

1 Invited reviews and synthesis

2 **Population genomics for wildlife conservation and management**

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4 Running title: Population genomics for wildlife

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19 **Abstract**

20 Biodiversity is under threat worldwide. Over the past decade, the field of population genomics
21 has developed across non-model organisms, and the results of this research have begun to be
22 applied in conservation and management of wildlife species. Genomics tools can provide precise
23 estimates of basic features of wildlife populations, such as effective population size, inbreeding,

24 demographic history, and population structure, that are critical for conservation efforts.
25 Moreover, population genomics studies can identify particular genetic loci and variants
26 responsible for inbreeding depression or adaptation to changing environments, allowing for
27 conservation efforts to estimate the capacity of populations to evolve and adapt in response to
28 environmental change and to manage for adaptive variation. While connections from basic
29 research to applied wildlife conservation have been slow to develop, these connections are
30 increasingly strengthening. Here we review the primary areas in which population genomics
31 approaches can be applied to wildlife conservation and management, highlight examples of how
32 they have been used, and provide recommendations for building on the progress that has been
33 made in this field.

34

35 **Keywords**

36 Adaptive capacity; conservation units; effective population size; genetic rescue; inbreeding
37 depression; population connectivity

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40 **1 Introduction**

41 **1.1 The need for population genomics in wildlife biology**

42 As increasing attention is focused on global change and loss of biodiversity (IPBES 2019), it is
43 critical to understand the changes and challenges that wildlife populations face and use the tools
44 now available for management and conservation of wildlife species. Central issues in wildlife
45 conservation include identifying populations and units for conservation, assessing population
46 size and connectivity, detecting hybridization, assessing the potential of populations to persist

47 and adapt to environmental change, and understanding the factors that affect this potential.
48 Genetic information can inform all of these issues and provide critical information for designing
49 management strategies to address them. The genomics revolution has democratized the field of
50 population genomics, allowing high-throughput sequencing to be applied in nearly any organism,
51 including natural populations of rare or difficult-to-study species (Luikart et al. 2019; Rajora
52 2019). As a result, genomics approaches are an important part of the toolkit for a basic
53 understanding of wildlife biology, such as disease or population dynamics, and to inform direct
54 conservation and management actions for wildlife populations and their habitats.

55 Natural populations face a number of threats, including habitat loss and alteration, direct
56 mortality from exploitation, invasive species, emerging infectious disease, pollution, and climate
57 change. These threats are pervasive and global, so that an estimated 1 million species of plants
58 and animals are at risk of extinction within the next few decades (IPBES 2019). Threats to
59 wildlife populations often act synergistically, and genetic factors are central to the challenges
60 confronting wildlife. For instance, loss of genetic diversity and inbreeding due to population
61 declines and fragmentation can reduce population fitness directly, but also can reduce a
62 population's ability to adapt to novel conditions produced by invasive species or climate change
63 (Ceballos et al. 2017). Genetics and genomics concepts, and the ability to efficiently study
64 genetic factors in nature, are important for quantifying and mitigating threats to wildlife
65 populations.

66 Several years ago, spurred by technological advances in high-throughput sequencing, a
67 set of reviews and perspective articles assessed the potential for the field of conservation
68 genomics (Primmer 2009; Allendorf et al. 2010; Steiner et al. 2013). Genomics concepts and
69 approaches have a wide range of applications in conservation, from seed sourcing for restoration

70 to understanding community-level effects of genomic diversity (Hand et al. 2015, Holliday et al.
71 2017; Breed et al. 2019; Rajora 2019). Here we focus on applications of population genomics to
72 wildlife, which we define as natural populations of vertebrate species that are the focus of
73 specific attention for conservation or population management (although most of the tools and
74 concepts we discuss are applicable to all of biodiversity). Over the last decade, the field has
75 made substantial progress in understanding how to apply population genomics in wildlife and
76 what questions can be addressed. It is timely to take stock of the progress that has been made to
77 date, learn from some of the successes, and identify avenues for future progress in wildlife
78 genomics research. Additionally, a critical need is to translate wildlife population genomics
79 research to conservation actions, requiring concrete steps toward integrating the two.

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82 **1.2 Technical advances in population genomics**

83 Traditional conservation genetics has relied on techniques including allozyme and microsatellite
84 genotyping or sequencing of mitochondrial DNA to provide a wealth of knowledge about natural
85 populations (Allendorf 2017). However, these techniques provide data on a limited number of
86 genetic markers across individuals. Advances in next-generation sequencing technology have
87 led to a proliferation of techniques for population genomics studies, all of which have the
88 potential to provide fine-scale genetic data across the genome of multiple individuals (Holliday
89 et al. 2019). Multiple genomics techniques provide sequence data on a reduced representation of
90 the genome, such as the transcriptome or a pre-selected set of loci targeted with primers or
91 hybridization probes (Meek & Larsen 2019). Anonymous reduced-representation techniques
92 provide sequence data from loci spread across all parts of the genome, which are determined by

93 the molecular protocol, such as the choice of restriction enzymes used in the restriction-site
94 associated DNA sequencing (RADseq) family of techniques (Andrews et al. 2016). Finally,
95 whole-genome sequencing (WGS) produces data from every part of the genome, and it is
96 increasingly feasible for most taxa (Fuentes-Pardo & Ruzzante 2017). Importantly for studies of
97 wildlife species, many of these techniques, including transcriptome, RADseq, and WGS, do not
98 require any prior genomic knowledge for the species.

99 The line between genetics and genomics, and whether it is even useful to make a
100 distinction, is subject to differing opinions. The vast increase in the amount of data provided by
101 genomics techniques can allow new questions to be addressed, such as detection of genes
102 associated with important traits or fitness, that were not tractable with traditional techniques; this
103 has been called “narrow-sense genomics” (Garner et al. 2015; Hohenlohe et al. 2019a). With the
104 availability of reference genome assemblies, placing genetic markers on chromosomes provides
105 important information about physical linkage and recombination and connects genetic markers
106 directly to candidate genes. This new perspective can be integral to a truly genomics study, and
107 what Allendorf (2017) calls “the death of beanbag genetics.” Conversely, in a “broad-sense
108 genomics” approach (Garner et al. 2015), high-throughput sequencing tools can be used to
109 address questions that were already tractable with traditional genetic techniques. The advantage
110 of using newer techniques is increased statistical power and resolution with more markers, and in
111 many cases increased efficiency and cost-effectiveness (Walters & Schwartz 2020).

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114 **1.3 Applications to wildlife**

115 Below we highlight a number of recent applications of population genomics to understanding
116 wildlife populations. Progress in this field has revealed several general trends. First, all of the
117 techniques described above, from traditional genetics tools through the wide range of next-
118 generation sequencing approaches, have important roles to play. Determining which approach is
119 best in a particular case depends on many factors, including the resources available and the data
120 required to address a specific scientific question (Hohenlohe et al. 2019a). Second, population
121 genomics studies are increasingly able to address multiple scientific questions with high
122 precision from a single genomic dataset. For instance, genomic data can allow population
123 structure to be assessed from the perspective of both neutral and adaptive connectivity, with
124 different implications for conservation actions (Funk et al. 2012). WGS data from a relatively
125 small number of individuals can provide information across a range of time scales, from
126 demographic history and phylogenetic relationships among widely separated populations over
127 the last two million years, to inbreeding within the last century (Saremi et al. 2019). In part this
128 is the result of new analytical approaches made possible by genomic datasets, such as
129 demographic reconstruction (discussed below) and runs of homozygosity (ROH; Box 1).

130 Third, many approaches that are most useful for wildlife also combine multiple
131 population genetics or genomics approaches. For instance, many applications of genetics tools
132 in wildlife require the ability to genotype a set of genetic markers consistently over time across
133 many individuals, for instance in long-term monitoring of populations. Next-generation
134 sequencing tools can efficiently provide a large amount of data, from which a highly optimized
135 set of marker loci can be extracted for specific objectives like parentage analysis, population
136 assignment, or monitoring of adaptive loci (Hess et al. 2015; Meek et al. 2016; Förster et al.
137 2018; von Thaden et al. 2020). These marker panels may have relatively few loci (e.g., orders of

138 magnitude fewer than the genomic dataset on which they are based) and miss large parts of the
139 genome, so they may not be considered “genomics” in a strict sense. Nonetheless, when a
140 selected panel of marker loci is developed from a genome-wide dataset to include adaptively
141 significant loci, it is able to address questions about adaptive variation in wildlife populations
142 that were previously intractable with traditional genetics studies.

143 A particular need in wildlife studies is the ability to use low-quality and/or low-quantity
144 DNA, including DNA extracted from archival, environmental, and non-invasive samples. A
145 wide range of genetics and genomics techniques can be applied to low-quality DNA samples,
146 although some are more challenging than others (Andrews et al. 2018a). In difficult-to-study
147 species, it can be very useful to combine genotyping of non-invasive samples at traditional
148 markers such as microsatellites with genomic sequencing of a few individuals, such as captive
149 individuals, for which higher-quality DNA samples are available (for instance in snow leopards,
150 *Panthera uncia*; Janecka et al. 2020). In addition to microsatellites, panels of single-nucleotide
151 polymorphisms (SNPs) optimized from large genomic datasets can also be genotyped using low-
152 quality DNA samples (Andrews et al. 2018; von Thaden et al. 2020). Particularly in threatened
153 wildlife species in which genetic variation has been lost in living populations but remains in
154 archival museum or field-collected ancient samples, techniques for analyzing low-quality DNA
155 samples open a window into the genetic past that can inform current conservation efforts (Bi et
156 al. 2013; van der Valk et al. 2019a).

