers have been strongly criticized as general tools for population
genetics, phylogenetics, and conservation outside of specific contexts (Zink and Barrowclough
2008; Edwards and Bensch 2009; Galtier et al. 2009; Paz-Vinas et al. 2021; Schmidt and
Garroway 2021a).

194 In contrast, microsatellites and whole-genome data both capture genome-wide diversity. 195 Genetic diversity estimated from ~10 microsatellite loci is well correlated (83%) with genomewide diversity (Mittell et al. 2015). We therefore expected relationships between Red List status 196 and genetic diversity estimated from mitochondrial versus nuclear data to differ, with nuclear 197 markers being more promising predictors of threat status. Indeed, we did not detect a 198 199 correlation between mtDNA and microsatellite markers for the bird species that overlapped in 200 our data (Fig. 4). However, the general trends we found were in the same direction across all marker types. We suspect the general, species-level trends captured by our own and previously 201 202 published models could be driven by particularly significant declines in abundance or range extent in some species, which could cause genetic diversity declines in both mitochondrial and 203 204 nuclear DNA. The similar trends we detect across marker types suggest that most threatened 205 species have likely undergone a genetic bottleneck, but not all species with low genetic diversity 206 are considered threatened. In other words, Least Concern species may be equally likely to have experienced a decline that caused a reduction in genetic diversity at some point in their history, 207 but for reasons we discuss in the following section, these low levels of genetic diversity may not 208 209 necessarily be of conservation concern. Alternatively, these species could be miscategorized.

210

211 Low versus declining genetic diversity

Many reasons might explain the mismatch between Red List status and species-level genetic 212 213 diversity. Declines in genetic diversity can often be difficult to detect due to time lags between 214 the ecological causes of demographic decline and their evolutionary consequences (Landguth 215 et al. 2010; Pflüger et al. 2019), and due to non-linear relationships between range loss and genetic diversity loss (Pflüger et al. 2019). Previous work has shown that genome-wide genetic 216 217 diversity is not strongly correlated with IUCN estimates of present abundance (Willoughby et al. 2015). Furthermore, changes in nuclear DNA genetic diversity following habitat disturbance are 218 219 variable across taxa. For example, with regard to habitat disturbance related to urbanization, 220 mammals generally lose diversity in highly urbanized areas, but at different rates depending on species (DiBattista 2008; Schmidt et al. 2020; Habrich et al. 2021); bird species either lose or 221 gain genetic diversity in more urban areas (Schmidt et al. 2020); while changes in amphibian 222 223 genetic diversity are more idiosyncratic depending on species and location (Schmidt and Garroway 2021b). Variation in response rate to local and contemporary habitat changes can 224 obscure the relationship between a species' genetic diversity and its Red List status over time. 225 The inability of our models to accurately identify threatened species also indicates a potential 226

227 problem with using species-level estimates of genetic diversity as a criterion to assess

228 conservation status, because species have variable levels of genetic diversity at mutation-drift

- 229 equilibrium. The natural census size of species will also cause variation in equilibrium levels of
- 230 genetic diversity at the species level (Eo et al. 2011; Romiguier et al. 2014; Buffalo 2021). For

instance, there were many species with relatively low genetic diversity that are classified as

Least Concern (Fig. 2), an observation that has generated suggestions to include genetic

diversity in species risk assessment (Willoughby et al. 2015; Garner et al. 2020). Canteri et al.

- note that only a few non-threatened (4%) and threatened (10%) bird species had notably low genetic diversity. Brüniche-Olsen et al. report that 9 species had heterozygosity $<9\times10^{-4}$ (13th
- 235 generic diversity. Draniene Olsen et al. report that 5 species had heterozygosity (3×10
- 236 percentile), 6 of which were listed as threatened.

237 The demographic histories of individual populations can also contribute to variation in genetic

- 238 diversity across species, especially for species where only few sites or sequences were
- sampled. A species with low contemporary genetic diversity that also has a low long-term
- 240 effective population size and stable abundance is not necessarily of high priority for
- conservation, at least in terms of genetic vulnerability (e.g., Reed 2010; Fraser et al. 2014). The
- data we present suggest that demographically stable species (Least Concern or stable
- population trends) have a wide range of genetic diversity levels (Figs. 2, 3). This variability
- poses an issue for the possibility of integrating genetic diversity into Red List classifications by
- setting thresholds that are determined through interspecific comparisons, because they may not
 translate into meaningful conservation gains for the classified species.

