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CONSERVATION
and the **GENOMICS** of
POPULATIONS
THIRD EDITION



Fred W.
ALLENDORF

W. Chris
FUNK

Sally N.
AITKEN

Margaret
BYRNE

Gordon
LUIKART

Conservation and the Genomics of Populations

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Third Edition

Fred W. Allendorf

Division of Biological Sciences, University of Montana, USA

W. Chris Funk

Department of Biology, Colorado State University, USA

Sally N. Aitken

*Department of Forest and Conservation Sciences, Faculty of Forestry,
University of British Columbia, Canada*

Margaret Byrne

*Biodiversity and Conservation Science, Department of Biodiversity,
Conservation and Attractions, Australia*

Gordon Luikart

Flathead Lake Biological Station, University of Montana, USA

With illustrations by

Agostinho Antunes

University of Porto, Portugal

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Front cover image: Yellow-spotted monitor (*Varanus panoptes*) in Litchfield National Park,
Northern Territory, Australia. The collapse of this species is perhaps the most high-profile loss
caused by the invasion of the cane toad (Guest Box 14). Photo by Ed Kanze.

Back cover image: Old growth Sitka spruce (*Picea sitchensis*) in Carmanah Walbran Provincial Park,
British Columbia, Canada. The climber is sampling the tree from different
locations in order to estimate somatic mutation rates (Section 12.1). Photo by T.J. Watt.

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We dedicate this book to Michael E. Soulé, who died while we were working on this edition (Crooks et al. 2020). Michael was instrumental in the founding of the field of conservation biology by inspiring his basic science friends to apply their efforts to conserve biodiversity and by organizing a series of meetings in the late 1970s. He also co-authored the first book that applied the principles of genetics to conservation (Frankel & Soulé 1981).

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Preface to the Third Edition

I have always loved, and will always love, wild nature: Plants and animals. Places that are still intact. Though others might avoid the word, I insist that we talk about “love” in conservation, because we only protect what we love.

(Michael E. Soulé 2018)

The field of conservation genetics has changed dramatically since the second edition of this book was published in 2013. One-third of the references in this edition were written after the publication of the second edition. We have changed the title to reflect the growing and profound influence that genomics has had on applying genetics to problems in conservation. We have witnessed an extraordinary explosion of knowledge of the genetics and genomics of natural populations because genomic approaches have become more affordable and accessible. It has been a real challenge to add the new literature while keeping the book to a reasonable size. To accomplish this, we have put the Appendix and the References online. We understand that this is inconvenient, but we wanted to avoid an unwieldy book. Approximately 10% of the second edition was taken up by the References. The References and Appendix can be downloaded from the following companion website: www.oup.com/companion/AllendorfCGP3e.

We are excited to add Margaret Byrne and Chris Funk as coauthors. The five of us met in Missoula in July 2019 to plan our efforts (see Figure P.1). We have added [Chapter 24](#), which deals with the practical considerations of being a conservation geneticist and applying genetics to problems in conservation. We invited Helen R. Taylor to help write this chapter; she is the primary author of [Chapter 24](#).

This edition was written largely in the midst of the COVID-19 pandemic. Millions of people worldwide

have died from this tragic event. We send our deepest condolences to those who have lost loved ones from this global pandemic. The disease spillover from wildlife to humans is intimately linked to the topic of this book: conservation of biodiversity. This tragedy demonstrates that human health and well-being are inextricably tied to the health and well-being of the natural world. We hope this book furthers biodiversity conservation for the benefit of nature and humans.

Our guiding principle in writing has been to provide the conceptual basis for understanding the genetics of biological problems in conservation. We have not attempted to review the extensive and ever-growing literature in this area. Rather, we have tried to explain the underlying concepts and to provide examples and key citations for further consideration. We also have strived to provide enough background so that students can read and understand the primary literature.

There is a wide variety of computer programs available to analyze genetic and genomic data to estimate parameters of interest. However, the ease of collecting and analyzing data has led to an unfortunate and potentially dangerous reduction in the emphasis on understanding theory in the training of population and conservation geneticists. Understanding theory remains crucial for correctly interpreting outputs from computer programs and statistical analyses. For example, the most powerful



Figure P.1 The authors (left to right: Chris Funk, Margaret Byrne, Sally Aitken, Fred Allendorf, and Gordon Luikart) on the campus of the University of Montana.

software programs that estimate important parameters, such as effective population size (Chapter 7) and gametic disequilibrium (Chapter 10), can be misleading if their assumptions and limitations are not understood. We are still disturbed when we read statements in the literature that the loci studied are not linked because they are not in linkage (gametic) disequilibrium.

We have striven for a balance of theory, empirical examples, and statistical analysis (see Figure P.2). Population genomics provides unprecedented power to understand genetic variation in natural populations. Nevertheless, application of this information requires sound understanding of population genetics theory. To quote Joe Felsenstein: “We have the same situation in population genomics. People have vast amounts of data and do completely half-ass things with it because they don’t know any better. And, I wish there was some way of persuading people that we need to train students in the development and properties of the methods. And that means population genetics.”

The molecular tools being used by population geneticists continue to change rapidly. It has been difficult to decide which techniques to include in Chapters 3 and 4. We present some techniques

that are seldom or no longer used (e.g., allozymes) because they are crucial for understanding much of the previous conservation genetics literature.

We also have included a comprehensive Glossary. Words included in the Glossary are **bolded** the first time they are used in each chapter. Many of the disagreements and long-standing controversies in population and conservation genetics result

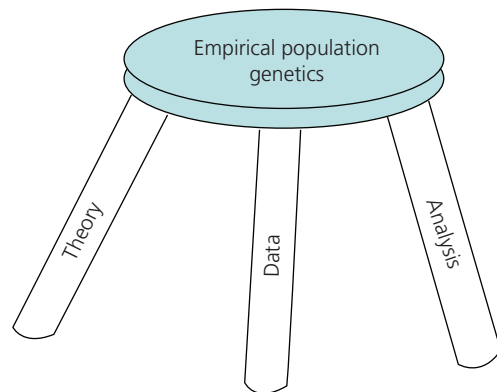


Figure P.2 The application of population genetics to understand genetic variation in natural populations relies upon a combination of understanding theory, collecting data, and understanding analysis.

from people using the same words to mean different things. It is important to define and use words precisely.

Many of our colleagues have written Guest Boxes that present their own work in conservation genetics. Each chapter contains a Guest Box that provides further consideration of the topics from that chapter. These boxes provide the reader with broader voices in conservation genetics from some of the major contributors to the literature in conservation genetics from around the world.

We have lost some special colleagues since the publication of the second edition. We have dedicated this edition to Michel Soulé, who co-authored

a Guest Box in the first two editions of this book. We were saddened to learn that Elaina Tuttle, who wrote a Guest Box in the previous edition, passed away in 2016. Fred's good friend and colleague Ian Jamieson passed away in 2015. Ian had an important influence on Fred's understanding of genetic load (Box 17.1), population viability, and rugby.