157 A variety of other technical advances and available resources facilitate the use of
158 population genomics in wildlife species. Increasingly, sequencing technology is advancing to
159 the point that it can be used in the field with only a backpack full of equipment and supplies
160 (Kreherwinkel et al. 2019). Increasing numbers of wildlife species have reference genome

161 assemblies available, and these provide a number of benefits, including improved identification
162 of loci, linking genetic markers to candidate genes, and haplotype-based or other analyses that
163 are not possible otherwise (Brandies et al. 2019; Luikart et al. 2019; Box 1). If a reference
164 genome is not available for a particular species, one from a closely related species can be used to
165 align short-read sequence data (e.g., Janecka et al. 2020 aligned WGS data from snow leopards
166 against the tiger genome assembly, both in the genus *Panthera*), and it can also provide a
167 backbone for creating a reference genome assembly for the focal species. The growing number
168 of reference genome assemblies is facilitated by large collaborative initiatives focused on
169 taxonomic groups, such as Australian mammals (<https://ozmammalsgenomics.com>), birds
170 (Zhang et al. 2014; <https://b10k.genomics.cn/index.html>), or all eukaryotes (Lewin et al. 2018).
171 Transcriptomic and epigenetic databases also provide complementary information, especially
172 useful for genome annotation and gene functional insights.

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175 **2 Understanding wildlife populations**

176 **2.1 Population size and demographic history**

177 Perhaps the most basic aspect of wildlife populations that can be addressed with population
178 genomics tools is population size. The number of individuals is a key factor in determining
179 demographic viability of populations and in determining management actions, such as harvest
180 quotas based on numbers of adults, recruitment rates, and knowledge of source-sink dynamics.
181 Genetics tools, such as marker panels designed for individual identification, can be used in
182 genetic mark-recapture studies to estimate population densities, including non-invasive samples
183 such as scat and hair (Mills et al. 2000; von Thaden et al. 2020). Genetic marker panels that are

184 able to estimate close kinship relationships can similarly be used to estimate population size
185 (Bravington et al. 2016; Clendenin et al. 2020). As described above, genomics tools can provide
186 efficient methods for designing such marker panels from strict filtering of a much larger set of
187 loci.

188 Population size is critical not only for demographic viability of wildlife populations, but
189 also because of its effect on genetic diversity. This is captured by the effective population size
190 (N_e), defined as the size of an ideal, panmictic population that would experience the same loss of
191 genetic variation, through genetic drift, as the observed population. N_e is usually smaller than
192 the observed “census” population size (N_c), due to a number of factors common in natural
193 populations, particularly wildlife taxa, including fluctuating population size, variance in
194 reproductive success, and overlapping generations, although there is wide variation in the N_e/N_c
195 ratio (Charlesworth 2009). N_e influences the likelihood of accumulation of deleterious variants,
196 inbreeding depression, and the capacity of populations to adapt to environmental change or
197 disease, important factors in wildlife populations that are declining or have experienced
198 bottlenecks.

199 Population genomics approaches can be used to estimate N_e (Browning & Browning
200 2015; Kardos et al. 2017). For instance, Nunziata and Weisrock (2018) used simulations to test
201 the potential for RADseq data sets to estimate N_e and declines in N_e over time. They found that
202 RADseq data are effective for precisely estimating N_e and for detecting declines in N_e over
203 contemporary time scales (20 generations). Grossen et al. (2018) used RADseq to generate
204 >100,000 SNPs to test the genetic effects of reintroduction of Alpine ibex (*Capra ibex*) in
205 Switzerland and found markedly reduced N_e in reintroduced populations compared to the source
206 population or the closely related Iberian ibex (*C. pyrenaica*) (Figure 1A). Nunziata et al. (2017)

207 also found that demographic model inference of changes in N_e based on ddRAD data from two
208 salamander species (*Ambystoma talpoideum* and *A. opacum*) agreed with population size changes
209 inferred from mark-recapture data; because this study included ddRAD sequencing on samples
210 collected decades ago, temporal trends in N_e could be estimated for these two species using both
211 mark-recapture and ddRAD. Jensen *et al.* (2018) compared variation at >2000 SNPs in Pinzón
212 giant tortoise (*Chelonoidis duncanensis*) samples from a single island in the Galápagos Island
213 from before and after a bottleneck that reduced their population size (N_e) to just 150-200 in the
214 mid 20th century. They found that the extent and distribution of genetic variation in the historical
215 and contemporary samples was very similar, which they attributed to a successful *ex situ* head-
216 start and release program.

217 Even in the absence of historical samples, population genomic data can be used to
218 uncover the demographic history of populations, including population bottlenecks and
219 expansions. Because loss of genetic diversity and consequences for population fitness depend
220 strongly on not only the severity but also the time scale of population bottlenecks, reconstructing
221 demographic history in wildlife species can help explain current levels of genetic diversity.
222 While historical trends can be estimated from large SNP datasets, WGS from a few individuals is
223 effective in producing demographic reconstructions using methods based on the sequentially
224 Markovian coalescent (SMC; Li & Durbin 2011; Terhorst *et al.* 2017) or the site frequency
225 spectrum (SFS; Liu & Fu 2015). SMC may better detect older population fluctuations, and SFS
226 more recent ones (Patton *et al.* 2019). This approach has provided additional insights into the
227 Alpine ibex case, suggesting that despite a dramatic demographic recovery, Alpine ibex carry a
228 persistent genomic signature of their reintroduction history (Grossen *et al.* 2020; Figure 1B; Box
229 1). Demographic analyses by Ekblom *et al.* (2018) using WGS of 10 Scandinavian wolverines

230 (*Gulo gulo*) uncovered a long-term decline of the population from an N_e of 10,000 well before
231 the last glaciation to <500 after this period, indicating that this population has been declining for
232 thousands of years. Two subspecies of gorilla also provide an illustrative contrast: in Graur's
233 gorilla (*Gorilla beringei graueri*), population declines have led to loss of genetic diversity and
234 increased inbreeding, while the mountain gorilla (*G. beringei beringei*) population has remained
235 small but genetically stable over the past century (van der Valk et al. 2019). This study was
236 enabled by WGS of both museum and contemporary samples. Historical demographic
237 reconstruction can link population changes to environmental shifts, with the potential to predict
238 the effect of ongoing environmental changes on population distributions and genetic diversity
239 (Prates et al. 2016).

240 Low genetic variation and small N_e do not necessarily mean that a population will suffer
241 from inbreeding depression. Genetic load, the negative consequences of deleterious variation
242 that can accumulate from genetic drift, may be purged in small populations, and some
243 populations appear to experience few negative fitness effects despite low genetic variation.
244 Testing for inbreeding depression requires combining genetic data with fitness data or delving
245 deeper into the function of alleles prevalent in small populations due to genetic drift. One
246 approach for assessing the potential for inbreeding depression is to predict the physiological and
247 fitness consequences of specific allelic variants at high frequency or fixed in small, inbred
248 populations (e.g., Grossen et al. 2020). Benazzo et al. (2017) found several private and
249 deleterious amino acid changes fixed due to genetic drift in Apennine brown bears (*Ursus arctos*
250 *marsicanus*) that are predicted to result in energy deficit, muscle weakness, skeletal and cranial
251 anomalies, and reduced aggressiveness. Arguably the strongest evidence for inbreeding
252 depression comes from studies that show a negative correlation between fitness and inbreeding

253 coefficients. Huisman et al. (2016) found strong evidence for inbreeding depression in red deer
254 (*Cervus elaphus*) by examining the relationship between several different fitness metrics and
255 inbreeding coefficients estimated using SNPs. In contrast, inbreeding coefficients calculated
256 from a deep and fairly complete pedigree in the same population found evidence for inbreeding
257 depression for fewer traits (Huisman et al. 2016), highlighting the emerging consensus that
258 genomic estimates are better for quantifying inbreeding than pedigrees (Kardos et al. 2016b).
259 Estimates of ROH, especially from WGS data, are particularly effective at both quantifying
260 inbreeding coefficients and understanding candidate loci underlying inbreeding depression (Box
261 1).

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264 **2.2 Population structure and connectivity**

265 A long-standing goal of population genetics, and critical source of information for conservation
266 and management actions in wildlife, is to identify distinct populations and understand the
267 relationships among them. Characterizing population structure, the distribution of genetic
268 variation within and among populations, is key for inferring the relative importance of different
269 evolutionary processes (gene flow, drift, and selection) across populations. Given that gene flow
270 infuses new genetic variation into populations, there is also a strong interest in wildlife and
271 conservation biology in understanding the amount of gene flow among populations, particularly
272 those isolated in fragmented landscapes (Crooks & Sanajayan 2006; Walters & Schwartz 2020).

273 The first step in inferring population structure using genetic or genomic data is to
274 delineate populations. What constitutes a population is not always obvious for natural
275 populations, and it is important to distinguish demographic and genetic connectivity (Waples &

276 Gaggiotti 2006; Lowe & Allendorf 2010). This is particularly true for continuously distributed
277 populations, but also for species distributed in discrete habitat patches, which may or may not be
278 equivalent to populations (Funk *et al.* 2005). Fortunately, population genomics provides
279 increased power to delineate populations, detect cryptic population structure, and quantify how
280 genetically distinct populations are. For example, Oh *et al.* (2019) identified a genetically very
281 divergent population of greater sage-grouse (*Centrocercus urophasianus*) in eastern Washington
282 using WGS of representative individuals, which has important implications for conservation of
283 this imperiled species (Figure 2A). The scale of genomic data also allowed the researchers to
284 link population structure to adaptive divergence at candidate loci associated with detoxification
285 of the birds' primary food, sagebrush (*Artemisia* spp.). In another example, mitogenomic
286 (Hofman *et al.* 2015) and RADseq-generated SNP data (Funk *et al.* 2016) revealed evidence for
287 a low level of historic gene flow in island foxes (*Urocyon littoralis*) among island populations,
288 which suggests recent human movement of foxes. In these examples, genetic and genomic data
289 confirmed the expected delineation of populations by geography, but also quantified the
290 distinctiveness among them.

