

The long-standing significance of genetic diversity in conservation

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Abstract

Since allozymes were first used to assess genetic diversity in the 1960s and 1970s, biologists have attempted to characterize gene pools and conserve the diversity observed in domestic crops, livestock, zoos and (more recently) natural populations. Recently, some authors have claimed that the importance of genetic diversity in conservation biology has been greatly overstated. Here, we argue that a voluminous literature indicates otherwise. We address four main points made by detractors of genetic diversity's role in conservation by using published literature to firmly establish that genetic diversity is intimately tied to evolutionary fitness, and that the associated demographic consequences are of paramount importance to many conservation efforts. We think that responsible management in the Anthropocene should, whenever possible, include the conservation of ecosystems, communities, populations and individuals, and their underlying genetic diversity.

KEYWORDS

conservation biology, conservation genetics, population genetics – empirical, population genetics – theoretical

Genetic diversity, along with species and ecosystem diversity, is one of the three main pillars of biodiversity. The realization of genetic diversity's role in the conservation of biodiversity was fuelled by the discovery and characterization of widespread protein variation and the long-observed notion that close inbreeding was associated with declines in fitness (Brown, 1978; Lewontin, 1974). Historically, genetic diversity was characterized using allozyme and later microsatellite loci, and was typically reported as observed heterozygosity, mean allelic diversity and (in allozymes) the proportion of polymorphic loci. More recently, single nucleotide polymorphisms (SNPs) have largely replaced microsatellites. Because SNPs are typically biallelic due to mutation-drift equilibrium, genetic diversity at the nucleotide level is reported as observed heterozygosity or as SNP density. In addition, the distribution of structural variants is emerging as an orthologous measure of

genetic diversity (e.g., Weissensteiner et al., 2020). Whether one considers allozymes, microsatellites, SNPs or structural variants, population geneticists use these empirical assessments of genetic diversity to support one of the core goals of conservation genetics: maintaining genetic diversity across individuals in ways that support persistence of populations and species, even in the face of ongoing threats such as fragmentation and global climate change (Crandall et al., 2000; Moritz, 2002).

Recently, Teixeira and Huber (2021) argued against the perceived importance of neutral genetic diversity for the conservation of wild populations and species. While we respect their Perspective, a deeper dive into decades of conservation genetics literature contradicts many of their arguments. Here, we address four key points made by Teixeira and Huber that are counter to a robust literature focused on the genetics of wild and captive populations.

TABLE 1 Exemplar studies demonstrating positive relationships between genetic diversity and fitness