247 A pressing conservation issue for population genetic diversity that has been highlighted at the policy level are recent, ongoing declines in abundance and loss of distinct populations (Hoban 248 249 et al. 2021). Declines in genetic diversity are not necessarily cause for alarm; for example, they 250 might lead to inbreeding and the eventual exposure of phenotypes associated with recessive 251 alleles in homozygous states. This can cause deleterious alleles to be selectively purged, which 252 reduces negative effects of inbreeding and enables populations to persist with low levels of genetic diversity (Mathur and DeWoody 2021; Kardos et al. 2021). While purging deleterious 253 alleles can help counteract ill effects of inbreeding, it cannot be relied on to do so, especially in 254 255 the long term. Many more populations will have gone extinct due to complications associated with low genetic diversity than those that persist in spite of it (Spielman et al. 2004; Frankham et 256 257 al. 2019). Species-level genetic diversity estimates obtained by averaging across population-258 level estimates can obscure declines in species with high diversity, especially in unmonitored 259 and opportunistically sampled populations. Declines are ideally assessed with intraspecific data 260 sampled over time, but unfortunately, this is difficult to do at scale (but see Leigh et al. 2019).

- Repurposing publicly available genetic data can allow us to overcome this to an extent by substituting space for time (or impact for time) to study environmental factors related to declir
- substituting space for time (or impact for time) to study environmental factors related to decline using data from multiple populations per species (Schmidt et al. 2020; Habrich et al. 2021;
- 264 Schmidt and Garroway 2021b). Overall, we conclude that continued interspecific comparisons
- of Red List rankings and average species genetic diversity are unproductive because the nature
- and causes of genetic diversity loss are variable across genetic markers, populations, species,
- and species' ranges. Below we list ways in which genetic diversity can be incorporated into
- 268 species risk assessments to improve its protection.
- 269

270 A way forward

271 Red List rankings are used extensively for conservation planning, often at the species or

- 272 regional level, such as prioritizing actions for species at the highest risk levels (Critically
- 273 Endangered and Endangered) and identifying at risk regions or Key Biodiversity Areas
- 274 (Hoffmann et al. 2008). The Red List process of compiling information from experts also allows

analysis of threats to individual species, species in a region, and globally (Rodrigues et al.

- 276 2006). Change in the Red List Index over time is a useful global indicator of biodiversity loss
- (Tittensor et al. 2014; though see Fraixedas et al. 2022 for a critique of other aspects of the Red
 List). It is apparent, however, that these patterns are currently not related to genetic diversity in
- List). It is apparent, however, that these patterns are currently not related to genetic diversity a way that is meaningful for conservation, as has been pointed out previously (Nabholz et al.
- 280 2008; Rivers et al. 2014; Doyle et al. 2015; Willoughby et al. 2015). This is not surprising,
- because the Red List was not developed to assess genetic diversity. Given its focus on
- demographic change, it was important to test whether the Red List might encompass genetic
- diversity and remove the need to further develop tools to assess genetic erosion. The takeaway
- from these extended analyses is that the Red List, on its own, cannot account for the genetic
- diversity patterns of individual species, and is not reliable for conserving and recovering genetic
- diversity. Genetic diversity assessments, in combination with the use of well-verified proxies or indicators of genetic diversity (Hanson et al. 2017; Hoban et al. 2020, 2022) and other
- conservation assessment tools, are needed to assess species' vulnerability to genetic erosion.
- 289 Where do we go from here? To our minds, it is time to shift attention away from policy tools that
- 290 were not designed to capture genetic information when the goal is to conserve genetic diversity
- (Hoban et al. 2022). Nuclear genetic data are increasingly available for a wider variety of
- species (Leigh et al. 2021), enhancing our ability to look more deeply into genetic diversity
 status below the species level (Hoban et al. 2022). Additionally, as more genomes become fully
 sequenced, there are more proposals for assessing genetic erosion status using genome level
- sequenced, there are more proposals for assessing genetic erosion status using genome level statistics (van Oosterhout 2020, 2021; Bertorelle et al. 2022). The majority of species will lack
- 296 genetic data for the foreseeable future. This highlights the need to develop effective proxies that
- are directly connected to genetic diversity (Hoban et al. 2020, 2021). For example, proxies could
- include the proportion of populations with low effective size (which will slow genetic erosion), or
- the proportion of distinct populations lost (Hoban et al. 2020, 2021, 2022).
- 300 The rapid collection and use of these genetic, genomic, and proxy metrics in a coordinated way 301 across thousands of species is important to help the scientific community advance understanding and inform decision making. Producing and aggregating these data, however, 302 would require considerable effort. Data would ideally be aggregated in centralized databases 303 that can be expanded and updated over time, similar to updates to the Red List. Rather than 304 tailoring new data to suit old metrics, the increasing availability of abundant, fine-scale genetic 305 306 data can enable conservation geneticists to develop and adopt improved metrics. Fortunately, additional tools are forthcoming. The ongoing development of a suite of genetic Essential 307 Biodiversity Variables (Hoban et al. 2022) means that policymakers can begin to move beyond 308 309 the Red List to safeguard genetic diversity in all species.
- 310