291 In other cases, geographic delineation of populations is not so clear. Landscape genetics
292 combines population genetics, landscape ecology, and spatial statistics to understand the effects
293 of landscape and environmental heterogeneity on gene flow, genetic variation, and
294 microevolutionary processes, and to identify barriers between populations (Manel *et al.* 2003).
295 Genomics tools add statistical power and resolution to these studies, and also add the potential to
296 identify loci associated with adaptation within and among populations. This has led to the
297 distinction between neutral landscape genomics (addressing the questions of traditional
298 landscape genetics with genomics tools) and adaptive landscape genomics (Forester *et al.* 2018;

299 Storfer et al. 2018); we discuss genomics studies of adaptive genetic variation below. One
300 advantage of landscape genetics and genomics is that the unit of analysis can be either the
301 individual or the population, which facilitates studies of organisms that are continuously
302 distributed, rather than clustered in discrete patches. A focus of landscape genetics and genomics
303 studies of wildlife species has been to understand how anthropogenic habitat modification
304 influences patterns and rates of gene flow. For instance, Kozakiewicz *et al.* (2019) found that
305 urbanization impedes connectivity among bobcat (*Lynx rufus*) populations in southern
306 California, and the barrier effect of major highway corridors can be seen in the genetic separation
307 of wildlife populations (Figure 2B). Genomic data can also reconstruct the historical patterns of
308 gene flow among populations, whether natural or human-mediated (Figure 1B), and link these to
309 the geographic and climatic factors causing changes in gene flow over time. This puts
310 contemporary patterns of genetic variation and reductions in connectivity due to habitat
311 fragmentation in a historical context. As an example, Hotaling *et al.* (2017) analyzed SNPs
312 generated using RADseq with coalescent-based demographic modelling to investigate historical
313 patterns of gene flow in a rare, stream stonefly (*Lednia tumana*) in the Rocky Mountains of
314 Glacier National Park, Montana, USA. Their analyses supported divergence with gene flow
315 among three genetic clusters since the end of the Pleistocene (~13-17 kya), which they
316 interpreted as the result of south-to-north recession of ice sheets.

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319 **2.3 Hybridization and admixture**

320 An emerging view in evolutionary biology in the last few decades is that hybridization
321 between animal species is relatively common and plays an important role in evolution and

322 ecology. For instance, Toews *et al.* (2019) review the evidence that admixture between bird
323 species has been an important source of variation and has possibly led to the formation of new
324 species. Population genomic approaches can provide large sets of markers that increase the
325 ability to detect and quantify low levels of hybridization or admixture (the flow of genetic
326 variation into a species or population as a result of hybridization) (Luikart *et al.* 2019). Large
327 SNP datasets can estimate historic hybridization events among related taxa, using methods that
328 rely on shared allelic variation across a phylogeny (e.g. Foote & Morin 2016; Sinding *et al.*
329 2018). Additionally, mapping genomic data onto a reference genome assembly can identify
330 chromosomal tracts of ancestry. Because these blocks of ancestry break down through
331 recombination following a hybridization event, the distribution of their sizes can be used to infer
332 the history of hybridization and admixture in wildlife species, as well as evidence for selection in
333 admixed genomes (e.g. Leitwein *et al.* 2018, 2019).

334 Admixture can have both negative and positive effects on population fitness. In
335 snowshoe hares (*Lepus americanus*), Jones *et al.* (2018) found that brown winter coats likely
336 originated from an introgressed black-tailed jackrabbit (*L. californicus*) allele that has swept to
337 high frequency in parts of the snowshoe hare range with milder winter climates. Adaptive
338 introgression into this species may have allowed it to expand its range following Pleistocene
339 glaciation (Jones *et al.* 2019), and this genetic variation may play a key role in future adaptation
340 as snowshoe hares encounter reduced winter snow cover across more of their range.

341 Hybridization and admixture can also have negative consequences for fitness and local
342 adaptation in wildlife species, particularly with massive increases in human-facilitated
343 movement of organisms (Allendorf *et al.* 2001). One example is species invasions facilitated by
344 hybridization (e.g., feral swine, *Sus scrofa*; Smyser *et al.* 2020), which can negatively impact

345 native wildlife populations. More directly, hybridization between westslope cutthroat trout
346 (*Oncorhynchus clarkii lewisi*) and the widely introduced rainbow trout (*O. mykiss*) in western
347 North America reduces fitness of the native species (Muhlfeld et al. 2009). Muhlfeld *et al.*
348 (2017) amassed an impressive, multidecadal dataset consisting of >12,000 individuals from 582
349 sites genotyped at allozyme loci, microsatellite loci, and SNPs to infer the spatiotemporal
350 dynamics of hybridization between these two species. They found that hybridization was more
351 common in close proximity to historical stocking locations for rainbow trout, in warm water, and
352 with lower spring precipitation. Importantly, cold sites were not protected from invasion,
353 meaning that even cutthroat trout populations in high-elevation, cold water streams are not safe
354 from hybridization by invasive rainbow trout. Large population genomic data sets will have
355 greater power to detect and quantify even low rates of hybridization.

356 Identifying hybrids is also important from a legal standpoint, as hybrids between
357 endangered and non-endangered species may not be protected under some endangered species
358 laws (vonHoldt et al. 2017). The red wolf (*Canis rufus*) is listed as endangered under the U.S.
359 Endangered Species Act (ESA), but recent hybridization with coyotes (*Canis latrans*) as well as
360 historical hybridization with coyotes and other wolf taxa has resulted in substantial controversy.
361 Nonetheless, Waples et al. (2018) found that under any historical pattern of hybridization, red
362 wolves retain the basic features necessary to be considered a distinct population segment under
363 the law and thus are eligible to remain on the list. Another North American canid species,
364 eastern wolves (*Canis lycaon*), also has a complex history including recent hybridization.
365 Heppenheimer et al. (2019) argue that such admixed populations still retain genetic variation
366 representative of a distinct taxon and potentially important for local adaptation, warranting their
367 protection under wildlife conservation measures.

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370 **3 Adaptive Variation**

371 **3.1 The role of adaptive variation in wildlife**

372 Determining the genetic basis of adaptive traits has been a central goal in evolutionary biology
373 since the genesis of the field but has proved elusive for non-model species, such as wildlife.

374 Historically, testing for local adaptation and dissecting its genetic basis required controlled
375 breeding, common garden, and reciprocal transplant experiments, which are typically only
376 feasible for some model plant and animal species. Adaptive variation in wildlife populations
377 determines their long-term viability, potential for increases in distribution or population size, and
378 extinction probability. Wildlife populations face a variety of threats, including climate change
379 and other factors that can be projected into the future. The quick pace of environmental change
380 means that sensitive species will have to move, acclimate or respond plastically, or evolve to
381 avoid extinction (Dawson *et al.* 2011), but conservation actions can be targeted to facilitate these
382 processes if they can be based on data about the genetic basis of adaptive variation.

383 Additionally, some laws design to protect endangered wildlife such as the U.S. Endangered
384 Species Act take adaptive potential into consideration in endangered species listing and delisting
385 decisions (Funk *et al.* 2019).

386 Basic estimates of heritability of potentially adaptive traits can be informative. For
387 instance, Reed *et al.* (2011) developed an individual-based model to explore potential
388 evolutionary changes in migration timing and the consequences for population persistence in
389 Fraser River sockeye salmon (*Oncorhynchus nerka*). Assuming a heritability of migration
390 timing of 0.5, they predict that adult migration timing will advance by ~10 days in response to a

391 2°C increase in temperature and that quasi-extinction risk will only be 17% of that faced by
392 populations with no evolutionary potential. Many wildlife species that are the focus of long-term
393 studies have pedigree data that can be used to estimate heritability of phenotypic traits (e.g.,
394 deVillemereuil et al. 2018), and genomics tools can also be used in natural populations to
395 provide estimates of heritability by providing pairwise estimates of individual relatedness
396 (Gienapp et al. 2017). Beyond assessing whether adaptive phenotypic traits have a genetic basis,
397 population genomics now makes it possible to pinpoint the specific genes underlying this
398 variation in natural populations, and better understand the processes and potential for adaptation.
399 A genomic understanding of adaptive potential allows future projections of population viability
400 and distribution under alternative scenarios of environmental change (Box 2).

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403 **3.2 Identifying adaptive genetic variation**

404 Adaptive variation in contemporary wildlife populations is often most evident as differentiation
405 among populations or across a landscape where selective factors, such as interacting species or
406 climate, are heterogeneous. One analytical framework for identifying loci under selection is
407 outlier tests (Beaumont and Nichols 1996). These tests allow detection of loci with “outlying”
408 behavior, such as unusually high or low F_{ST} values, potentially indicative of divergent or
409 stabilizing selection, respectively. Although F_{ST} outlier tests have proved an important approach
410 for identifying loci under selection, a number of factors ranging from recombination rate
411 variation across the genome to demographic fluctuations can produce large variance in F_{ST} and
412 related statistics. Several recent papers have cautioned that they can be subject to high type I
413 error rates as a result (Whitlock and Lotterhos 2015; Hoban *et al.* 2016). Genotype-environment

414 associations (GEA) are another method for identifying loci under selection in a landscape
415 genomics framework (Forester *et al.* 2019). The goal of GEA is to identify loci that have allele
416 frequencies that are associated with environmental gradients hypothesized *a priori* to drive local
417 adaption (Rellstab *et al.* 2015). GEA analyses are more powerful than F_{ST} outlier tests because
418 they make use of an additional source of data (De Mita *et al.* 2013; Forester *et al.* 2018), but they
419 can only identify loci associated with the environmental gradients included as predictor variables
420 in the analysis. Environmental variables also may be strongly correlated with each other and
421 with geographic distance, making associations with individual variables difficult to detect.