Species	Ecosystem	GD marker	GD estimator	Reference
Reproductive success				
Atlantic salmon (<i>Salmo salar</i>)	Diadromous	Microsatellite	r	Garant et al. (2005)
Kangaroo rat (<i>Dipodomys spectabilis</i>)	Terrestrial	Pedigree	F, r	Willoughby et al. (2019)
Black stilt (<i>Himantopus novaeseelandiae</i>)	Terrestrial	Microsatellite	H	Hagen et al. (2011)
Grey seal (<i>Halichoerus grypus</i>)	Marine	Microsatellite	r	Pomeroy et al. (2001)
Helmeted honeyeater (<i>Lichenostomus melanops</i>)	Terrestrial	SNP	F	Harrisson et al. (2019)
Kakapo (<i>Strigops habroptilus</i>)	Terrestrial	Microsatellite	r	White et al. (2015)
Leadbeater's possum (<i>Gymnobelideus leadbeateri</i>)	Terrestrial	SNP	H	Zilko et al. (2020)
Little spotted kiwi (<i>Apteryx owenii</i>)	Terrestrial	Microsatellite	H, F, A	Taylor et al. (2017)
Long-finned pilot whale (<i>Globicephala melas</i>)	Marine	Microsatellite	H, r	Amos et al. (2001)
Mandrill (<i>Mandrillus sphinx</i>)	Terrestrial	Microsatellite	H, r	Charpentier et al. (2005)
Mysid shrimp (<i>Americamysis bahia</i>)	Estuarine	Pedigree, AFLP	H, A	Markert et al. (2010)
Red-breasted flycatcher (<i>Ficedula parva</i>)	Terrestrial	Microsatellite	H	Mitrus et al. (2020)
Red deer (<i>Cervus elaphus</i>)	Terrestrial	SNP	F	Huisman et al. (2016)
Wandering albatross (<i>Diomedea exulans</i>)	Terrestrial	Microsatellite	H, r	Amos et al. (2001)
Viability/survival (adults and juveniles)				
Alpine marmot (<i>Marmota marmota</i>)	Terrestrial	Microsatellite	H	Silva et al. (2006)
Chalk-hill blue butterfly (<i>Polyommatus coridon</i>)	Terrestrial	Microsatellite	H, A	Vandewoestijne et al. (2008)
Chatham Island black robin (<i>Petroica nigra</i>)	Terrestrial	Pedigree	F	Kennedy et al. (2014)
Chinook salmon (<i>Oncorhynchus tshawytscha</i>)	Diadromous	Microsatellite	H	Rosengrave et al. (2016)
Common frog (<i>Rana temporaria</i>)	Terrestrial	Microsatellite	H, A, r	Lesbarreres et al. (2005)
Common toad (<i>Bufo bufo</i>)	Terrestrial	Allozyme	H, A	Hitchings and Beebee (1998)
European tree frog (<i>Hyla arborea</i>)	Terrestrial	Microsatellite	H, F	Andersen et al. (2004)
Florida panther (<i>Puma concolor coryi</i>)	Terrestrial	Microsatellite	H	Johnson et al. (2010)
Glanville fritillary butterfly (<i>Melitaea cinxia</i>)	Terrestrial	Allozyme	H	Saccheri et al. (1998)
Golden eagle (<i>Aquila chrysaetos</i>)	Terrestrial	SNP	H	Doyle et al. (2016)
Golden lion tamarin (<i>Leontopithecus rosalia</i>)	Terrestrial	Pedigree	F	Dietz et al. (2000)
Great reed warbler (<i>Acrocephalus arundinaceus</i>)	Terrestrial	Microsatellite	H, A	Hansson et al. (2001)
Great tit (<i>Parus major</i>)	Terrestrial	Pedigree	F	Szulkin et al. (2007)
Harbor seal (<i>Phoca vitulina</i>)	Marine	Microsatellite, SNP	H	Hoffman et al. (2014)
Harp seal (<i>Phoca groenlandica</i>)	Marine	Microsatellite	A	Kretzmann et al. (2006)
Imperial eagle (<i>Aquila adalberti</i>)	Terrestrial	SNP	H	Doyle et al. (2019)
North Island robin (<i>Petroica longipes</i>)	Terrestrial	Pedigree	F	Jamieson et al. (2007)
Red flour beetle (<i>Tribolium castaneum</i>)	Terrestrial	Microsatellite	H	Szűcs et al. (2017)
Rock iguana (<i>Cyclura nigriventris</i>)	Terrestrial	Pedigree	H, F	Moss et al. (2019)
Wolf (<i>Canis lupus</i>)	Terrestrial	Pedigree	F	Liberg et al. (2005)
Size, weight, growth rate				
American crow (<i>Corvus brachyrhynchos</i>)	Terrestrial	Microsatellite	H, r	Townsend et al. (2010)
American oyster (<i>Crassostrea virginica</i>)	Marine	Allozyme	H	Singh and Zouros (1978)

(Continues)

TABLE 1 (Continued)