311 References

- Bazin, E., Glémin, S., and Galtier, N. 2006. Population size does not influence mitochondrial
 genetic diversity in animals. Science. **312**(5773): 570–572. doi:10.1126/science.1122033.
- Bertorelle, G., Raffini, F., Bosse, M., Bortoluzzi, C., Iannucci, A., Trucchi, E., Morales, H.E., and
 van Oosterhout, C. 2022. Genetic load: genomic estimates and applications in non-model
 animals. Nat. Rev. Genet. 23(8): 492–503. doi:10.1038/s41576-022-00448-x.
- Brüniche-Olsen, A., Kellner, K.F., Anderson, C.J., and DeWoody, J.A. 2018. Runs of

- homozygosity have utility in mammalian conservation and evolutionary studies. Conserv.
 Genet. **19**(6): 1295–1307. doi:10.1007/s10592-018-1099-y.
- Brüniche-Olsen, A., Kellner, K.F., Belant, J.L., and Dewoody, J.A. 2021. Life-history traits and
 habitat availability shape genomic diversity in birds: Implications for conservation. Proc. R.
 Soc. B Biol. Sci. 288(1961). doi:10.1098/rspb.2021.1441.
- Buffalo, V. 2021. Quantifying the relationship between genetic diversity and population size
 suggests natural selection cannot explain Lewontin's paradox. Elife 10.
 doi:10.7554/eLife.67509.
- Canteri, E., Fordham, D.A., Li, S., Hosner, P.A., Rahbek, C., and Nogués-Bravo, D. 2021. IUCN
 Red List protects avian genetic diversity. Ecography. 44(12): 1808–1811.
 doi:10.1111/ecog.05895.
- Chamberlain, S. 2020. rredlist: "IUCN" Red List Client. Available from https://cran.r project.org/package=rredlist.
- Charlesworth, B., and Charlesworth, D. 2010. Elements of evolutionary genetics. Roberts &
 Company Publishers, Greenwood Village, Colorado, USA.
- DiBattista, J.D. 2008. Patterns of genetic variation in anthropogenically impacted populations.
 Conserv. Genet. 9(1): 141–156. doi:10.1007/s10592-007-9317-z.
- Doyle, J.M., Hacking, C.C., Willoughby, J.R., Sundaram, M., and DeWoody, J.A. 2015.
 Mammalian Genetic Diversity as a Function of Habitat, Body Size, Trophic Class, and
 Conservation Status. J. Mammal. **96**(3): 564–572. doi:10.1093/jmammal/gyv061.
- Edwards, S., and Bensch, S. 2009. Looking forwards or looking backwards in avian
 phylogeography? A comment on Zink and Barrowclough 2008. Mol. Ecol. 18: 2930–2933.
- Eo, S.H., Doyle, J.M., and DeWoody, J.A. 2011. Genetic diversity in birds is associated with
 body mass and habitat type. J. Zool. 283(3): 220–226. doi:10.1111/j.14697998.2010.00773.x.
- Fernandes, J.A., Irigoien, X., Goikoetxea, N., Lozano, J.A., Inza, I., Pérez, A., and Bode, A.
 2010. Fish recruitment prediction, using robust supervised classification methods. Ecol.
 Modell. 221(2): 338–352. doi:10.1016/j.ecolmodel.2009.09.020.
- Fraixedas, S., Roslin, T., and Laine, A. 2022. Nationally reported metrics can't adequately guide
 transformative change in biodiversity policy. Proc. Natl. Acad. Sci. **119**(9): 1–4.
- Frankham, R., Ballou, J.D., Ralls, K., Eldridge, M., Dudash, M.R., Fenster, C.B., Lacy, R.C., and
 Sunnucks, P. 2019. Inbreeding and loss of genetic diversity increase extinction risk. *In A* Practical Guide for Genetic Management of Fragmented Animal and Plant Populations.
 Oxford University Press. doi:10.1093/oso/9780198783411.001.0001.
- Fraser, D.J., Debes, P. V, Bernatchez, L., and Hutchings, J.A. 2014. Population size, habitat
 fragmentation, and the nature of adaptive variation in a stream fish. Proc. R. Soc. B Biol.
 Sci. 281: 20140370. doi:10.1098/rspb.2014.0370.
- Galtier, N., Nabholz, B., Glémin, S., and Hurst, G.D.D. 2009. Mitochondrial DNA as a marker of
 molecular diversity: A reappraisal. Mol. Ecol. 18(22): 4541–4550. doi:10.1111/j.1365 294X.2009.04380.x.
- 358 Garner, B.A., Hoban, S., and Luikart, G. 2020. IUCN Red List and the value of integrating