422 Within populations, adaptive variation and genomic signatures of selection can be
423 detected if samples are available over multiple generations (Mathieson & McVean 2013;
424 Gompert 2015). This is possible for many wildlife species that have been the subject of long-
425 term studies, and also where museum specimens can be used as historical genetic samples
426 (Dehasque *et al.* 2020). For example, Epstein *et al.* (2016) identified two genomic regions
427 showing signatures of selection in response to an epidemic disease – devil facial tumor disease
428 (DFTD) in Tasmanian devils (*Sarcophilus harrisii*) – by applying RADseq to samples collected
429 both before and after the disease appeared in three independent populations that were the focus
430 of long-term field studies. Signatures of selection in this case are shifts in allele frequency and
431 linkage disequilibrium at specific genomic locations, and concordant signatures across
432 populations are evidence for an adaptive response. Similarly, Bi *et al.* (2019) applied sequence
433 capture methods to museum and contemporary samples from two chipmunk species (*Tamias*
434 spp.) spanning a century and identified significant shifts in allele frequencies. Neither of these
435 studies specifically included phenotypic data on potential adaptive traits; nonetheless, both

436 identified specific candidate genes with known function that may affect fitness under changing
437 selection regimes in natural populations.

438 A complementary approach to determine the genetic basis of adaptative variation in
439 natural populations is genome-wide association studies (GWAS) (e.g., Béréños et al. 2015;
440 Husby et al. 2015). The goal of GWAS is to identify loci and alleles underlying phenotypic
441 variation by gathering large-scale genomic and phenotypic data on a set of individuals. For
442 instance, using some of the same long-term Tasmanian devil population studies described above,
443 Margres *et al.* (2018) used GWAS to identify loci associated with three DFTD-related
444 phenotypes and found that genetic factors explained a large proportion of the variance in
445 infection status and survival after infection of female Tasmanian devils. This study used a
446 hybrid RADseq and sequence capture approach and a pre-designed panel of nearly 16,000
447 markers that included some candidate selected loci from Epstein et al. (2016). GWAS often
448 require large sample sizes for sufficient statistical power (Kardos *et al.* 2016a), but this case
449 illustrates how GWAS can be complementary to selection studies, providing a multi-pronged
450 population genomics approach to understand the genetic basis of adaptation in wildlife
451 populations. All of these sources of data can be applied to predictive models of adaptation (Box
452 2) and to guide monitoring and genetic management of wildlife populations (discussed below).

453

454

455 **3.3 Genetic Drift and Deleterious Variation**

456 In addition to identifying loci that can provide the capacity to adapt to environmental change or
457 local conditions, population genomics can also reveal the genetic basis of reduced fitness in
458 small populations. A central paradigm in conservation genetics is that genetic drift in small

459 populations can cause inbreeding depression, reduce individual fitness, decrease population size,
460 and increase extinction probability, what has been referred to as the “extinction vortex” (Soulé &
461 Mills 1998). Deleterious alleles can rise to high frequency due to genetic drift, and mating
462 between close relatives in a small population can increase the expression of recessive deleterious
463 alleles in the homozygous state and reduce genome-wide heterozygosity, reducing individual
464 fitness. Identifying populations with low genetic variation, small effective population sizes, and
465 evidence of inbreeding depression is of paramount importance for the conservation of wildlife
466 populations.

467 Population genomics provides tools to understand the genetic basis of reduced fitness in
468 small wildlife populations and potentially address the issues through management actions. For
469 example, Apennine brown bears (*Ursus arctos marsicanus*) are a small, isolated population in
470 Italy. Bennazo et al. (2018) used whole-genome sequencing to discover that all variation was
471 lost in the mitochondrial genome and parts of the nuclear genome, and several deleterious alleles
472 were fixed, with predicted effects on physiology, development, and behavior. These analyses are
473 possible with annotated reference genomes, on which regions of reduced variation can be
474 mapped and the functional consequences of mutations in specific genes can be predicted (e.g. by
475 analyzing genomic data from island foxes [*Urocyon littoralis*] with the domestic dog [*Canis*
476 *domesticus*] reference genome, Robinson et al. 2016; also see Box 1).

477 In addition to current population size, the demographic history of a population can have
478 important and sometimes counter-intuitive effects on population fitness. For instance, the long-
479 term effective population size is lower in a population that has been small for a long time,
480 compared to one with a recent rapid decline. Nonetheless, the genetic or mutational load – the
481 fitness cost of accumulated deleterious mutations – can be lower in the first case and more severe

482 in the second, because strongly deleterious mutations can be purged during an extended period of
483 small size with inbreeding (Robinson et al. 2018; van der Valk et al. 2019a,b). In wildlife
484 species, this means that reduced population fitness may be more of a problem in recent
485 anthropogenic declines compared to populations that were small before human influence.
486 Conversely, the genetic effects of a population bottleneck can linger even after the population
487 has recovered demographically. Grossen et al. (2020) found that population bottlenecks in
488 successfully reintroduced Alpine ibex populations (Figure 1) had purged highly deleterious
489 mutations while allowing mildly deleterious ones to accumulate. As a result of all of these
490 factors, there may often be little relationship between genetic diversity or genetic load and
491 current population size, so that these genetic factors may not be reflected in conservation status
492 assessments such as IUCN listing (Diez-del-Molino et al. 2018; van der Valk et al. 2019b).

493

494

495 **4 Informing management actions**

496 Although application of population genomics to wildlife conservation and management has been
497 slow to develop (Shafer et al. 2015), population genomics studies are already generating
498 information that can help wildlife managers and conservation practitioners make difficult
499 management decisions (Walters & Schwartz 2020). We highlight specific examples of the
500 application of population genomics to conservation and management of wildlife populations
501 here.

502

503 **4.1 Identifying population units**

504 One of the most important first steps for managing populations is to identify and delineate the
505 boundaries of intraspecific conservation units (CUs), such as evolutionarily significant units
506 (ESUs) and management units (MUs). We define an ESU as a classification of populations that
507 have substantial reproductive isolation and adaptive differences so that the population represents
508 a significant evolutionary component of the species (Funk et al. 2012). An MU is a local
509 population that is managed as a distinct unit because of its demographic independence. An ESU
510 may contain multiple MUs. CUs may be further defined on the basis of specific adaptive
511 variation (e.g. Prince et al. 2017). These definitions implicitly rely on multiple concepts of
512 connectivity among populations, including demographic and multiple aspects of genetic
513 connectivity, which may be substantially different; for instance, the level of migration needed to
514 avoid inbreeding depression and loss of adaptive genetic variation may be much lower than that
515 needed to maintain demographic connectivity and directly increase population size through
516 immigration (Lowe & Allendorf 2010).

517 Population genomics tools can be applied to estimate multiple aspects of population
518 structure and connectivity, and in some cases have led to changes in management. The
519 population genomics work of Andrews et al. (2018b) revealed that one population (of canary
520 rockfish, *Sebastes pinniger*) listed under the U.S. ESA did not actually merit listing as a discrete
521 population, while a second (yelloweye rockfish, *S. ruberrimus*) harbored previously unknown
522 genetic differentiation (Walters & Schwartz 2020). Genomics studies have more power than
523 previous microsatellite studies to quantify overall (genome-wide) population differentiation; for
524 instance, McCartney-Melstad *et al.* (2018) applied RADseq data to the declining foothill yellow-
525 legged frogs (*Rana boylei*) and found five extremely differentiated clades that can serve as
526 management units for this species of conservation concern. Barbosa et al. (2018) used reduced

527 representation sequencing data following the framework of Funk et al. (2012) to delineate CUs
528 in Cabrera voles (*Microtus cabreræ*): ESUs on the basis of overall differentiation, MUs on the
529 basis of differentiation at neutral loci, and adaptive units (AUs) on the basis of outlier loci
530 (Figure 3). Previous results from environmental niche modeling and landscape genetics
531 connectivity analysis are also informative for designing strategies in this species (Barbosa et al.
532 2018). Once populations are delineated, the genomic data can also provide high-throughput
533 genotyping panels for assigning individuals to populations, and adaptive loci may be particularly
534 useful for this effort (Larson et al. 2014). For example, in anadromous fish species in which
535 multiple breeding populations mix during the oceanic phase where they may be subject to
536 harvest, breeding populations can be distinguished on the basis of some combination of neutral
537 and adaptive genetic markers (Waples et al. 2020).

538

539

540 **4.2 Genetic Monitoring**

541 Genetic monitoring of natural populations has played an important role in conservation,
542 and the advent of population genomics presents new opportunities for improving the utility of
543 genetic monitoring for wildlife (Mimura et al. 2017; Flanagan et al. 2018; Hunter et al. 2018;
544 Leroy et al. 2018). First, as described above, genomics tools can be used to rapidly design a
545 relatively small set of genetic markers that can be genotyped efficiently across many individuals,
546 often using minimally invasive sampling (Carroll et al. 2018). These marker panels can be
547 designed for specific goals, such as estimating population size or detecting hybridization. More
548 important, population genomics tools also allow monitoring of allele frequency changes at
549 adaptive loci. Monitoring changes at these loci can track changes in adaptive potential as a result

550 of environmental change or management actions, such as assisted migration or genetic rescue, so
551 that management strategies can be continually updated (Flanagan et al. 2018). Monitoring of
552 deleterious variants, such as those that cause inbreeding depression, could also be informative to
553 detect genomic erosion in small populations (Leroy et al. 2018). If monitoring reveals that
554 genetic problems are accumulating, or that a population is not showing evidence of an adaptive
555 response to environmental stressors, it would suggest more active management strategies.
556 Conversely, monitoring genetic variation at adaptive loci can inform managers on whether
557 evolutionary rescue is possible. For instance, in the case of Tasmanian devils and their
558 transmissible cancer described above, population genomics studies have revealed loci associated
559 with a rapid response to selection and with particular disease-related traits. Genetic monitoring
560 panels could specifically assay these loci to ensure that sufficient variation exists, both in natural
561 and in captive populations (Hohenlohe et al. 2019b).