Fred W. Allendorf
W. Chris Funk
Sally N. Aitken
Margaret Byrne
Gordon Luikart
12 February 2021

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Otto, Andy Overall, Jim Patton, Bret Payseur, Rod Peakall, Jill Pecon-Slattery, Eleni Petrou, Robert Pitman, Craig Primmer, Reg Reisenbichler, Bruce Rieman, Pete Ritchie, Bruce Rittenhouse, Bruce Robertson, Rob Robichaux, Marina Rodriguez, Rafael Ribeiro, Beth Roskilly, Norah Saarman, Mike Schwartz, Jim Seeb, Brad Shaffer, Pedro Silva, Stephen Smith, Pia Smets, Doug Soltis, Pam

Soltis, Paul Spruell, Dave Tallmon, Mark Tanaka, Barb Taylor, Dave Towns, Kathy Traylor-Holzer, Daryl Trumbo, Hayley Tumas, Susannah Tysor, Dragana Obrecht Vidacovic, Randal Voss, Hartmut Walter, Robin Waples, Tongli Wang, John Wenburg, Andrew Whiteley, Mike Whitlock, Jeannette Whitton, Briana Whitaker, Jack Woods, and Sam Yeaman.

Guest Box Authors

Helen R. Taylor Royal Zoological Society of Scotland, Edinburgh, Scotland, UK (helentaylor23@gmail.com). Primary author of Chapter 24.

Kenneth K. Askelson Biodiversity Research Centre, and Department of Zoology, University of British Columbia, Vancouver, British Columbia, Canada (askelson@zoology.ubc.ca). Chapter 20.

Rachael A. Bay Department of Evolution and Ecology, University of California Davis, Davis, California, USA (rbay@ucdavis.edu). Chapter 16.

Mark A. Beaumont School of Biological Sciences, University of Bristol, Bristol, UK (m.beaumont@bristol.ac.uk). Appendix.

Oliver F. Berry Environomics Future Science Platform, The Commonwealth Scientific and Industrial Research Organisation, Crawley, Western Australia, Australia (oliver.berry@csiro.au). Chapter 13.

Iris Biebach Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland (iris.biebach@ieu.uzh.ch). Chapter 18.

Shane C. Campbell-Staton Department of Ecology and Evolutionary Biology and Institute for Society and Genetics, University of California Los Angeles, Los Angeles, California, USA (scampbellstaton@princeton.edu). Chapter 8.

James F. Crow Laboratory of Genetics, University of Wisconsin, Madison, Wisconsin, USA. Deceased (1916–2012). Chapter 5.

Janine E. Deakin Institute for Applied Ecology, University of Canberra, Canberra, Australia (janine.deakin@canberra.edu.au). Chapter 3.

Eleanor E. Dormontt School of Biological Sciences, The University of Adelaide, Adelaide, Australia (eleanor.dormontt@adelaide.edu.au). Chapter 22.

Nicolas Dussex Centre for Palaeogenetics and Department of Bioinformatics and Genetics, Swedish Museum of Natural History, Stockholm, Sweden (nicolas.dussex@gmail.com). Chapter 6.

Holly B. Ernest Wildlife Genomics and Disease Ecology Lab, University of Wyoming, Laramie, Wyoming, USA (holly.ernest@uwyo.edu). Chapter 19.

Peter J.S. Fleming Vertebrate Pest Research Unit, New South Wales Department of Primary Industries, Orange, New South Wales, Australia (peter.fleming@dpi.nsw.gov.au). Chapter 13.

Yasmin Foster Department of Zoology, University of Otago, Dunedin, New Zealand (y.al.foster@gmail.com). Chapter 6.

Armando Geraldés Biodiversity Research Centre and Departments of Zoology and Botany, University of British Columbia, Vancouver, British Columbia, Canada (geraldes@mail.ubc.ca). Chapter 20.

J. Paul Grobler Genetics Department, University of the Free State, Bloemfontein, South Africa (groblerjp@ufs.ac.za). Chapter 23.

Kyle D. Gustafson Department of Biological Sciences, Arkansas State University, Jonesboro, Arkansas, USA (kgustafson@astate.edu). Chapter 19.

Philip W. Hedrick School of Life Sciences, Arizona State University, Tempe, Arizona, USA (philip.hedrick@asu.edu). Chapter 12.

Paul A. Hohenlohe Department of Biological Sciences, Institute for Bioinformatics and

Evolutionary Studies, University of Idaho, Moscow, Idaho, USA (hohenlohe@uidaho.edu). Chapter 4.

Jo Howard-McCombe School of Biological Sciences, University of Bristol, Bristol, UK (j.howard-mccombe@bristol.ac.uk). Appendix.

Darren Irwin Biodiversity Research Centre and Department of Zoology, University of British Columbia, Vancouver, British Columbia, Canada (irwin@zoology.ubc.ca). Chapter 20.

Marty Kardos Northwest Fisheries Science Center, National Marine Fisheries Service, Seattle, Washington, USA. (martin.kardos@noaa.gov). Chapter 17.

Lukas F. Keller Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland (lukas.keller@ieu.uzh.ch). Chapter 18.

Antoinette Kotzé Foundational Research and Services, South African National Biodiversity Institute, Pretoria, South Africa (A.Kotze@sanbi.org.za). Chapter 23.

Linda Laikre Division of Population Genetics, Department of Zoology, Stockholm University, Stockholm, Sweden (linda.laikre@popgen.su.se). Chapter 7.

Andrew J. Lowe School of Biological Sciences, The University of Adelaide, Adelaide, Australia (andrew.lowe@adelaide.edu.au). Chapter 22.

Juha Merilä Ecological Genetics Research Unit, Organismal and Evolutionary Biology Research Programme, University of Helsinki, Helsinki, Finland, and Research Division for Ecology and Biodiversity, School of Biological Sciences, The University of Hong Kong, Hong Kong, SAR (merila@hku.hk). Chapter 15.

Paolo Momigliano Ecological Genetics Research Unit, Organismal and Evolutionary Biology Research Programme, University of Helsinki, Helsinki, Finland (Paolo.momigliano@helsinki.fi). Chapter 15.

Sarah P. Otto Biodiversity Research Center, University of British Columbia, Vancouver, British Columbia, Canada (otto@zoology.ubc.ca). Chapter 1.

Sally Potter Australian Museum Research Institute, Australian Museum, Sydney, New South

Wales, Australia and Research School of Biology, Australian National University, Acton, Australia (sally.potter@anu.edu.au). Chapter 3.

Uma Ramakrishnan National Centre for Biological Sciences, Tata Institute of Fundamental Research, Bangalore, India (uramakri@ncbs.res.in). Chapter 9.

Bruce C. Robertson Department of Zoology, University of Otago, Dunedin, New Zealand (bruce.robertson@otago.ac.nz). Chapter 6.

Robert H. Robichaux Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona, USA (robichau@email.arizona.edu). Chapter 21.

Lee A. Rollins Evolution and Ecology Research Centre, Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, New South Wales, Australia (l.rollins@unsw.edu.au). Chapter 14.