- 359 genetics. Conserv. Genet. **21**(5): 795–801. doi:10.1007/s10592-020-01301-6.
- Habrich, A.K., Lawrence, E.R., and Fraser, D.J. 2021. Varying genetic imprints of road networks
 and human density in North American mammal populations. Evol. Appl. 14(6): 1659–1672.
 doi:10.1111/eva.13232.
- Hanson, J.O., Rhodes, J.R., Riginos, C., and Fuller, R.A. 2017. Environmental and geographic
 variables are effective surrogates for genetic variation in conservation planning. Proc. Natl.
 Acad. Sci. U. S. A. **114**(48): 201711009. doi:10.1073/pnas.1711009114.
- Hoban, S., Archer, F.I., Bertola, L.D., Bragg, J.G., Breed, M.F., Bruford, M.W., Coleman, M.A.,
 Ekblom, R., Funk, W.C., Grueber, C.E., Hand, B.K., Jaffé, R., Jensen, E., Johnson, J.S.,
 Kershaw, F., Liggins, L., MacDonald, A.J., Mergeay, J., Miller, J.M., Muller-Karger, F.,
 O'Brien, D., Paz-Vinas, I., Potter, K.M., Razgour, O., Vernesi, C., and Hunter, M.E. 2022.
 Global genetic diversity status and trends: towards a suite of Essential Biodiversity
 Variables (EBVs) for genetic composition. Biol. Rev. doi:10.1111/brv.12852.
- Hoban, S., Bruford, M., D'Urban Jackson, J., Lopes-Fernandes, M., Heuertz, M., Hohenlohe, 372 373 P.A., Paz-Vinas, I., Sjögren-Gulve, P., Segelbacher, G., Vernesi, C., Aitken, S., Bertola, L.D., Bloomer, P., Breed, M., Rodríguez-Correa, H., Funk, W.C., Grueber, C.E., Hunter, 374 M.E., Jaffe, R., Liggins, L., Mergeay, J., Moharrek, F., O'Brien, D., Ogden, R., Palma-Silva, 375 C., Pierson, J., Ramakrishnan, U., Simo-Droissart, M., Tani, N., Waits, L., and Laikre, L. 376 2020. Genetic diversity targets and indicators in the CBD post-2020 Global Biodiversity 377 378 Framework must be improved. Biol. Conserv. 248: 108654. 379 doi:10.1016/j.biocon.2020.108654.
- Hoban, S., Bruford, M.W., Funk, W.C., Galbusera, P., Griffith, M.P., Grueber, C.E., Heuertz, M.,
 Hunter, M.E., Hvilsom, C., Stroil, B.K., Kershaw, F., Khoury, C.K., Laikre, L., and Lopes-,
 M. 2021. Global commitments to conserving and monitoring genetic diversity are now
 necessary and feasible. Bioscience: 1–13. doi:10.1093/biosci/biab054.
- Hoffmann, M., Brooks, T.M., da Fonseca, G.A.B., Gascon, C., Hawkins, A.F., A., James, R.E.,
 Langhammer, P., Mittermeier, R.A., Pilgrim, J.D., Rodrigues, A.S.L., and Silva, J.M.C.
 2008. Conservation planning and the IUCN Red List. Endanger. Species Res. 6(2): 113–
 125. doi:10.3354/esr00087.
- Kardos, M., Armstrong, E.E., Fitzpatrick, S.W., Hauser, S., Hedrick, P.W., Miller, J.M., Tallmon,
 D.A., and Funk, W.C. 2021. The crucial role of genome-wide genetic variation in
 conservation. Proc. Natl. Acad. Sci. **118**(48): e2104642118.
 doi:10.1073/pnas.2104642118.
- Kuhn, M. 2021. caret: Classification and Regression Training. Available from https://cran.r project.org/package=caret.
- Laikre, L., Hoban, S., Bruford, M.W., Segelbacher, G., Allendorf, F.W., Gajardo, G., GonzalezRodriguez, A., Hedrick, P.W., Heuertz, M., Hohenlohe, P.A., Jaffé, R., Johannesson, K.,
 Liggins, L., MacDonald, A.J., Orozco-terWengel, P., Reusch, T.B.H., Rodríguez-Correa, H.,
 Russo, I.R.M., Ryman, N., and Vernesi, C. 2020. Post-2020 goals overlook genetic
 diversity. Science. 2121: 1083–1085. doi:10.1126/science.abb2748.
- Landguth, E.L., Cushman, S.A., Schwartz, M.K., McKelvey, K.S., Murphy, M., and Luikart, G.
 2010. Quantifying the lag time to detect barriers in landscape genetics. Mol. Ecol. 19(19):
 4179–4191. doi:10.1111/j.1365-294X.2010.04808.x.
- Lawrence, E.R., Benavente, J.N., Matte, J.-M., Marin, K., Wells, Z.R.R., Bernos, T.A., Krasteva,