562

563

564 **4.3 Assisted gene flow, genetic rescue, and translocations**

565 As wildlife populations become increasingly isolated in a fragmented world, managers
566 are faced with the decision of whether or not to restore gene flow by moving individuals between
567 populations to rescue them from population declines caused by the loss of genetic variation.
568 Genetic rescue is an increase in population fitness and decrease in extinction probability caused
569 by gene flow (Tallmon et al. 2004; Whiteley et al. 2015; Bell et al. 2019). Genetic rescue may
570 occur by reducing inbreeding depression via masking deleterious alleles expressed in the
571 homozygous state, or by infusing additive genetic variation on which selection can act so that
572 populations can adapt to changing environments (evolutionary rescue). Fitzpatrick and Funk

573 (2019) outline a variety of ways in which population genomics can help managers with decisions
574 regarding genetic rescue. First, genomics tools can help identify populations suffering from low
575 genetic variation and inbreeding depression, as outlined above, and map regions of low variation
576 across the genome (Box 1). Second, genomics can help identify the best potential source
577 populations that are not too adaptively divergent from the target recipient population. A fine-
578 scale genomic view could potentially identify source populations that best reduce genomic
579 regions of homozygosity while minimizing disruption of local adaptation. Finally, if and when
580 genetic rescue is implemented, genomic data can be used to monitor changes in genetic ancestry
581 across loci and the relative fitness of immigrants, residents, and hybrids to test whether gene
582 flow is increasing fitness as desired (Miller et al. 2012).

583 A number of genetic rescue attempts have been conducted in wildlife populations, and
584 some general trends are emerging (Bell et al. 2019). A risk of genetic rescue is outbreeding
585 depression – reduced fitness when assisted migration comes from a divergently adapted source
586 population. Some authors have suggested that outbreeding depression may be a low risk in most
587 cases (Frankham 2015; Chan et al. 2019; Fitzpatrick et al. 2020). In many wildlife species, the
588 problems of small populations and inbreeding depression may be the fairly recent effect of
589 human-caused fragmentation; in this case, these populations would not be expected to be highly
590 divergent adaptively, and assisted migration is more likely appropriate (Ralls et al. 2018). In
591 contrast, attempts at genetic rescue could impede ongoing evolutionary rescue if populations are
592 already rapidly evolving to a novel environmental condition, such as a disease (Hohenlohe et al.
593 2019b). In this case, population genomics tools can identify the pace and genetic nature of this
594 adaptation and inform management decisions.

595

596

597 **4.4 Managing for specific genetic variants**

598 For threatened and declining populations, a major concern is that adaptive alleles might
599 be lost by environmental stressors caused by humans. Prince et al. (2017) made the surprising
600 discovery that variation in a major life history trait in salmon—migration timing—is
601 underpinned by the same single locus across multiple populations in two different species,
602 Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*O. mykiss*). Thompson et al.
603 (2019) then went on to test the effects of a recently constructed dam on adaptive potential at this
604 locus, given that the dam selects against the spring-run phenotype because fish with this
605 phenotype historically spawned upstream of the dam. They found a dramatic reduction in the
606 frequency of the spring-run phenotype and allele underlying this phenotype. Simulations suggest
607 that the dam could lead to the complete loss of this allele in the near future. This situation
608 highlights a conundrum: in general, it may be inadvisable to manage populations on the basis of
609 a single allelic variant, because it could neglect important factors across the rest of the genome.
610 But in this case, a substantial ecological role and associated phenotypes could be lost with the
611 loss of this single allele.

612 Most genetic variation that is important to management is likely to be polygenic,
613 although there may be wide variation among populations and taxa. The number of loci affecting
614 fitness or adaptive capacity depends on the population history, and whether large-effect or small-
615 effect allelic variation plays a bigger role in either adaptive or deleterious variation (Grossen et
616 al. 2020). Population genomics tools are able to identify dozens to hundreds of candidate loci
617 associated with a trait or with fitness, and lead to high-throughput genotyping assays that could
618 target these loci (perhaps in combination with others). Most studies do not have the statistical

619 power to resolve the specific effects of each locus or even identify them with high confidence
620 (Hoban et al. 2016), and this will remain an unavoidable problem with the sample sizes available
621 in many wildlife populations (Margres et al. 2018). Thus, active management to favor particular
622 alleles could not be supported in these cases. But management strategies with genetic
623 monitoring could be designed to maintain variation at these loci, for instance in captive
624 populations and with the additional goal of maintaining variation genome-wide (Hogg et al.
625 2019), so that adaptive evolution is possible in the wild.

626

627

628 **4.5 *Ex situ* management**

629 Many wildlife species are kept in captivity, and some of these are either extinct in the wild or
630 limited to populations smaller than those in captivity, so that the captive populations represent
631 the majority of genetic variation in the species (e.g., Humble et al. 2020). These are often
632 subject to intensive genetic management and some degree of controlled breeding, and genomics
633 tools can be applied in multiple ways (Brandies et al. 2019). For instance, methods to estimate
634 demographic history, source population, or admixture can reveal much about captive individuals.
635 Genomics tools can rapidly provide marker sets for efficient genotyping. Even when pedigree
636 relationships are completely known, genomic data can provide more precise estimates of actual
637 genetic relatedness, inbreeding, and the proportion of the genome that is identical by descent
638 (Kardos et al. 2015; Box 2). Controlled breeding can be precisely designed to maximize
639 genome-wide diversity, to maintain genetic distinctiveness of source populations, or potentially
640 to manage for variation at particular loci as described above. Selection for traits that are favored

641 in captivity but maladaptive in the wild is a major problem for captive populations, and genetic
642 monitoring could focus on specific loci associated with adaptation to captivity.

643

644

645 **5 Improving connections between population genomics and conservation**

646 We have several different recommendations to improve translating the power of population
647 genomics research into better wildlife conservation and management decisions. Although
648 population genomics clearly provides unprecedented power to peer into the genomes of wildlife
649 species, a gap still remains between population genomics research and application to
650 conservation practice (Shafer *et al.* 2015; Garner *et al.* 2016).

651 Our first recommendation is for population genomicists to develop professional
652 relationships with managers and conservation practitioners. The old model of conducting
653 research, writing a paper on the results with a “conservation recommendations” section at the
654 end, and then expecting managers to find and use the research has been shown to be ineffective
655 at impacting management decisions. Fabian *et al.* (2019) surveyed Swiss professionals in nature
656 conservation and found that experience-based sources (e.g., personal exchange with colleagues
657 and experts) are more important than evidence-based sources (e.g., printed products and
658 journals). Articles in scientific journals were almost never consulted by conservation
659 practitioners. Given that conservation professionals have limited time to read scientific articles
660 and keep up with rapid pace of advancement in fields such as population genomics, it is essential
661 for scientists to build relationships and communicate directly with managers and conservation
662 practitioners if they want their science to improve conservation management and policy.
663 Holderegger *et al.* (2019) describe multiple frameworks, such as workshops, modes of

664 communication, and joint projects, that can facilitate connections between researchers and
665 practitioners.

666 A second recommendation is to let conservation and management questions guide
667 research. Oftentimes, a study or results that a researcher thinks are useful for conservation may
668 not be what a manager needs to know to make decisions that affect wildlife species. Ultimately,
669 research results can only guide conservation if they have bearing on management decisions.
670 Thus, researchers first need to know what decisions managers face and what management actions
671 are within the realm of possibility, and this communication should happen early in the research
672 process (Holderegger et al. 2019). Only then can researchers know what questions managers
673 need answered to help them decide the best management option. Building relationships with
674 managers, as above, is extremely helpful for learning about the problems and issues that
675 managers and conservation practitioners are faced with, where information gaps exist, and how
676 research can fill these information gaps. Relationships with managers will also provide
677 opportunities for researchers to communicate the types of questions genomics can and cannot
678 help answer.

679 Another recommendation for improving the translation of population genomics into
680 improved wildlife conservation and management is training for both aspiring population
681 genomics students and conservation practitioners, ideally together to foster direct interaction
682 between these groups. Population genomics workshops, for example, not only provide technical
683 training in the ever-expanding field of genomics; they can also provide opportunities for
684 conservation practitioners to gain exposure to the field to give them a better appreciation of the
685 capacity of population genomics, the steps involved, and how to apply it to the species they
686 manage and the questions they face. Fortunately, several genomics workshops now provide

687 venues to discuss the latest developments in population and conservation genomics, such as the
688 annual Population and Conservation Genomics workshop at the International Plant and Animal
689 Genomes Conference (<https://intlpag.org>), and hands-on training in population genomic analysis,
690 including the ConGen workshop at the University of Montana’s Flathead Lake Biological station
691 (<http://www.umt.edu/sell/cps/congen2019/>), the Genomics of Disease in Wildlife workshop at
692 Colorado State University (<https://gdworkshop.colostate.edu/>), and a variety of workshops
693 given across Europe by the G-BIKE (Genomic Biodiversity Knowledge for Resilient
694 Ecosystems) program (<https://sites.google.com/fmach.it/g-bike-genetics-eu/home>).