Nils Ryman Division of Population Genetics, Department of Zoology, Stockholm University, Stockholm, Sweden (nils.ryman@popgen.su.se). Chapter 7.

Michael K. Schwartz USDA Forest Service, National Genomics Center for Wildlife and Fish Conservation, Missoula Montana, USA (Michael.k.schwartz@usda.gov). Chapter 24.

Richard Shine Department of Biological Sciences, Macquarie University, New South Wales, Australia (rick.shine@mq.edu.au). Chapter 14.

Victoria L. Sork Department of Ecology and Evolutionary Biology and Institute of Environment and Sustainability, University of California Los Angeles, Los Angeles, California, USA (vlsork@ucla.edu). Chapter 11.

Danielle Stephens Zoological Genetics, Inglewood, South Australia, Australia (stephens@zoolgenetics.com). Chapter 13.

Robin S. Waples Northwest Fisheries Science Center, Seattle, Washington, USA (Robin.Waples@noaa.gov). Chapter 10.

Kelly R. Zamudio Department of Ecology and Evolutionary Biology, Cornell University Museum of Vertebrates, Cornell University, Ithaca, New York, USA (krz2@cornell.edu). Chapter 2.

List of Symbols

This list includes mathematical symbols with definitions and references to the primary chapters in which they are used. There is quite a bit of duplication, which reflects the general usage in

the population genetics literature. However, the specific meaning should be apparent from the context and chapter.

Symbol	Definition	Chapter
Latin Symbols		
\hat{x}	estimate of parameter x	Appendix (A)
A	number of alleles at a locus	3, 4, 5, 6
B	the number of lethal equivalents per gamete	17
CV_A	additive coefficient of variation	11
D	Jost's measure of differentiation	9
D	Nei's genetic distance	9, 20
D	coefficient of gametic disequilibrium	10, 13
D'	standardized measure of gametic disequilibrium	10
D_B	gametic disequilibrium caused by population subdivision	10
D_C	composite measure of gametic disequilibrium	10
E	probability of an event	A
e^2	environmental effect in heritability	11
e_μ	evolvability; the proportional change expected in a trait mean value under a unit strength of selection	11
f	inbreeding coefficient	6
F	realized proportion of genome that is identical by descent	17
F_{ij}	coefficient of coancestry	9
F_{IS}	departure from Hardy–Weinberg proportions within local demes or subpopulations	5, 6, 9, 11, 17, A
F_{IT}	overall departure from Hardy–Weinberg proportions	9
F_k	temporal variance in allele frequencies	A
F_P	pedigree inbreeding coefficient	6, 17, A
F_{SR}	proportion of the total differentiation due to differences among subpopulations within regions	9
F_{ROH}	proportion of the genome that is IBD as estimated by runs of homozygosity	17

Symbol	Definition	Chapter
F_{ST}	proportion of genetic variation due to differences among populations	3, 9, 12, 13, 14, 19, 21, A
$F2_{ST}$	F_{ST} value using the frequency of the most common allele and all other allele frequencies binned together	9
G	generation interval	7, 15, 21
G_{ST}	F_{ST} extended for three or more alleles	9
G'_{ST}	standardized measure of G_{ST}	9
h	gene diversity, computationally equivalent to H_e , especially useful for haploid marker systems	3, 7
h	degree of dominance of an allele	12
h	heterozygosity	6, 7
h^2	narrow sense heritability/proportion of phenotypic variance due to genotypic value	11
H_A	alternative hypothesis	A
H_B	broad sense heritability	11
H_e	expected proportion of heterozygotes	3, 5, 6, 7, 9, 14, 19, 22, A
H_o	observed heterozygosity	3, 6, 9, A
H_0	null hypothesis	A
H_N	narrow sense heritability	11, 15, 18, 21
H_S	mean expected heterozygosity	3, 9, 12, 19
H_T	total genetic variation	9, 12, 14, 19
K	carrying capacity	6, 18
k	number of gametes contributed by an individual to the next generation	7
k	number of populations	20, A
L	number of loci	17
m	proportion of migrants	9, 19, 20, 21
mk	mean kinship	22
mN	number of migrants per generation	9
MP	match probability	22
N	population size	5, 6, 7, 9, 12, A
n	sample size	3, A
n	ploidy level	3
N_b	number of breeders per reproductive cycle	7, 23
N_C	census population size	7, 15, 18, 23, A
N_C	proportion of individuals that reproduce in captivity	21
N_W	proportion of individuals that reproduce in the wild	21
N_e	effective population size	4, 7, 8, 9, 10, 11, 12, 15, 18, 21, 23, A
N_{eI}	inbreeding effective population size	7
N_{eV}	variance effective population size	7
N_f	number of females in a population	6, 7, 9
N_m	number of males in a population	6, 7, 9
NS	Wright's neighborhood size	9
P	proportion of loci that are polymorphic	3, 5
P	probability of an event	5, A

Symbol	Definition	Chapter
p	frequency of allele A_1 (or A)	5, 6, 8, 9, 11
p	proportion of patches occupied in a metapopulation	19
PE	probability of paternity exclusion; average probability of excluding (as father) a randomly sampled nonfather	22
PI_{av}	average probability of identity	22, 23
q	frequency of allele A_2 (or a)	5, 6, 8, 9, 11
Q	probability two alleles are identical in state	9
Q	probability of an individual's genotype originating from each population	20
Q_{ST}	proportion of total genetic variation for a phenotypic trait due to genetic differentiation among populations (analogous to F_{ST})	11
r	frequency of allele A_3	5
r	correlation coefficient	A
r	rate of recombination	4, 10
r	intrinsic population growth rate	6, 18
r_A	correlation between two traits	11
R	correlation coefficient between alleles at two loci	10
R	response to selection	11, 15
R	number of recaptured individuals	18
R	rate of adaptation to captivity	21
$R(g)$	allelic richness in a sample of g genes	5, 23
R_{ST}	analog to F_{ST} that accounts for differences length of microsatellite alleles	9, 20
S	self-incompatibility locus	8, 18
S	selection differential	11, 15, 21
S	effects of inbreeding on the probability of survival	17
S	selfing rate	9
s	selection coefficient (intensity of selection)	8, 9
s_x	standard deviation	A
s_x^2	sample variance	A
t	number of generations	6
V_A	proportion of phenotypic variability due to additive genetic differences between individuals	11, 12, 18
V_D	proportion of phenotypic variability due to dominance effects (interactions between alleles)	11
V_E	proportion of phenotypic variability due to environmental differences between individuals	2, 11, 18
V_G	proportion of phenotypic variability due to genetic differences between individuals	2, 11
V_I	proportion of phenotypic variability due to epistatic effects	11
V_k	variance of the number of offspring contributed to the next generation	7
V_m	increase in additive genetic variation per generation due to mutation	12, 18
V_P	total phenotypic variability for a trait	2, 11
V_q	binomial sampling variance	6
W	absolute fitness	8, 11
w	relative fitness	8, 11