- N., Habrich, A., Nessel, G.A., Koumrouyan, R.A., and Fraser, D.J. 2019. Geo-referenced
 population-specific microsatellite data across American continents, the MacroPopGen
 Database. Sci. Data 6(1): 14. doi:10.1038/s41597-019-0024-7.
- Lawrence, E.R., Benavente, J.N., Matte, J., Marin, K., Wells, Z.R.R., Bernos, T.A., Habrich, A.,
 Nessel, G.A., Koumrouyan, R.A., and Fraser, D.J. 2018. MacroPopGen Database: Georeferenced population-specific microsatellite data across the American continents.
 Available from https://doi.org/10.6084/m9.figshare.7207514.v2 [accessed 11 November
 2021].
- Leigh, D.M., Hendry, A.P., Vázquez-Domínguez, E., and Friesen, V.L. 2019. Estimated six per
 cent loss of genetic variation in wild populations since the industrial revolution. Evol. Appl.
 12(8): 1505–1512. doi:10.1111/eva.12810.
- Leigh, D.M., van Rees, C.B., Millette, K.L., Breed, M.F., Schmidt, C., Bertola, L.D., Hand, B.K.,
 Hunter, M.E., Jensen, E.L., Kershaw, F., Liggins, L., Luikart, G., Manel, S., Mergeay, J.,
 Miller, J.M., Segelbacher, G., Hoban, S., and Paz-Vinas, I. 2021. Opportunities and
 challenges of macrogenetic studies. Nat. Rev. Genet. doi:10.1038/s41576-021-00394-0.
- Li, H., Xiang-Yu, J., Dai, G., Gu, Z., Ming, C., Yang, Z., Ryder, O.A., Li, W.H., Fu, Y.X., and
 Zhang, Y.P. 2016. Large numbers of vertebrates began rapid population decline in the late
 19th century. Proc. Natl. Acad. Sci. U. S. A. **113**(49): 14079–14084.
 doi:10.1073/pnas.1616804113.
- Mathur, S., and DeWoody, J.A. 2021. Genetic load has potential in large populations but is
 realized in small inbred populations. Evol. Appl. 14(6): 1540–1557. doi:10.1111/eva.13216.
- 424 Mittell, E.A., Nakagawa, S., and Hadfield, J.D. 2015. Are molecular markers useful predictors of 425 adaptive potential? Ecol. Lett. **18**(8): 772–778. doi:10.1111/ele.12454.
- Nabholz, B., Mauffrey, J.F., Bazin, E., Galtier, N., and Glemin, S. 2008. Determination of
 mitochondrial genetic diversity in mammals. Genetics **178**(1): 351–361.
 doi:10.1524/genetics.107.072346
- 428 doi:10.1534/genetics.107.073346.
- 429 Nei, M. 1973. Analysis of gene diversity in subdivided populations. Proc. Natl. Acad. Sci. U. S.
 430 A. **70**(12): 3321–3323. doi:10.1073/pnas.70.12.3321.
- 431 van Oosterhout, C. 2020. Mutation load is the spectre of species conservation. Nat. Ecol. Evol.
 432 4(8): 1004–1006. doi:10.1038/s41559-020-1204-8.
- van Oosterhout, C. 2021. Conservation genetics: 50 Years and counting. Conserv. Lett. 14(2):
 1–2. doi:10.1111/conl.12789.
- Paz-Vinas, I., Jensen, E.L., Bertola, L.D., Breed, M.F., Hand, B.K., Hunter, M.E., Kershaw, F.,
 Leigh, D.M., Luikart, G., Mergeay, J., Miller, J.M., Van Rees, C.B., Segelbacher, G., and
 Hoban, S. 2021. Macrogenetic studies must not ignore limitations of genetic markers and
 scale. Ecol. Lett.: ele.13732. doi:10.1111/ele.13732.
- Petit-Marty, N., Vázquez-Luis, M., and Hendriks, I.E. 2021. Use of the nucleotide diversity in
 COI mitochondrial gene as an early diagnostic of conservation status of animal species.
 Conserv. Lett. 14(1): 1–7. doi:10.1111/conl.12756.
- Pflüger, F.J., Signer, J., and Balkenhol, N. 2019. Habitat loss causes non-linear genetic erosion
 in specialist species. Glob. Ecol. Conserv. **17**: e00507. doi:10.1016/j.gecco.2018.e00507.
- 444 Reed, D.H. 2010. Albatrosses, eagles and newts, Oh My!: Exceptions to the prevailing