695 A final recommendation is for the population genomics community to continue
696 streamlining and standardizing bioinformatics tools and population genomics analyses. Many
697 bioinformatic pipelines and population genomics analyses require fairly advanced computer and
698 programming skills, which acts as a barrier to entering the “genomics world” for many students,
699 scientists, and conservation practitioners. Bioinformatics tools and population genomics
700 analyses need to be developed that are more broadly accessible. Moreover, bioinformatics
701 pipelines and guidelines for best practices have not yet been standardized. Fortunately,
702 significant progress is being made in the development of more user-friendly programs and clear
703 guidelines for collecting and applying genomics to wildlife biology and management (Gomez-
704 Sanchez & Schlötterer 2018; Gruber et al. 2018; Ravindrin et al. 2019).

705

706

707 **6 Conclusions and Future Prospects**

708 Even in the relatively short time (approximately 10 years) since genomic data have been applied
709 to population genetic questions in non-model organisms, population genomics has already helped

710 answer a wide variety of questions in the biology of wildlife species. There has been a relatively
711 slow uptake of population genomics results in influencing policy decisions and wildlife
712 management actions (Shafer et al. 2015), with a number of factors contributing to significant
713 time lags: researchers learning how to apply population genomics in wildlife species, studies
714 being completed through publication of results, communicating results and interpretation of
715 genomic data to conservation practitioners, integrating genomic results into the many sources of
716 information that influence policy decisions or conservation actions, etc. Nonetheless, a decade
717 on, examples of direct connections between population genomics research and wildlife
718 conservation actions are now rapidly accumulating (Walters & Schwartz 2020). A remaining
719 question, however, is whether population genomics can help stem the tide of cataclysmic
720 biodiversity declines given the accelerating urgency of the problems.

721 Population genomics research is by nature intensive and focused on one or a few species.
722 It has, therefore, been applied to wildlife species that are high-profile or of significant economic
723 interest, such as captive populations or salmonid fish (Waples et al. 2020), although the
724 decreasing costs of genomic studies and proliferation of resources like reference genome
725 assemblies have allowed these techniques to spread across taxa, and this trend will continue.
726 Future directions include expanding the “omics” toolkit to include transcriptomics, epigenomics,
727 or proteomics, which may improve our understanding of adaptive capacity in wildlife
728 populations and the role of gene expression, epigenetics, and phenotypic plasticity in population
729 fitness. There may also be a role for genetic engineering techniques in wildlife, such as gene
730 therapy or gene drive approaches to cause alleles to spread in a population (Breed et al. 2019;
731 Rode et al. 2019). In species that suffer from a well-understood, relatively simple genetic
732 problem, it could be conceivable to use a “rescue drive” – an attempt to spread a favored allele

733 into a population to increase fitness (Rode et al. 2019). However, this approach carries
734 numerous poorly understood risks, including the pitfalls associated with focusing management
735 on a narrow set of genetic factors (Kardos & Shafer 2018). Another approach is to use gene
736 drive techniques to control or eradicate invasive species that negatively affect native wildlife
737 (Rode et al. 2019). While invasive species can often require active management, and some level
738 of risk may be acceptable compared to taking no action, the risks of such eradication or
739 suppression drives are still poorly known.

740 A future need in conservation is to understand how population genomics tools can be
741 applied more broadly beyond single focal species, for instance at the ecosystem level (Breed et
742 al. 2019). One avenue is metagenomics approaches, where genetic samples include multiple
743 species, for instance with environmental DNA (eDNA; Goldberg & Parsley 2020). Population
744 genomics focused on species that are central to ecosystem interactions may also reveal the
745 community effects of genomic diversity (Hand et al. 2015). These may often be plants, such as
746 the dominant tree species in a forest ecosystem in which many other species are affected by its
747 genetics, and genomics tools can be important for seed sourcing in restoration efforts (Breed et
748 al. 2019). In other cases, wildlife species may play a similar role.

749 The field of population genomics continues to change rapidly, with technological and
750 analytical advances expanding the tools that are available in wildlife biology at the same time as
751 the need for conservation knowledge and action becomes more urgent. While it may be very
752 difficult to keep up to date with all of the changes, it is critical for both researchers and wildlife
753 professionals to maintain a broad understanding of the population genomics tools that are
754 available and to foster communication between wildlife scientists and practitioners.

755

756

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762

763

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1188 **Data Accessibility**

1189 No new data was generated or analyzed as part of this review article.

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1192 **Author Contributions**

1193 All authors contributed to writing the manuscript.

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1196 **Box 1 Understanding Inbreeding: runs of homozygosity**

1197 Loss of genetic diversity and inbreeding in small populations is a central threat to many wildlife
1198 populations. With fine-scale genomic data, such as short-read WGS data, mapped to a reference
1199 genome, it is possible to identify runs of homozygosity (ROH) – chromosomal regions that have
1200 few or no heterozygous nucleotide sites because both chromosome copies derive from a single
1201 copy in a relatively recent common ancestor (Ceballos et al. 2018). The proportion of the

1202 genome that is in ROH, or identical by descent, has long been central to the concept of
1203 inbreeding, but being able to map these regions in the genome reveals several novel insights that
1204 illustrate the power of population genomics approaches. First, ROH provide precise estimates of
1205 individual-level inbreeding which are more accurate than other methods (Kardos et al. 2015).

1206 Further, the lengths of ROH reveal details of demographic history and the time scale of
1207 inbreeding (Grossen et al. 2020). Part A of the figure shows heterozygosity across the genome
1208 of several wolf (*Canis* spp.) individuals from Robinson et al. (2019); regions where
1209 heterozygosity is absent are ROH. Long ROH are expected in offspring from matings between
1210 close relatives, reflecting recent inbreeding, as seen in the severely declining (now extinct)
1211 population on Isle Royale, Michigan, USA. In contrast, mainland outbred wolves had relatively
1212 few long ROH (Robinson et al. 2019). Ethiopian wolves had low genome-wide heterozygosity
1213 due to long-term small effective population size in an isolated population, but few long ROH
1214 suggesting relatively little contemporary inbreeding. Because recombination breaks up
1215 haplotype blocks with each generation, smaller ROH reflect older inbreeding events, so that the
1216 distribution of ROH lengths tells the history of inbreeding in a population. Part B of the figure
1217 shows the distribution of ROH lengths in 10 puma (*Felis concolor*) individuals, with size classes
1218 corresponding to the number of generations since the individual's maternal and paternal lineages
1219 shared common ancestor for that chromosomal region (Saremi et al. 2019).

1220 Genes that cause inbreeding depression due to recessive deleterious alleles in the
1221 homozygous state or the loss of heterozygosity at particular genes can be mapped by comparing
1222 the locations of ROH across individuals. Further, the relative locations of ROH among
1223 individuals and populations can be informative for controlled breeding or genetic rescue
1224 attempts. For example, if two individuals share ROH due to common ancestry, their offspring

1225 will also have those regions of reduced diversity. However, if two individuals have different
1226 ROH, mating between them can produce offspring with lower inbreeding coefficients,
1227 potentially relieving inbreeding depression. Part C of the Figure shows the extent of ROH
1228 sharing among puma individuals (Saremi et al. 2019); many pairs show only minimal sharing of
1229 ROH, but two individuals from Florida (CYP47 and CYP51) share ROH across a relatively large
1230 portion of their genomes due to identity by descent from severe inbreeding.

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1233 **Box 2 Adaptive potential**

1234 Adaptive potential (also called evolutionary potential) is the ability of a population to evolve
1235 genetically-based changes in traits in response to changing environmental conditions (Funk *et al.*
1236 2019). This is a component of the broader concept of adaptive capacity, which also includes
1237 non-genetic responses to environmental change, such as phenotypic plasticity and dispersal
1238 (Dawson et al. 2011; Nicotra et al. 2015). Species or populations with high adaptive potential
1239 are thus predicted to be less vulnerable to environmental change and more likely to survive in
1240 parts of their current distribution. Currently, we have a poor understanding of adaptive potential
1241 in many wild populations, so we do not know the extent to which it can buffer populations from
1242 rapid environmental change.

1243 Adaptive potential depends on genetic variation in resilience traits among individuals
1244 within populations, as well as genetic differences in these traits among populations and across
1245 environmental gradients. Population genomics provides methods for estimating the genetic
1246 variation or heritability of traits that are expected to be important for adaptation, or for fitness
1247 *per se*. de Villemereuil et al. (2019) assessed adaptive potential in the hihi (*Notiomystis cincta*),

1248 an endangered New Zealand passerine (Chen 2019). Combining RADseq and long-term
1249 phenotypic and fitness data, they found a lack of genome-wide diversity, low heritability of traits
1250 under selection, and little additive genetic variance of fitness, all indicating low adaptive
1251 potential in the sole remaining natural population and in a reintroduced population. Genomic
1252 evidence for a response to selection under current environmental stressors can reveal genetic
1253 variation and adaptive potential, for example in the case of disease like transmissible cancer in
1254 Tasmanian devils (Epstein et al. 2016) or white-nose syndrome in bats (Auteri & Knowles 2020).

1255 Another approach for assessing adaptive potential, particularly in the face of climate
1256 change, is to examine patterns of local adaptation to climate conditions across the current species
1257 range, and then project future climatic changes and species' responses (e.g., Prates et al. 2016;
1258 Ruegg et al. 2018; Waterhouse et al. 2018). Adaptive differences among populations can
1259 contribute to adaptive potential and can also inform assisted migration efforts. For instance,
1260 Razgour *et al.* (2019) uncovered adaptive differences related to spatial variation in climate in two
1261 Mediterranean bat species (*Myotis escalerai* and *M. crypticus*) by analyzing ddRAD data with
1262 GEA. Incorporating this climate-adaptive potential into forecasts of range changes under climate
1263 change reduced projected range reductions, highlighting the importance of taking adaptive
1264 potential into consideration in climate change vulnerability predictions. The Figure shows this
1265 conceptual framework, reprinted from Razgour et al. (2019). Similarly, Bay *et al.* (2018)
1266 identified genomic variation associated with climate across the breeding range of yellow
1267 warblers (*Setophaga petechia*). They found that populations that will require the greatest shifts
1268 in allele frequencies at these adaptive loci to keep pace with climate change have already
1269 experienced the most severe population declines, suggesting that inability to adapt to a changing
1270 climate may already be causing declines.