Species	Ecosystem	GD marker	GD estimator	Reference
Blue mussel (<i>Mytilus edulis</i>)	Freshwater	Allozyme	H, F	Koehn and Gaffney (1984)
Common fruit fly (<i>Drosophila melanogaster</i>)	Terrestrial	SNP	F	Ørsted et al. (2019)
European eel (<i>Anguilla anguilla</i>)	Diadromous	Allozyme	H, A	Pujolar et al. (2005)
Gilthead sea bream (<i>Sparus aurata</i>)	Freshwater	Microsatellite	H, A	Borrell et al. (2011)
Rainbow trout (<i>Oncorhynchus mykiss</i>)	Freshwater	Allozyme	H	Danzmann et al. (1987)
Scots pine (<i>Pinus sylvestris</i>)	Terrestrial	Pedigree	F	Mullin et al. (2019)
Springtail (<i>Orchesella cincta</i>)	Terrestrial	AFLP	A	Ellers et al. (2011)
Tiger salamander (<i>Ambystoma tigrinum</i>)	Terrestrial	Allozyme	H	Mitton et al. (1986)
White-footed mouse (<i>Peromyscus leucopus</i>)	Terrestrial	Pedigree, SNP	H	Willoughby et al. (2017)
Disease/pathogen resistance				
Guppy (<i>Poecilia reticulata</i>)	Freshwater	Pedigree	F	Smallbone et al. (2016)
California sea lion (<i>Zalophus californianus</i>)	Marine	Microsatellite	R	Acevedo-Whitehouse et al. (2006)
House finch (<i>Carpodacus mexicanus</i>)	Terrestrial	Microsatellite	H	Hawley et al. (2005)
Soay sheep (<i>Ovis aries</i>)	Terrestrial	Microsatellite	H	Coltman et al. (1999)
Gamete quality				
Bladder campion (<i>Silene vulgaris</i>)	Terrestrial	AFLP	A	Keller and Taylor (2010)
European rabbit (<i>Oryctolagus cuniculus</i>)	Terrestrial	Microsatellite	H	Gage et al. (2006)
Flour beetle (<i>Tribolium castaneum</i>)	Terrestrial	Pedigree	F	Michalczyk et al. (2010)
Guppy (<i>Poecilia reticulata</i>)	Freshwater	Pedigree	F	Zajitschek and Brooks (2010)
Wild gourd (<i>Cucurbita pepo</i>)	Terrestrial	Pedigree	F	Hayes et al. (2005)

Note: Genetic diversity was measured as indicated by the "GD" marker column using relatedness (r), inbreeding coefficient (F), heterozygosity (H) or allelic diversity (A) as listed in the estimator column. Fitness-associated traits are indicated by subheadings within the table. These references do not represent a systematic or comprehensive survey of the literature, but are intended to provide the reader with a glimpse of the breadth and depth of the topical literature. There is ample evidence that as genetic diversity increases, fitness tends to increase as well, which leads to a reduced risk of extinction.

The first alleged problem with the use of genetic diversity in conservation is the lack of supporting evidence for the idea that higher levels of genetic diversity lead to an increase in fitness and long-term survival with a concomitant reduction in species extinction risk. Indeed, Teixeira and Huber (2021) write that "no simple general relationship exists between neutral genetic diversity and the risk of species extinction." Notwithstanding the paradoxical view of neutrality, such sweeping statements mischaracterize an impressive literature that spans decades. Textbook examples of the positive relationship between genetic diversity and fitness abound, including examples in fruit flies (*Drosophila melanogaster*) (Frankham, 1995), monkeyflower (*Mimulus guttatus*) (Willis, 1993) and field mice (*Peromyscus leucopus*) (Lacy et al., 2013), as well as many other diverse organisms that occupy a variety of ecosystems (Table 1; see also Chapman et al., 2009; Hedrick & Kalinowski, 2000). In one recent example, Scott et al. (2020) showed that individual heterozygosity predicted translocation success in threatened desert tortoises (Figure 1; Scott et al., 2020). While there is obviously variation in survival that is not explained by heterozygosity (Reed & Frankham, 2003), this does not undermine the

position that reduced genetic variability often imparts a substantial and negative effect on fitness in this and many other examples (Table 1).