- paradigm concerning genetic diversity and population viability? Anim. Conserv. 13(5): 448–
 457. doi:10.1111/j.1469-1795.2010.00353.x.
- Rivers, M.C., Brummitt, N.A., Nic Lughadha, E., and Meagher, T.R. 2014. Do species
 conservation assessments capture genetic diversity? Glob. Ecol. Conserv. 2: 81–87.
 doi:10.1016/j.gecco.2014.08.005.
- Rodrigues, A.S.L., Pilgrim, J.D., Lamoreux, J.F., Hoffmann, M., and Brooks, T.M. 2006. The
 value of the IUCN Red List for conservation. Trends Ecol. Evol. 21(2): 71–76.
 doi:10.1016/j.tree.2005.10.010.
- Romiguier, J., Gayral, P., Ballenghien, M., Bernard, A., Cahais, V., Chenuil, A., Chiari, Y.,
 Dernat, R., Duret, L., Faivre, N., Loire, E., Lourenco, J.M., Nabholz, B., Roux, C.,
 Tsagkogeorga, G., Weber, A.A.T., Weinert, L.A., Belkhir, K., Bierne, N., Glémin, S., and
 Galtier, N. 2014. Comparative population genomics in animals uncovers the determinants
- 457 of genetic diversity. Nature **515**(7526): 261–263. doi:10.1038/nature13685.
- Schmidt, C., Domaratzki, M., Kinnunen, R.P., Bowman, J., and Garroway, C.J. 2020. Continentwide effects of urbanization on bird and mammal genetic diversity. Proc. R. Soc. B Biol.
 Sci. 287(1920): 20192497. doi:10.1098/rspb.2019.2497.
- Schmidt, C., and Garroway, C.J. 2021a. The conservation utility of mitochondrial genetic
 diversity in macrogenetic research. Conserv. Genet. 22(3): 323–327. doi:10.1007/s10592021-01333-6.
- Schmidt, C., and Garroway, C.J. 2021b. The population genetics of urban and rural amphibians
 in North America. Mol. Ecol. 30(16): 3918–3929. doi:10.1111/mec.16005.
- Spielman, D., Brook, B.W., and Frankham, R. 2004. Most species are not driven to extinction
 before genetic factors impact them. Proc. Natl. Acad. Sci. U. S. A. **101**(42): 15261–15264.
 doi:10.1073/pnas.0403809101.
- 469 Tittensor, D.P., Walpole, M., Hill, S.L.L., Boyce, D.G., Britten, G.L., Burgess, N.D., Butchart, S.H.M., Leadley, P.W., Regan, E.C., Alkemade, R., Baumung, R., Bellard, C., Bouwman, 470 471 L., Bowles-Newark, N.J., Chenery, A.M., Cheung, W.W.L., Christensen, V., Cooper, D.H., 472 Crowther, A.R., Dixon, M.J.R., Galli, A., Gaveau, V., Gregory, R.D., Gutierrez, N.L., Hirsch, T.L., Höft, R., Januchowski-Hartley, S.R., Karmann, M., Krug, C.B., Leverington, F.J., Loh, 473 474 J., Kutsch Lojenga, R., Malsch, K., Marques, A., Morgan, D.H.W., Mumby, P.J., Newbold, 475 T., Noonan-Mooney, K., Pagad, S.N., Parks, B.C., Pereira, H.M., Robertson, T., Rondinini, C., Santini, L., Scharlemann, J.P.W., Schindler, S., Sumaila, U.R., Teh, L.S.L., Van Kolck, 476 477 J., Visconti, P., and Ye, Y. 2014. Biodiversity Targets. Science. 346(6206): 241-244. 478 doi:10.1126/science.1257484.
- Venables, W.N., and Ripley, B.D. 2002. Modern Applied Statistics with S. *In* Fourth. Springer,
 New York. Available from https://www.stats.ox.ac.uk/pub/MASS4/.
- Willoughby, J.R., Sundaram, M., Wijayawardena, B.K., Kimble, S.J.A., Ji, Y., Fernandez, N.B.,
 Antonides, J.D., Lamb, M.C., Marra, N.J., and DeWoody, J.A. 2015. The reduction of
 genetic diversity in threatened vertebrates and new recommendations regarding IUCN
 conservation rankings. Biol. Conserv. **191**: 495–503. doi:10.1016/j.biocon.2015.07.025.
- Xu, H., Cao, Y., Yu, D., Cao, M., He, Y., Gill, M., and Pereira, H.M. 2021. Ensuring effective
 implementation of the post-2020 global biodiversity targets. Nat. Ecol. Evol. 5(4): 411–418.
 doi:10.1038/s41559-020-01375-y.