Symbol	Definition	Chapter
Greek Symbols		
α	probability of a false positive (Type I) error	A
β	probability of a false negative (Type II error)	A
Δ	change in value from one generation to the next	6, 7, 8
δ	proportional reduction in fitness due to selfing	17
θ	population scaled mutation rate	12
λ	factor by which population size increases each time unit	18, 19
μ	population mean	A
μ	neutral mutation rate	12
π	nucleotide diversity	3, 5
π	probability of an event	A
σ_x^2	population variance	A
Φ_{ST}	analogous to F_{ST} but incorporates genealogical relationships among alleles	9
X^2	chi-square statistic	A
Other Symbols		
x	number of observations or times that an event occurs	A
\bar{x}	sample mean	A
\bar{x}^2	sample variance (second moment)	A
\bar{x}^3	skewness of sample distribution (third moment)	A

List of Abbreviations

Abbreviation	Meaning		
ABC	approximate Bayesian computation	eDNA	environmental DNA
AFLP	amplified fragment length polymorphism	EM	expectation maximization
AMOVA	analysis of molecular variance	EST	expressed sequence tag
ANOVA	analysis of variance	EPBC Act	Australian Environment Protection and Biodiversity Conservation Act 1999
BAMBI	Baltic Sea Marine Biodiversity	ESA	United States Endangered Species Act
<i>Bd</i>	<i>Batrachochytrium dendrobatidis</i>	ESU	evolutionarily significant unit
BIC	Bayesian Information Criterion	FAO	Food and Agriculture Organization of the United Nations
BLAST	Basic Local Alignment Search Tool	FCA	frequency correspondence analysis
BLUP	best linear unbiased prediction	FIE	fisheries induced evolution
BOLD	Barcode of Life Data Systems	Gb	gigabase
bp	base pair	GBS	genotyping-by-sequencing
BSC	biological species concept	GCM	global climate model
CBD	Convention on Biological Diversity	GEA	genotype–environment association
CBOL	Consortium for the Barcode of Life	GEBV	genomic-estimated breeding value
cDNA	complementary DNA	GEOBON	Group on Earth Observations Biodiversity Observation Networks
CITES	Convention on International Trade in Endangered Species of Wild Fauna and Flora	GD	gametic disequilibrium
CKMR	close-kin mark–recapture	GO	gene ontology
cM	centimorgan	GWAS	genome-wide association study
CMS	cytoplasmic male sterility	HDFW	Hawai‘i Division of Forestry and Wildlife
CMR	capture–mark–recapture	HFC	heterozygosity–fitness correlation
cpDNA	chloroplast DNA	HIV	human immunodeficiency virus
CPSG	Conservation Planning Specialist Group	HW	Hardy–Weinberg
CRISPR	clustered regularly interspaced short palindromic repeats	IAM	infinite allele model
CTSG	Conservation Translocation Specialist Group	IBD	identical by descent
CU	conservation unit	iBOL	International Barcode of Life Initiative
CWD	chronic wasting disease	ICES	International Council for the Exploration of the Sea
DAPC	discriminant analysis of principal components	IPCC	Intergovernmental Panel on Climate Change
ddRAD	double digest RAD	IPBES	Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services
<i>df</i>	degrees of freedom	ISSR	inter-simple sequence repeat
DFTD	devil facial tumor disease	ITS	internal transcribed spacer
DNA	deoxyribonucleic acid	IUCN	International Union for Conservation of Nature
DPS	distinct population segment	LD	linkage disequilibrium
DDT	dichlorodiphenyltrichloroethane		

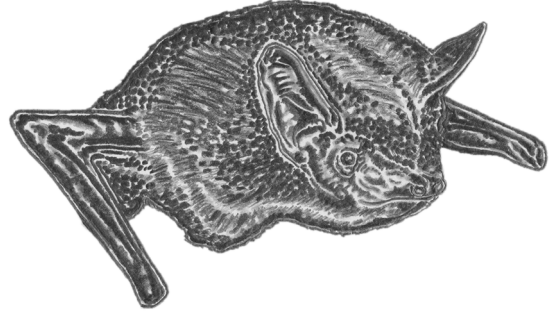
LDE	language development enzyme	PVA	population viability analysis
LE	lethal equivalent	qPCR	quantitative polymerase chain reaction
LOD	log of odds ratio	QTL	quantitative trait locus
LoF	loss of function	RADS	restriction site-associated DNA markers
MAC	minor allele count	RADseq	restriction site-associated DNA sequencing
MAF	minor allele frequency	RAPD	randomly amplified polymorphic DNA
Mb	megabase pairs, equal to million base pairs	RCP	representative concentration pathway
MCMC	Markov chain Monte Carlo	RDA	redundancy analysis
MDS	multidimensional scaling	rDNA	ribosomal DNA
MHC	major histocompatibility complex	REML	restricted maximum likelihood
ML	maximum likelihood	RFLP	restriction fragment length polymorphism
MLE	maximum likelihood estimate	RIL	recombinant inbred line
MMPA	US Marine Mammal Protection Act	RNA	ribonucleic acid
MOU	memorandum of understanding	ROH	runs of homozygosity
MP	match probability	RONA	risk of nonadaptedness
MRCA	most recent common ancestor	RRV	raccoon rabies virus
MSMC	multiple sequentially Markovian coalescent	RZSS	Royal Zoological Society of Scotland
mRNA	messenger RNA	SARA	Species at Risk Act of Canada
mtDNA	mitochondrial DNA	SDM	species distribution model
MU	management unit	siRNA	small interfering RNA
MVP	minimum viable population	SFS	site frequency spectrum
MYA	million years ago	SGS	spatial genetic structure
NCA	nested clade analysis	siRNA	small interfering RNA
NCDE	Northern Continental Divide Ecosystem	SMM	stepwise mutation model
NCPA	nested clade phylogeographic analysis	SNP	single nucleotide polymorphism
NEMBA	South African National Environmental Management: Biodiversity Act	SSR	simple sequence repeat
NGS	next-generation sequencing	STR	short tandem repeat
NGO	nongovernment organization	<i>Taq</i>	DNA polymerase enzyme from <i>Thermus aquaticus</i>
NOAA	US National Oceanic and Atmospheric Administration	TMRCa	time to most recent common ancestor
OTU	operational taxonomic unit	UNDRIP	UN Declaration on the Rights of Indigenous Peoples
PAW	Partnership for Action Against Wildlife Crime	UPGMA	unweighted pair group method with arithmetic averages
PCA	principal component analysis	US	United States
PCoA	principal coordinates analysis	USA	United States of America
PCR	polymerase chain reaction	USDA	US Department of Agriculture
PDF	probability density function	USFS	US Forest Service
PE	probability of paternity exclusion	USFWS	US Fish and Wildlife Service
PHR	Pearl and Hermes Reef	VNTR	variable number tandem repeat
PI	probability of identity	VSA	verified subspecies ancestry
PMRN	probabilistic maturation reaction norm	WNS	white-nose syndrome
PSC	phylogenetic species concept	WWF	World Wide Fund for Nature
PSMC	pairwise sequentially Markovian coalescent	YSE	Yellowstone Ecosystem

PART I

Introduction



Introduction



Christmas Island pipistrelle, Example 1.1

The extinction of species, each one a pilgrim of four billion years of evolution, is an irreversible loss. The ending of the lines of so many creatures with whom we have traveled this far is an occasion of profound sorrow and grief. Death can be accepted and to some degree transformed. But the loss of lineages and all their future young is not something to accept. It must be rigorously and intelligently resisted.