The second criticism of using genetic diversity as a metric for identifying species of conservation concern is that endangered species do not always have less genetic diversity than species of lesser conservation need. Teixeira and Huber (2021) posit that "if genetic diversity is indeed a major factor affecting the health and survival of populations in the wild, then one would expect endangered species to show, on average, lower levels of diversity." Although there are many species-specific traits that can influence genetic diversity irrespective of conservation need (e.g., fecundity, mutation rate, breeding system), we have previously identified and reported the reduction of genetic diversity in threatened vs. nonthreatened species (Willoughby et al., 2015) as have Li et al. (2016)—see Figure 2—despite the fact that species of conservation concern are not identified based on any genetic diversity criteria. We continue to argue that identification of this trend, despite the influence of outlier species, suggests that genetic diversity should be considered in conjunction with other listing criteria and

we have made explicit recommendations to this end (Willoughby et al., 2015). For example, range size has long been used by the International Union for the Conservation of Nature (IUCN) to ascribe conservation status but does not completely capture conservation need, particularly during this time of globally shifting climates (Rattis et al., 2018; Runge et al., 2015). The evaluation of several lines of evidence, including genetic diversity, is needed to accurately identify species that most require conservation action in order to prevent extinctions.

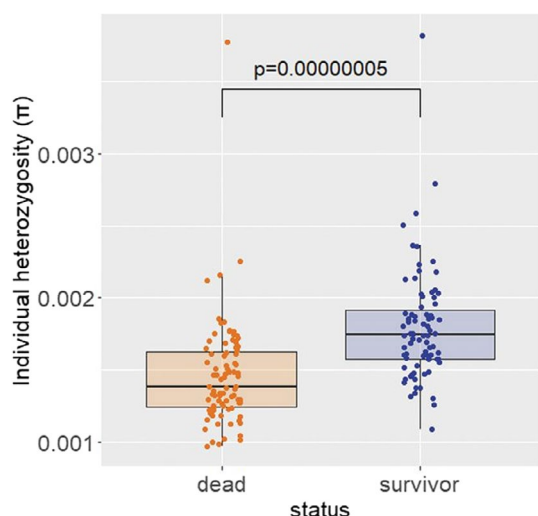


FIGURE 1 Genetic diversity in Mojave desert tortoises (*Gopherus agassizii*) that survived translocation was significantly higher than in individuals that did not survive. Individual heterozygosity was measured using ~6.7 million SNPs from RADSeq data sequenced for 87 dead (orange) and 79 surviving (blue) tortoises. Hence, lower genetic diversity was related to reduced fitness which contributes to extirpations and extinctions. Figure reproduced from Scott et al. (2020) [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/mec.16051)]

A third claim that purportedly undermines the utility of genetic diversity in conservation is that neutral diversity does not predict adaptive potential (Teixeira & Huber, 2021). Geneticists have long recognized that neutral diversity, which is now often measured as mean genome-wide diversity, is related to and correlated with functional diversity (Borrell et al., 2011; Fernandez-Fournier et al., 2021; Mackintosh et al., 2019; Nam et al., 2020; Willoughby et al., 2017). For example, Fernandez-Fournier et al. (2021) rank-ordered populations of yellow warblers (*Setophaga petechia*) and lodgepole pines (*Pinus contorta*) by mean genome-wide genetic diversity as well as by adaptive genetic diversity and found no difference in the rankings. This traditional conservation genetics framework, whereby adaptive diversity is characterized by neutral or genome-wide diversity, makes sense because adaptive loci often represent a small proportion of the genome or consist of many loci of small effect (Benestan et al., 2016; Mathur & DeWoody, 2021; Sella & Barton, 2019). Furthermore, many perturbations which threaten population persistence (fragmentation, bottlenecks, etc.) are expected to affect neutral and adaptive diversity similarly because drift overwhelms selection in small populations. Finally, diversity which may be neutral now could become adaptive in the future (Harrison et al., 2014). Excluding genetic diversity (neutral and/or functional) from conservation practice seems short-sighted and potentially catastrophic for species on the brink, particularly because we have only just begun to compile whole-genome data sets in these nonmodel species.