- Zink, R.M., and Barrowclough, G.F. 2008. Mitochondrial DNA under siege in avian
- 489 phylogeography. Mol. Écol. **17**(9): 2107–2121. doi:10.1111/j.1365-294X.2008.03737.x.

491 **Disclaimer:** Any use of trade, firm, or product names is for descriptive purposes only and does
 492 not imply endorsement by the United States Government.

493 **Acknowledgements:** We would like to thank Matthew Thorstensen, Deborah Leigh, and Alicia

- 494 Korpach for their feedback on the manuscript. CJG and CS were supported by a Natural
- 495 Sciences and Engineering Research Council of Canada Discovery Grant.

497 **Table 1.** Relationship between Red List categories and genetic diversity. Model summaries for

ordinal regressions (response variable is all 5 Red List categories ranked 1-LC, 2-NT, 3-VU, 4-

- 499 EN, 5-CR) and logistic regressions (binary response variable, threatened vs non threatened) for 500 mtDNA, microsatellite, and whole-genome (WGS) data. Coefficients (beta) are given with
- 501 standard errors (SE) and model accuracy from confusion matrices (Figs. S1-S2) with 95%
- 502 confidence intervals (CI).
- 503

n	accuracy	95% CI	beta	SE
215	0.66	0.60 - 0.73	-3.17	0.89
143	0.64	0.56 – 0.72	-4.67	1.13
80	0.74	0.67 – 0.83	-2.99	1.6
120	0.57	0.47 – 0.66	-4.3	1.38
134	0.63	0.55 – 0.72	-0.63	0.91
1048	0.84	0.82 - 0.86	-69.75	11.95
68	0.69	0.57 – 0.80	-748.8	232.9
	0.79	0.73 – 0.84	-3.09	1.02
	0.78	0.71 – 0.85	-6.06	1.45
	0.81	0.71 – 0.89	-3.59	1.81
	0.63	0.53 – 0.71	-3.26	1.48
	0.68	0.59 – 0.76	-0.65	0.98
	0.90	0.88 – 0.92	-124.29	21.61
	0.79	0.68 - 0.88	-939.54	338.82
	n 215 143 80 120 134 1048 68	n accuracy 215 0.66 143 0.64 80 0.74 120 0.57 134 0.63 1048 0.84 68 0.69 0.79 0.78 0.81 0.63 0.63 0.68 0.90 0.79	$\begin{array}{c ccccc} n & accuracy & 95\% \ Cl \\ 215 & 0.66 & 0.60 - 0.73 \\ 143 & 0.64 & 0.56 - 0.72 \\ 80 & 0.74 & 0.67 - 0.83 \\ 120 & 0.57 & 0.47 - 0.66 \\ 134 & 0.63 & 0.55 - 0.72 \\ 1048 & 0.84 & 0.82 - 0.86 \\ 68 & 0.69 & 0.57 - 0.80 \\ \hline & & 0.79 & 0.73 - 0.84 \\ 0.78 & 0.71 - 0.85 \\ 0.81 & 0.71 - 0.89 \\ 0.63 & 0.53 - 0.71 \\ 0.68 & 0.59 - 0.76 \\ \hline & 0.90 & 0.88 - 0.92 \\ 0.79 & 0.68 - 0.88 \\ \hline \end{array}$	naccuracy95% Clbeta2150.660.60 - 0.73-3.171430.640.56 - 0.72-4.67800.740.67 - 0.83-2.991200.570.47 - 0.66-4.31340.630.55 - 0.72-0.6310480.840.82 - 0.86-69.75680.690.57 - 0.80-748.80.790.73 - 0.84-3.090.780.71 - 0.85-6.060.810.71 - 0.89-3.590.630.53 - 0.71-3.260.680.59 - 0.76-0.650.900.88 - 0.92-124.290.790.68 - 0.88-939.54