(Gary Snyder 1990, p. 176)

The key for conservation genomics will be for the academic and policy spheres to communicate in an effort to maintain a firm grasp on conceptual advances (driven by academic research) and on-site conservation needs (recognized by practitioners).

(Aaron B.A. Shafer et al. 2015, p. 85)

We are living in a time of unprecedented extinctions (Dirzo et al. 2014; Pimm et al. 2014; Humphreys et al. 2019). Current extinction rates have been estimated to be 1,000 times background rates and are increasing (Pimm et al. 2014). Approximately 25% of mammals, 14% of birds, 42% of turtles and tortoises, 40% of amphibians, 34% of conifers, and 35% of selected dicot plant taxa are threatened with extinction (IUCN 2019). Most of these extinction risk projections are based primarily on population declines owing to habitat loss, overharvesting, and pollution. For example, the Christmas Island pipistrelle bat was declared extinct by the International Union for Conservation of Nature (IUCN) in 2017 (Example 1.1). Climate change is anticipated to further increase extinction risks for many species (Urban 2015).

The true picture is likely much worse than this because the conservation status of most of the

world's species remains poorly known. In addition, estimates indicate that less than 30% of the world's arthropod species have been described (Hamilton et al. 2010). Only ~6% of the world's described species have been evaluated for the IUCN Red List (Table 1a in IUCN 2019). Few invertebrate species (2%) have been evaluated, and the evaluations that have been done have tended to focus on mollusks and crustaceans. Among the insects, only the swallowtail butterflies, dragonflies, and damselflies have received much attention. A recent analysis has concluded that the number of extinctions of seed plants is more than four times that on the Red List (Humphreys et al. 2019).

Protecting biodiversity poses perhaps the most difficult and important questions ever faced by science (Pimm et al. 2001). The problems are difficult because they are so complex and cannot be approached by the reductionist methods that have

Example 1.1 Extinction

The nighttime forests of Christmas Island in the Indian Ocean fell silent in 2009 when the last Christmas Island pipistrelle, an echolocating bat, was no longer detected with ultrasound recording devices (Matacic 2017). This species was common until the 1980s, but surveys in the 1990s revealed a drastic decline of unknown cause (Martin et al. 2012). A survey in early 2009 indicated that some 20 bats remained. An attempt to capture these animals for a captive breeding program failed. The last bat evaded capture and was no longer detected with recording devices after 27 August that year. The Christmas Island pipistrelle was officially designated as extinct in 2017 by the IUCN (Matacic 2017).

worked so well in other areas of science. Moreover, solutions to these problems require a major readjustment of our social and political systems. An analysis of progress toward international biodiversity targets has concluded that efforts will not result in an improved state for biodiversity in the near future (Tittensor et al. 2014). Biodiversity conservation is arguably the greatest scientific and social challenge currently faced by humanity because biodiversity loss threatens the continued existence of our species and the future of the biosphere itself.

Genetics and genomics have an important role to play in the protection of biodiversity. The earliest applications of genetics to conservation began in the early 1980s at the very beginning of conservation biology (Soulé & Wilcox 1980). “**Genomic**” techniques revolutionized the use of genetics in conservation beginning around 2010 (Allendorf et al. 2010). Applications of genomics to conservation require a fundamental understanding of the theory of population genetics, as well as application of the latest techniques. We have strived to accomplish this goal in this work.

1.1 Genetics and civilization

Genetics has a long history of application to improve human well-being, but also to suppress and discriminate against people (Box 1.1). The domestication of animals and cultivation of plants is thought to have been the key step in the

development of civilization (Diamond 1997). Early peoples directed genetic change in domestic and agricultural species to suit their needs. It has been estimated that the dog was domesticated some 35,000 years ago (Skoglund et al. 2015), followed by goats and sheep around 10,000 years ago (Darlington 1969; Zeder 2008). Wheat and barley were the first crops to be domesticated in the eastern hemisphere ~10,000 years ago; beans, squash, and maize were domesticated in the western hemisphere at about the same time (Kingsbury 2009).

The initial genetic changes brought about by cultivation and domestication were not due to intentional selection but apparently were inadvertent and inherent in cultivation itself. Genetic change under domestication was later accelerated by thousands of years of purposeful selection as animals and crops were selected to be more productive or to be used for new purposes. This process became formalized in the discipline of agricultural genetics after the rediscovery of Mendel’s principles at the beginning of the 20th century.

The “success” of these efforts can be seen everywhere. Humans have transformed much of the landscape of our planet into croplands and pasture to support the over 7 billion humans alive today. It has been estimated that 35% of the Earth’s ice-free land surface is now occupied by crops and pasture (Foley et al. 2007), and that 24% of the primary terrestrial productivity is used by humans (Haberl et al. 2007). Recently, we have begun to understand the cost at which this success has been achieved. The replacement of wilderness by human-exploited environments is causing the rapidly accelerating loss of species and ecosystems throughout the world. The continued growth of the human population and its direct and indirect effects on environments imperils a large proportion of the wild species that now remain.

Aldo Leopold inspired a generation of ecologists to recognize that the actions of humans are embedded into an ecological network that should not be ignored (Meine 1998):

A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong when it tends otherwise.

(Leopold 1949, p. 262)

Box 1.1 Eugenics: The dark origins of population genetics and conservation

As conservation geneticists, we recognize the importance of genetic diversity in maintaining healthy natural populations, and in facilitating adaptation to new environmental conditions and challenges. However, both population genetics and the American conservation movement have their roots in the human eugenics movement of a century ago, which viewed genetic diversity among human populations as grounds for discrimination and prejudice. We acknowledge this unfortunate part of the history of both population genetics and conservation, and denounce how it has been used to suppress and disadvantage people.

Many of the early statistical methods that still underlie genetic analysis were developed by devout eugenicists. Francis Galton, a cousin of Charles Darwin, coined the term eugenics in 1883 (Galton 1883, p. 24). Simply put, the field of eugenics viewed human traits as the product of genes, some trait variants more valuable than others, and therefore some human races as better than others (Rohlf's 2020). Galton also developed the concept of linear regression analysis, initially termed "reversion to the mean" or "reversion to mediocrity," which remains widely used in analysis of data of many types. Ronald A. Fisher, who was one of the founders of population genetics, and who developed the

statistical method analysis of variance, was also a staunch eugenicist. Much of *The Genetical Theory of Natural Selection* (Fisher 1930) was devoted to Fisher's concern with the genetic effects of the lower fertility of the English upper class. US President Theodore Roosevelt and his conservation chief Gifford Pinchot, considered fathers of the conservation movement in their country, were both part of the eugenics movement (Wohlforth 2010). The racism that exists in many societies and affects the daily lives of people of color has historical connections to eugenics.