The fourth point used to dismiss the usefulness of conserving genetic diversity is that to do so requires a better understanding of functional genetic diversity, demographic history and ecological relationships for conservation (Teixeira & Huber, 2021). We think this is a straw man; one would be hard pressed to find a respectable conservation geneticist who thought otherwise. Indeed, we have argued elsewhere (Brüniche-Olsen et al., 2019; Willoughby et al., 2015) that the IUCN should incorporate measures of genetic/

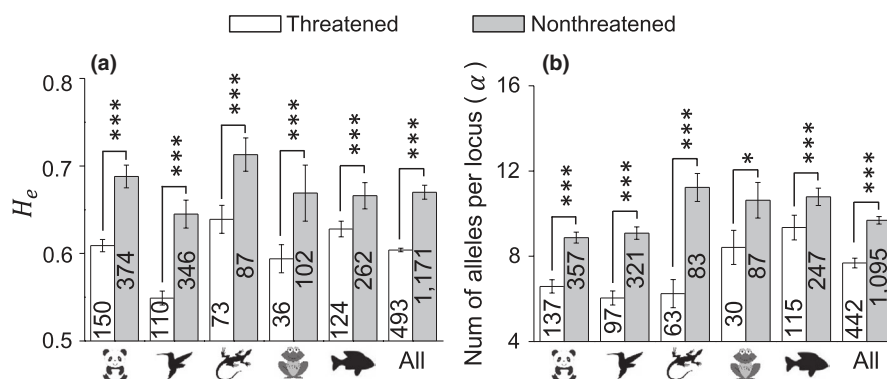


FIGURE 2 Threatened and endangered species have, on average, significantly lower levels of genetic diversity than nonthreatened species (from left to right: mammals, birds, reptiles, amphibians, fishes, all groups combined). Significance was estimated using permutation tests on expected heterozygosity (H_e ; left) and number of alleles (α ; right) per microsatellite locus between nonthreatened and threatened species with a null hypothesis that mean genetic diversity of nonthreatened species is equal to that of threatened species. Column number indicates the numbers of species compared in each category, and the one-tailed p values of the test are shown above the columns. * $p < .05$, *** $p < .01$. Figure from Li et al. (2016)

genomic diversity (e.g., heterozygosity or effective population size) as explicit criteria in Red Listing decisions to more accurately indicate the likelihood of future extinction and the associated need for conservation. However, it would be folly to suggest that demographic, environmental or ecological factors should be ignored or subsumed by genetic concerns as all are clearly integral to population persistence.

We agree with Teixeira and Huber (2021) that the global conservation emergency has “fostered the development and implementation of imperfect ... conservation strategies.” Our perspective—one shared by others (e.g. Hoban et al., 2020; Peart et al., 2020)—is that the consideration of genetic diversity in conservation has a strong theoretical justification, is backed by decades of empirical research and literature, and is empirically tractable for many species given current data and technological limitations. Furthermore, genetic diversity has predictive value (Scott et al., 2020) and, in the absence of knowledge of what variants are adaptive, approximates standing genetic variation and adaptive potential. We recognize that no one approach will be perfectly suited to characterizing all species and ecosystems, but we see no need to disregard informative data sets and thus we strongly support the use of genetics in establishing conservation priorities.

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CONFLICT OF INTEREST

None known, other than two of the authors are on the journal's Editorial Board.

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All authors contributed similarly to the contents of this manuscript.

DATA AVAILABILITY STATEMENT

Not applicable.

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