505

504

507 **Table 2.** Relationship between IUCN population trend and genetic diversity. Model summaries

for population trend ordinal regressions (decreasing, D = -1; stable, S = 0; increasing, I = 1) for

509 mtDNA, microsatellite, and whole-genome (WGS) data. Coefficients (beta) are given with

standard errors (SE) and model accuracy from confusion matrices (Fig. S3) with 95%

511 confidence intervals (CI).

microsatellites					
taxon	n	accuracy	95% CI	beta	SE
birds	203	0.47	0.40 - 0.54	1.27	0.90
mammals	126	0.53	0.44 – 0.62	5.65	1.52
amphibians	72	0.67	0.55 – 0.77	0.16	0.10
reptiles	99	0.57	0.46 – 0.67	-2.08	1.51
fish	94	0.65	0.54 – 0.74	-1.62	1.26
mtDNA					
birds	984	0.52	0.49 – 0.55	-14.69	5.02
WGS					
birds	67	0.64	0.52 – 0.76	-176.80	146.80

512



- 515 Figure 1. A toy comparison of a model that identifies general trends in data but does not make accurate predictions (A) and a model that both captures trends and predicts species risk status 516 well (B). Models can usefully capture general trends while at the same time having poor 517 predictive accuracy (A, C). General relationships between species Red List status and genetic 518
- 519
- diversity have been detected, but to date their predictive accuracy has not been assessed. 520 Models need to predict well if they are to be considered good conservation tools. With high
- overlapping levels of genetic diversity between Red List categories (Least Concern, LC, and 521
- 522 Critically Endangered, CR) models may be able to detect lower genetic diversity in CR than LC
- 523 species, but these models perform poorly when used to predict CR species (confusion matrix,

- 524 C). With less overlap across categories (B), models would be better able to correctly classify
- 525 species' risk status (D). The large variance in genetic diversity and prevalence of Least Concern
- 526 species suggests that Red List status is not related to genetic diversity in a way that is
- 527 informative for conservation policy.





Figure 2. Relationship of avian mitochondrial genetic diversity (*a*) whole-genome genetic
diversity (*b*), and microsatellite genetic diversity (*c*) to IUCN Red List categories (CR = critically
endangered; EN = endangered; VU = vulnerable; NT = near-threatened; LC = least concern).
Most species are classified as Least Concern. The genetic diversity of least concern species is
extremely variable and generally encompasses the entire range of genetic diversity across all
Red List categories for all genetic markers.



- **Figure 3.** Relationship of mitochondrial genetic diversity (*a*), whole-genome genetic diversity
- 538 (*b*), and microsatellite genetic diversity (*c*) to IUCN Red List population trend categories. IUCN 539 population trends are unrelated to species genetic diversity.





542 (gene diversity) in birds are not correlated (r = 0.22; -0.05 – 0.46 95% CI; n = 54 species).

543 Highlighted species show mismatches between mitochondrial genetic diversity, nuclear genetic

diversity, and IUCN Red List conservation status. For example, the endangered Galápagos

545 penguin has lower nuclear genetic diversity than other species in our data set, but mitochondrial

546 diversity comparable to several other species. The Marbled murrelet is also endangered, yet

has relatively high mitochondrial and nuclear diversity. Mitochondrial genetic diversity is thus not

a reliable proxy for genome-wide diversity, which is a quantity of interest for conservation.

549

551 Supplementary information for: The IUCN Red List is not sufficient to protect genetic

- 552 diversity
- 553 Figs. S1-S3





Figure S1. Confusion matrices for ordinal (left column) and binary (right column) logistic
regressions for mitochondrial (mtDNA) and whole genome sequence (WGS) data for birds. For
all models, Least concern (1; left) or non-threatened (0; right) were the best-predicted
categories.





562 **Figure S2.** Confusion matrices for ordinal (left column) and binary (right column) logistic

regressions for microsatellite data. For all models, Least concern (1; left) or non-threatened (0;

right) were the best-predicted categories.





Figure S3. Confusion matrices for population trend models (Decreasing population trend = -1;
Stable = 0; Increasing = 1). The best predicted classes are the most common ones (mtDNA,
WGS, mammals, and birds: Decreasing is most common; fish, amphibians, reptiles: Stable).