The fields of population genetics and conservations have fortunately progressed a great deal in the past century away from this past. However, they still suffer from the low ethnic and racial diversity typical of ecology and evolutionary biology more broadly (e.g., Graves 2019). The field of conservation genetics will improve further as the diversity of scientists in this field increases, and members of under-represented groups are welcomed warmly and equitably into the community of research and practice. Just as genetic diversity increases the resilience and adaptability of plant and animal populations, the diversity of people in this field will bring new ideas and practices for conserving biodiversity.

The organized actions of humans are controlled by sociopolitical systems that operate into the future on a timescale of a few years at most (e.g., the next election). All too often our systems of conservation are based on the economic interests of humans in the immediate future. We tend to disregard, and often mistreat, elements that lack immediate economic value but that are essential to the stability of the ecosystems upon which our lives and the future of our children depend.

In 1974, Otto Frankel published a landmark paper entitled "Genetic conservation: our evolutionary responsibility," which set out conservation priorities:

First, ... we should get to know much more about the structure and dynamics of natural populations and communities. ... Second, even now the geneticist can play a part in injecting genetic considerations into the planning of reserves of any kind. ... Finally, reinforcing the grounds for nature conservation with an evolutionary perspective

may help to give conservation a permanence which a utilitarian, and even an ecological grounding, fail to provide in men's minds.

(Frankel 1974, p. 63)

Frankel, an agricultural plant geneticist, came to similar conclusions to Leopold, a wildlife biologist, by a very different path. In Frankel's view, we cannot anticipate the future world in which humans will live in a century or two. Therefore, it is our responsibility to "keep evolutionary options open." It is crucial to apply our understanding of genetics and evolution to conserving the natural ecosystems that are threatened by human civilization (Cook & Sgrò 2018).

1.2 Genetics, genomics, and conservation

Darwin (1896, p. 99) was the first to consider the importance of genetics and evolution in the persistence of natural populations. He expressed concern

that deer in British nature parks may be subject to loss of vigor because of their small population size and isolation. Voipio (1950) presented the first comprehensive consideration of the application of population genetics to the management of natural populations. He was primarily concerned with the effects of **genetic drift** (Chapter 6) in game populations that were reduced in size by trapping or hunting and fragmented by habitat loss.

The modern concern for genetics in conservation began in the 1970s when Frankel (1970, 1974) began to raise the alarm about the loss of primitive crop varieties and their replacement by genetically uniform cultivars. It is not surprising that these initial considerations of conservation genetics dealt with species that were used directly as resources by humans. Seventy-five percent of crop diversity was lost between 1900 and 2000, and only a few livestock breeds now dominate among domesticated farm animals (FAO 2010). Conserving the genetic resources of wild relatives of agricultural species remains an important area of conservation genetics (Hanotte et al. 2010). For example, the commercial production of sugarcane was saved by the use of germplasm from wild relatives (Soltis & Soltis 2019). However, diversity of crop wild relatives is poorly represented in gene banks (Castañeda-Álvarez et al. 2016). At the same time, geneticists are seeking stress-related genes from wild progenitors of some crops to assist in breeding efforts for new climates (Warschewsky et al. 2014).

The application of genetics and evolution to conservation in a more general context did not blossom until around 1980, when three books established the foundation for applying the principles of genetics and evolution to conservation of biodiversity (Soulé & Wilcox 1980; Frankel & Soulé 1981; Schonewald-Cox et al. 1983). Today conservation genetics is a well-established discipline, with its own journals (e.g., *Conservation Genetics* and *Conservation Genetics Resources*) and two textbooks, including this one and Frankham et al. (2010).

The subject matter of papers published on conservation genetics is extremely broad. However, most articles dealing with conservation and genetics fit into one of the five general categories below:

1. Management and reintroduction of captive populations, and the restoration of biological communities.
2. Description and identification of individuals, genetic population structure, kin relationships, and taxonomic relationships.
3. Detection and prediction of the effects of habitat loss, fragmentation, isolation, and genetic rescue.
4. Detection and prediction of the effects of hybridization and introgression.
5. Understanding the relationships between fitness of individuals or local adaptation of populations and environmental factors.

These topics are listed in order of increasing complexity and decreasing uniformity of agreement among conservation geneticists. Although the appropriateness of captive breeding in conservation has been controversial, procedures for genetic management of captive populations are well developed with relatively little controversy. The relationship between specific genotypes and fitness or adaptation has been a particularly vexing issue in evolutionary and conservation genetics, but new genomic methods have made this more tractable to study. Many recent studies have shown that natural selection can bring about rapid genetic changes in populations that may have important implications for conservation (Homola et al. 2019).

As in other areas of genetics, model organisms have played an important research role in conservation genetics (Frankham 1999). Many important theoretical issues in conservation biology cannot be answered by empirical research on threatened species (e.g., how much gene flow is required to prevent the inbreeding effects of small population size?). Such empirical questions are often best resolved in species that can be raised in captivity in large numbers with a rapid generation interval (e.g., the fruit fly *Drosophila*, the guppy, deer mouse, and the fruit fly analog in plants, *Arabidopsis thaliana*). Such laboratory investigations can also provide excellent training opportunities for students. We have tried to provide examples from both model and threatened species. Where possible we have chosen examples from threatened species or wild populations, even though many of

the principles were first demonstrated with model species.

1.2.1 Using genetics to understand basic biology

Molecular genetic descriptions of individuals are also used to understand the basic biology of populations. For example, genetic information can provide valuable insight into the demographic structure of populations (Escudero et al. 2003; Palsbøll et al. 2007). The total population size can be estimated from the number of unique genotypes sampled in a population for species that are difficult to census (Luikart et al. 2010). Moreover, many demographic models assume a single randomly mating population. The distribution of genetic variation over a species range can be used to identify what geographic units can be considered separate demographic units. Consider a population of trout found within a single small lake that might appear to be a demographic unit (Example 9.2). Under some circumstances these trout could actually represent two or more separate reproductive (and demographic) groups with little or no exchange between them (e.g., Ryman et al. 1979).

Genetic analysis can also be used to detect cryptic effects of climate change on the distribution of species. A massive heatwave affected many marine species along the coast of Western Australia in 2011 (Gurgel et al. 2020). The amount of underwater forest cover of two forest-forming seaweeds quickly recovered so that there was no apparent effect of the heatwave. However, genetic analysis of both species before and after the extreme event indicated substantial loss of genetic diversity of both species. Thus, this marine heatwave resulted in a massive and cryptic loss of genetic diversity that may compromise their ability to respond to future environmental change.