1271 **Figure 1:** Two types of genomic data have been used to estimate population size and
1272 demographic history in Alpine ibex (*Capra ibex*). Several reintroduced populations in
1273 Switzerland were derived from the same Italian source population, Gran Paradiso (GP). (A)
1274 Contemporary estimates of N_e across multiple populations of Alpine ibex and a related species
1275 based on RADseq-derived SNP loci and analysis of linkage disequilibrium. Note that confidence
1276 limits, particularly the upper limit, can be large or even infinite. Reproduced from Grossen et al.
1277 (2018). (B) WGS data can provide estimates of current N_e (shown as numbers in bold) as well as
1278 reconstruction of demographic history. Generation 3023 represents current populations.
1279 Reproduced from Grossen et al. (2020).

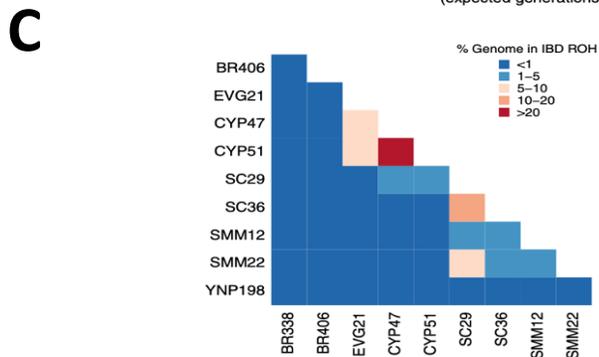
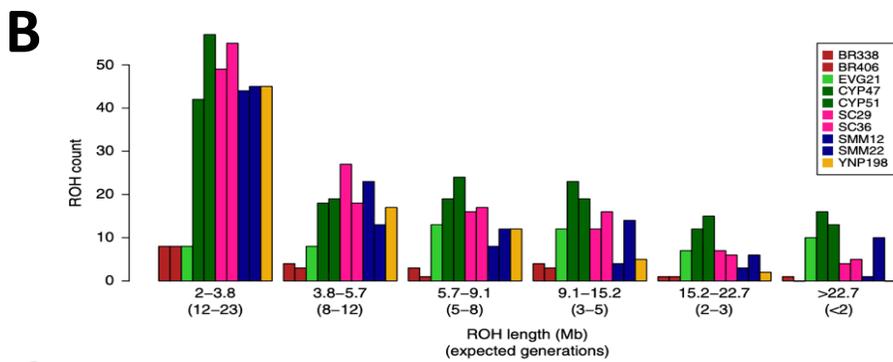
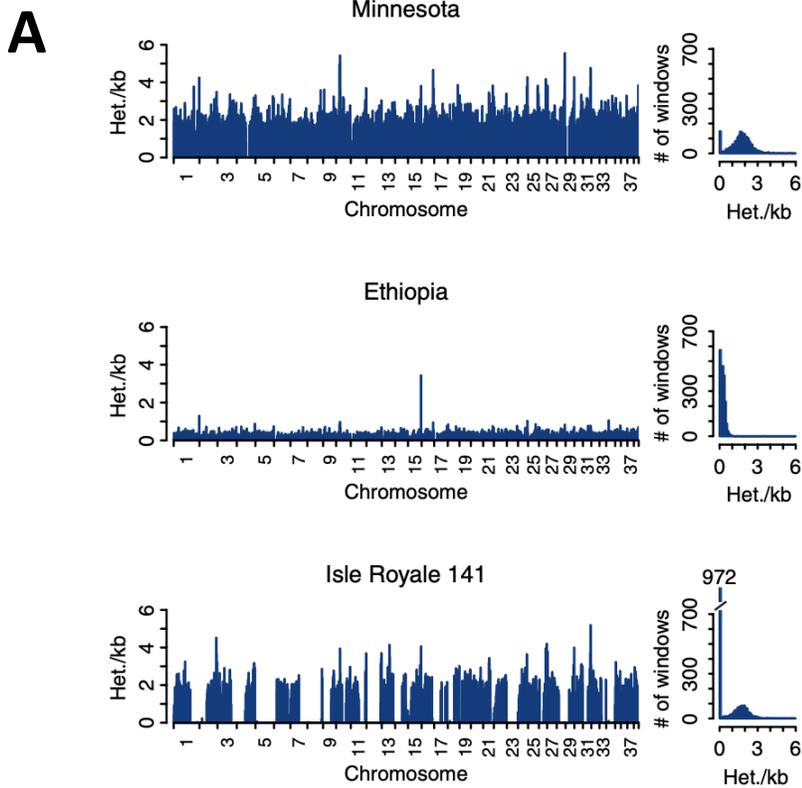
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1283 **Figure 2.** Inferring population structure in wildlife species. (A) Principal Components Analysis
1284 based on WGS reveals distinct populations of sage-grouse. The Gunnison sage-grouse (GU;
1285 *Centrocercus minimus*) had previously been recognized as a separate species, while the genetic
1286 distinctiveness of the Washington population (WA) of greater sage-grouse (*C. urophasianus*)
1287 from all other populations of this species was revealed by this study. Reproduced from Oh et al.
1288 (2019). (B) Genomic analysis of bobcat (*Lynx rufus*) populations in southern California show
1289 the effect of major highway corridors on gene flow. Colored points represent individuals
1290 assigned to genetic population groups, and red and black lines represent major highways.
1291 Reproduced from Kozakiewicz et al. (2019).

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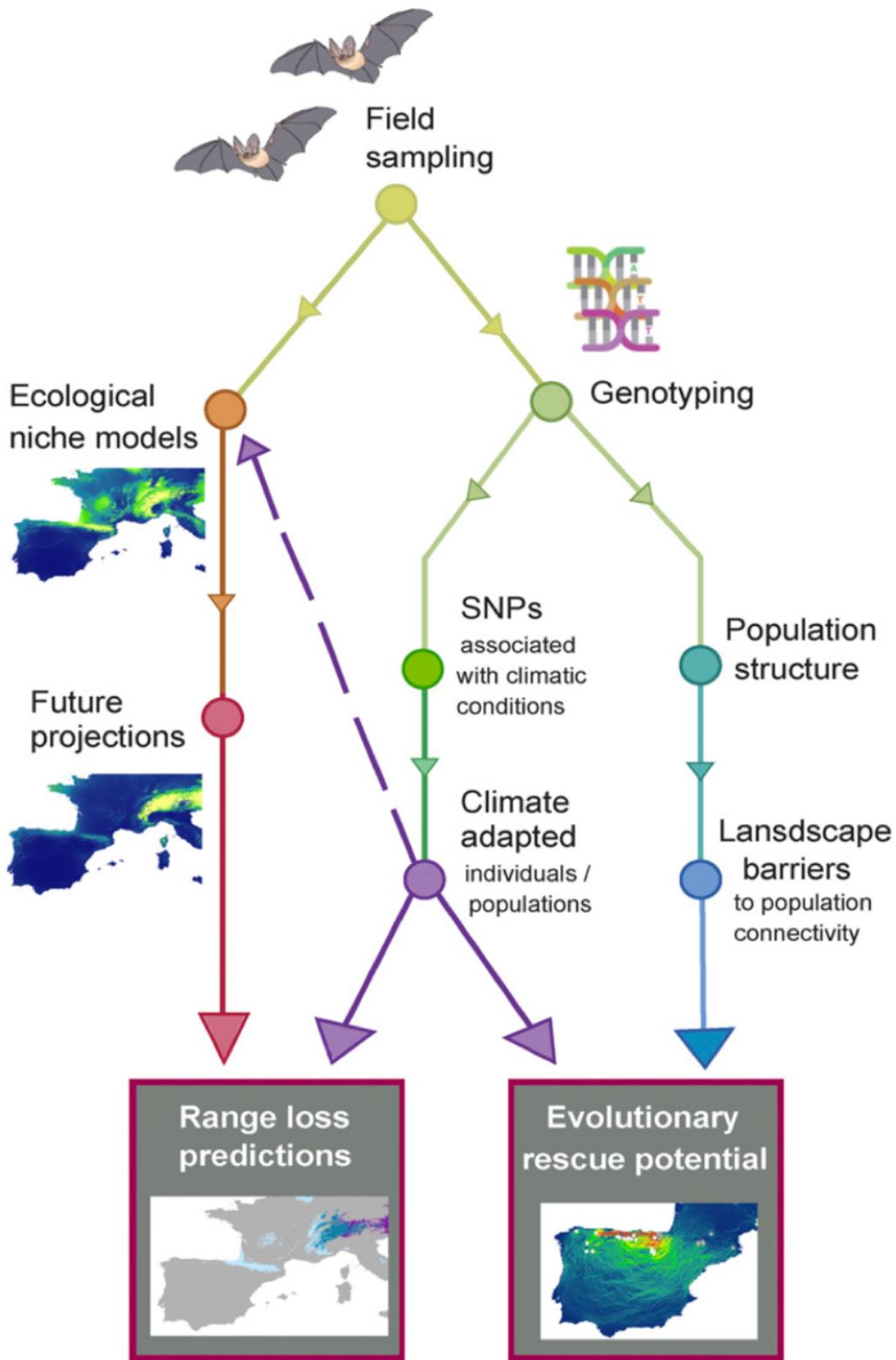
1295 **Figure 3:** Designation of conservation units in Cabrera voles (*Microtus cabrerae*) across the
1296 Iberian Peninsula. Genome-wide variation estimated from reduced representation sequencing
1297 provides greater resolution of evolutionarily significant units (ESUs) than previous microsatellite
1298 results. Neutral and adaptive variation facilitated delineation of management units (MUs) and
1299 adaptive units (AUs), respectively. Reproduced from Barbosa et al. (2018).