Molecular genotyping can also be used to verify the presence of rare species (Chapter 22). For example, wolverines had not been seen in the state of California since 1922 (Moriarty et al. 2009). When photographic evidence suggested the presence of a wolverine in the Sierra Nevada Mountains in 2008, genetic analysis of scat and hair confirmed its

presence. In addition, the comparison of the genotype of this individual with samples throughout the west indicated that this individual most likely originated in the Sawtooth Mountains of Idaho, nearly 600 km away.

Genetic analysis has also been used to document some other amazing animal journeys. A cougar originating from the Black Hills of South Dakota left its genetic fingerprints across northern North America from South Dakota to Minnesota to Wisconsin to New York (Hawley et al. 2016). Finally, a cougar killed by a vehicle in Connecticut turned out to be this same animal that had traveled over 2,400 km!

1.2.2 Invasive species and pathogens

Invasive species are recognized as one of the top two threats to global biodiversity (Chapter 14). Studies of genetic diversity and the potential for rapid evolution of invasive species may provide useful insights into what causes species to become invasive (Sakai et al. 2001; Lee & Gelembiuk 2008). More information about the genetics and evolution of invasive species or native species in invaded communities, as well as their interactions, may lead to predictions of the relative susceptibility of ecosystems to invasion, identification of key alien species, and predictions of the subsequent effects of removal (e.g., Roe et al. 2019).

Moreover, genetic descriptions of populations can be used to reconstruct the invasion history and to identify the source populations of biological invasions (Signorile et al. 2016). This information can also be used to detect possible human-mediated translocations and to better manage invasions by identifying transportation pathways that can be targeted for more stringent control.

Similarly, genetic descriptions of population connectivity (e.g., gene flow) can be used to reconstruct pathways of host movement and pathogen spread. Knowing corridors or barriers to movement and spread can help managers monitor, predict, and prevent infectious disease transmission and outbreaks (Blanchong et al. 2008). Study of the genetics of pathogens can also provide valuable information

about the genetic population structure and demography of host species (Biek et al. 2006).

1.2.3 Conservation genomics

Recent advances in molecular genetics, including sequencing of the entire genomes of many species, have revolutionized applications of genetics (e.g., medicine, forestry, and agriculture). We currently have complete genome sequences from thousands of species, as well as many individuals within species (Ellegren 2014). The Earth BioGenome Project intends to characterize the genomes of all of Earth's eukaryotic biodiversity over a 10-year period. This coming explosion of information has transformed our understanding of the amount, distribution, and functional significance of genetic variation in natural populations (Allendorf et al. 2010; Shafer et al. 2015).

Now is a crucial time to explore the potential applications of this information revolution for conservation genetics, as well as to recognize limitations in applying genomic tools to conservation issues. The ability to examine hundreds or thousands of genetic markers with relative ease has made it possible to answer many important questions in conservation that have been intractable until now (Figure 1.1).

1.2.3.1 Genetic engineering

Some have proposed that genetic engineering (or genetic modification) should be used to introduce adaptive variants to prevent extinction (e.g., Thomas et al. 2013), but this approach is not likely to be of general utility (Hedrick et al. 2013a). It might be applicable in a very few individual cases, for example, for some long-lived plants, where disease resistance is primarily due to single genes. In general, however, identification of "missing" adaptive single-gene variants in endangered species and increasing their frequency in populations without causing harmful side effects is infeasible in the wild except in a small number of special cases (e.g., where novel pathogens have been introduced; Kardos & Shafer 2018). However, such research is starting to play an important role in agriculture, identifying valuable variants in domesticated

species that live in managed environments (Zhu et al. 2020).

Furthermore, when genetically based fitness reductions have been documented in endangered populations, they almost always have been traced not to a lack of adaptive diversity, but to increased frequency of detrimental alleles and increased homozygosity caused by genetic drift and inbreeding (Hedrick et al. 2013a). Those were the factors causing low fitness in Florida panthers and Swedish vipers. In these cases, fitness was increased by genetic rescue, the introduction of unrelated individuals from other populations. The introduction of specific adaptive alleles by genetic engineering in these cases, as proposed by Thomas et al. (2013), will not overcome the genome-wide effects of inbreeding depression.

Nevertheless, there are some situations in which genetic engineering should be considered as a conservation genetics technique (Strauss et al. 2015). Many native trees in the northern temperate zone have been devastated by introduced diseases for which little or no genetic resistance exists (e.g., European and North American elms, and the North American chestnut). Adams et al. (2002) suggested that transfer of resistance genes by genetic modification is perhaps the only available method for preventing the loss of important tree species when no native variation in resistance to introduced diseases exists. Transgenic trees have been developed for both American elm and American chestnut, and are now being tested for stable resistance to Dutch elm disease and chestnut blight (Popkin 2018). The use of genetic engineering to improve agricultural productivity has been controversial but is now widespread for some crops. There will no doubt continue to be a lively debate about the use of these procedures to prevent the extinction of natural populations.

The loss of foundation tree species is likely to affect many other species as well. For example, whitebark pine is currently one of the two most important food resources for grizzly bears in the Yellowstone National Park ecosystem (Mattson & Merrill 2002). However, most of the whitebark pine in this region is projected to be extirpated because of an exotic pathogen, and with predicted geographic shifts in the climatic niche-based habitat of this

species in the next century (Warwell et al. 2007; McLane & Aitken 2012).

1.3 What should we conserve?

Conservation can be viewed as an attempt to protect the genetic diversity produced by evolution over the previous 3.5 billion years on our planet. This is an overwhelming task. Over 2 million species have been described and perhaps 100 million species have yet to be described (Soltis & Soltis 2019). Darwin (1859) was the first to represent this diversity in a diagram that he referred to as the “Tree of Life.” The first comprehensive Tree of Life for all described species was published in 2015 (Figure 1.2; Hinchcliff et al. 2015).

Genetic diversity is one of three forms of biodiversity recognized by the IUCN as deserving conservation, along with species and ecosystem diversity. Unfortunately, genetics has been generally ignored by the member countries in their National Biodiversity Strategy and Action Plans developed to implement the Convention on Biological Diversity (CBD) (Laikre et al. 2010a; Hoban et al. 2020).

We can consider the implications of the relationship between genetic diversity and conservation at many levels: genes, individuals, populations, varieties, subspecies, species, genera, and so on. Genetic diversity provides a retrospective view of the evolutionary history of taxa (phylogenetics), a snapshot of the current genetic structure within and among populations (population and ecological genetics), and a glimpse ahead to the future evolutionary