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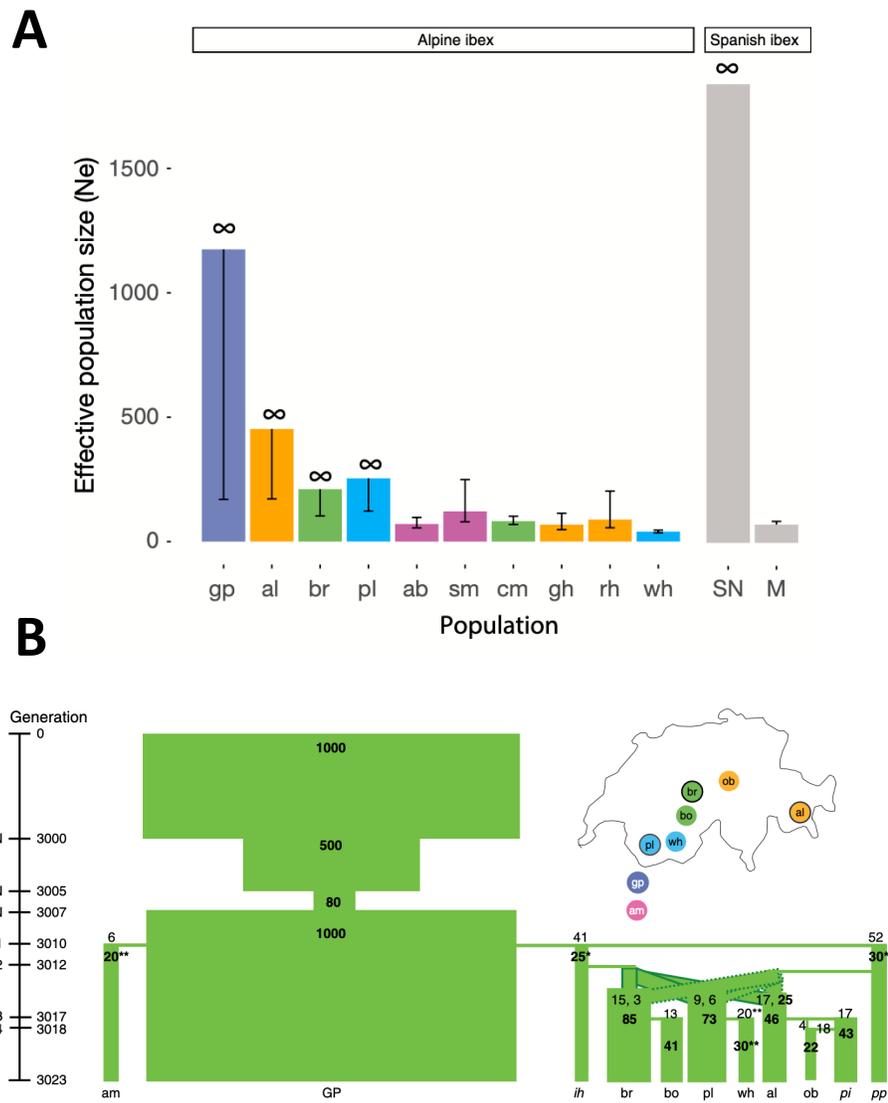
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Figure for Box 1



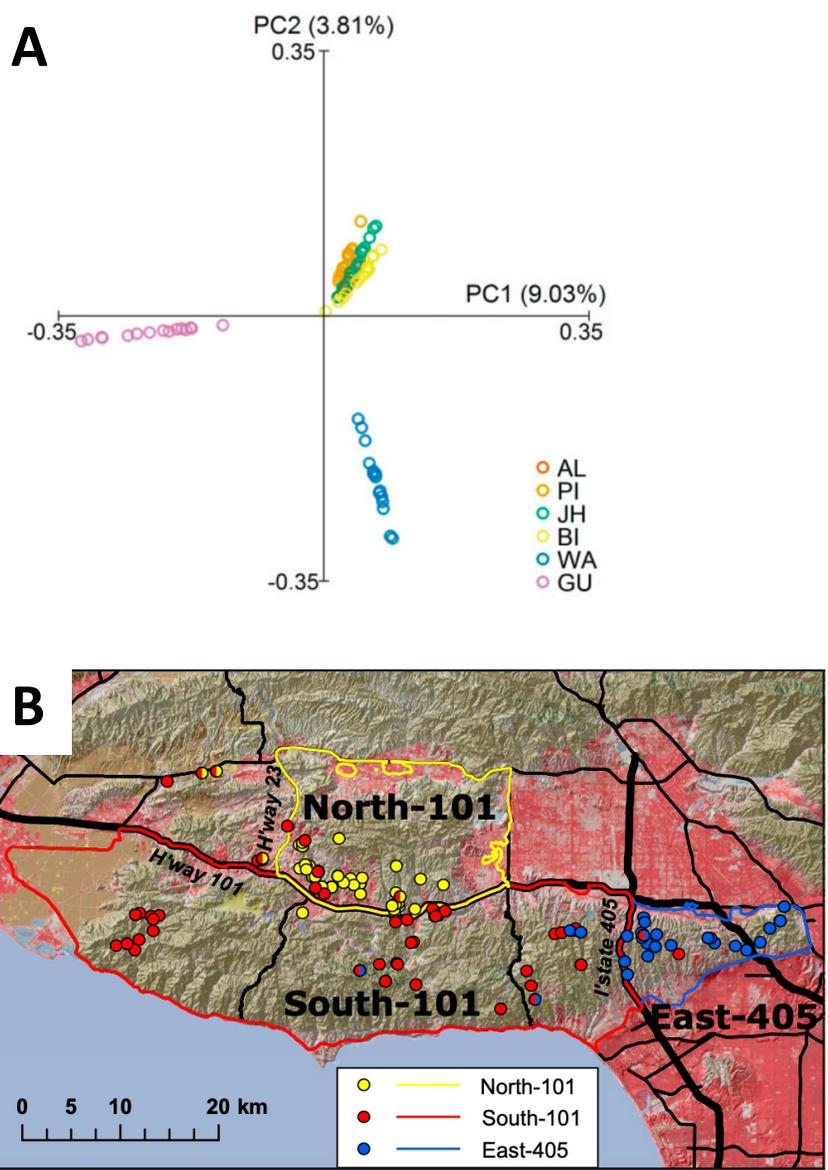
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1308 **Figure for Box 2**

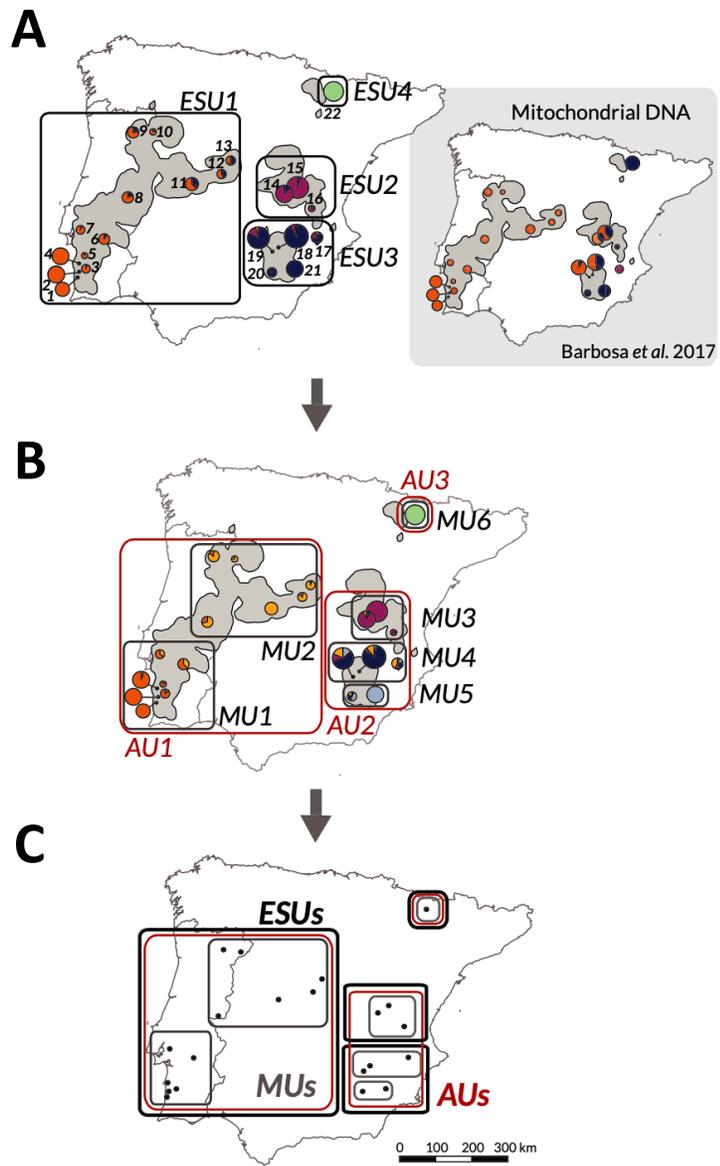


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Figure 1



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 1315 **Figure 2**
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Figure 3