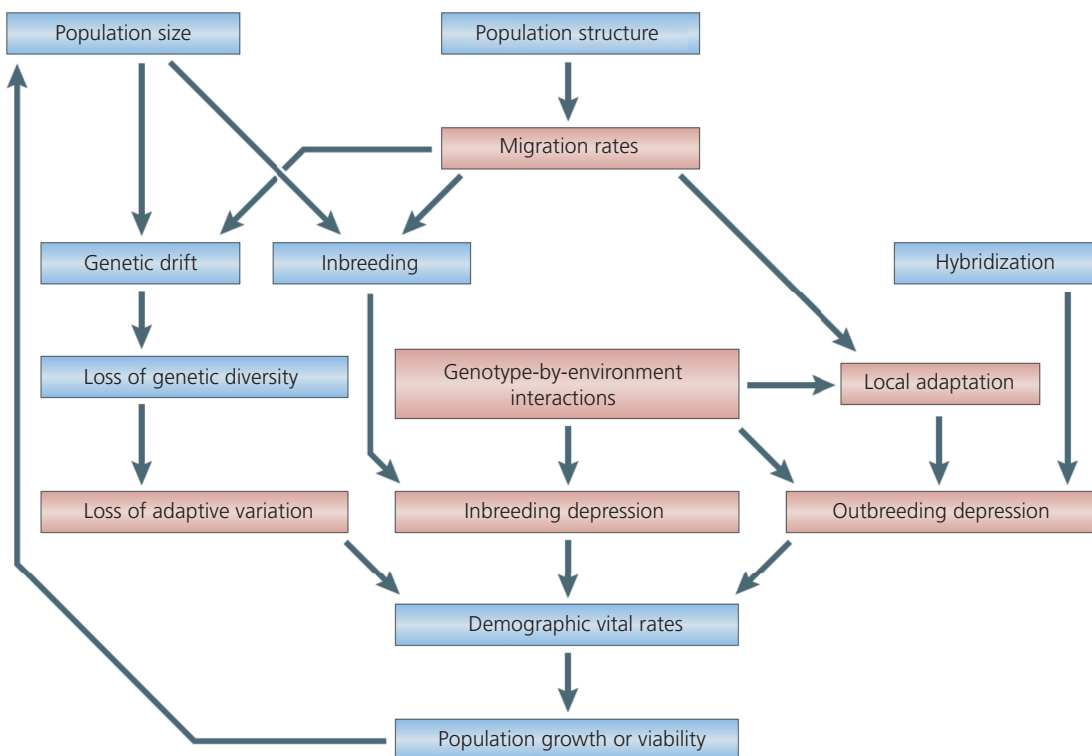


Figure 1.1 Schematic diagram of interacting factors in conservation of natural populations. Traditional conservation genetics, using neutral markers, provides direct estimates of some interacting factors (blue). Conservation genomics can address a wider range of factors (red). It also promises more precise estimates of neutral processes (blue) and understanding of the specific genetic basis of all of these factors. For example, traditional conservation genetics can estimate overall migration rates or inbreeding coefficients, whereas genomic tools can assess gene flow rates that are specific to adaptive loci or founder-specific inbreeding coefficients. From Allendorf et al. (2010).

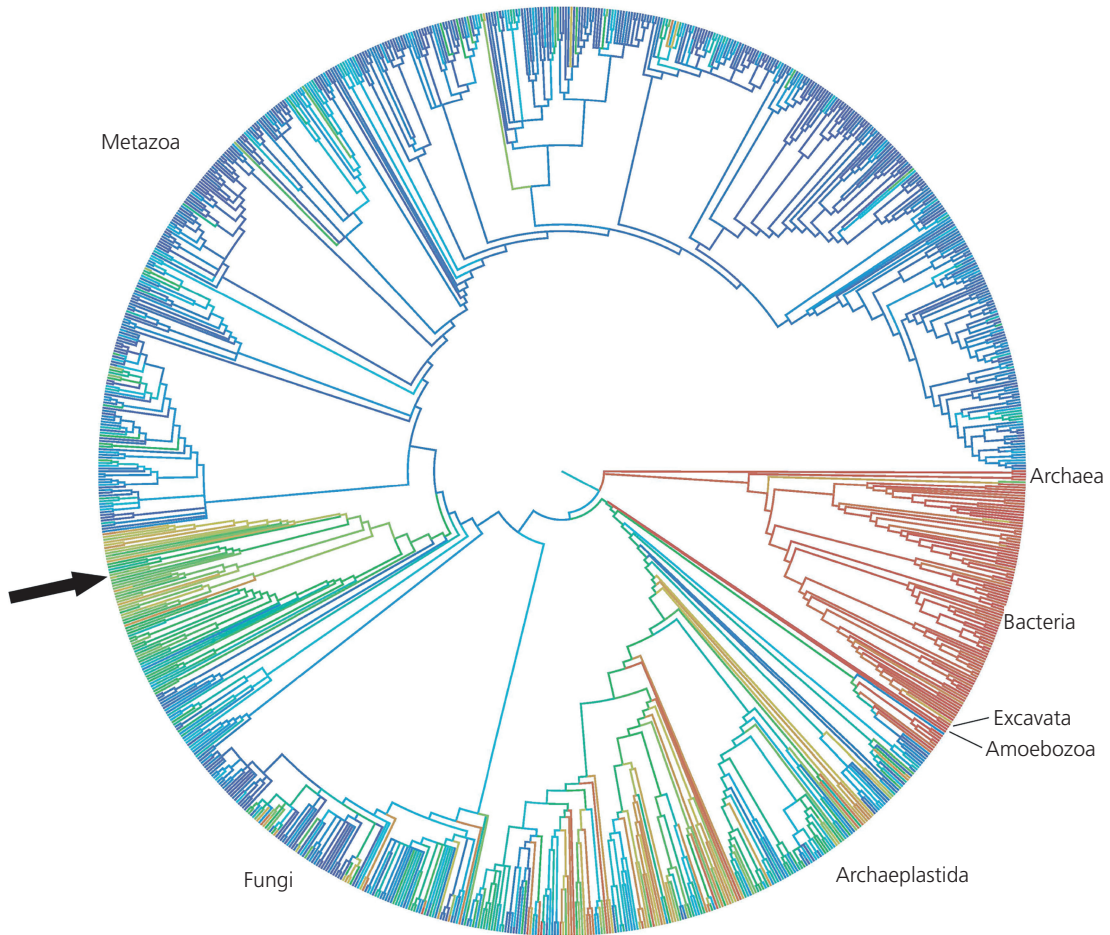


Figure 1.2 Comprehensive Tree of Life showing phylogenetic relationships among over two million described species. The arrow indicates the position of humans in this tree. Redrawn from Soltis & Soltis (2019).

potential of populations and species (evolutionary biology). Genomic tools have provided new insights into all of these areas.

1.3.1 Phylogenetic diversity

While species have historically been prioritized for conservation efforts and resources based on their charismatic appeal and high profile, scientifically justified methods have been developed to identify those species that should be of highest importance from an evolutionary standpoint. The amount of genetic divergence based upon **phylogenetic** relationships is often considered when

setting conservation priorities for different species (Mace et al. 2003; Rosauer & Mooers 2013). For example, the United States Fish and Wildlife Service (USFWS) assigns priority for listing under the Endangered Species Act (ESA) on the basis of “taxonomic distinctiveness” (USFWS 1983). Species of a **monotypic** genus receive the highest priority. The tuatara is an extreme example that raises several important issues about assigning conservation value and allocating our conservation efforts based upon taxonomic distinctiveness (Example 1.2).

Faith (2008) recommended integrating evolutionary processes into conservation decision-making by considering phylogenetic diversity. Faith provides