

MOLECULAR APPROACHES IN NATURAL RESOURCE CONSERVATION AND MANAGEMENT

Recent advances in molecular genetics and genomics have been embraced by many scientists in natural resource conservation. Today, several major conservation and management journals are using the “genetics” editors of this book to deal solely with the influx of manuscripts that employ molecular data. The editors have attempted to synthesize some of the major uses of molecular markers in natural resource management in a book targeted not only at scientists but also at individuals actively making conservation and management decisions. To that end, the text features contributors who are major figures in molecular ecology and evolution – many having published books of their own. The aim is to direct and distill the thoughts of these outstanding scientists by compiling compelling case histories in molecular ecology as they apply to natural resource management.

J. Andrew DeWoody is Professor of Genetics and University Faculty Scholar at Purdue University. He earned his MS in genetics at Texas A&M University and his PhD in zoology from Texas Tech University. His recent research in genetics, evolution, and ecology has been funded by organizations including the National Science Foundation, the U.S. Department of Agriculture (USDA) National Research Initiative, the Great Lakes Fishery Trust, and the National Geographic Society. His research is published in more than thirty-five journals, and he has served as Associate Editor for the *North American Journal of Fisheries Management*, the *Journal of Wildlife Management*, and *Genetica*.

John W. Bickham is Professor in the Department of Forestry and Natural Resources (FNR) and Director of the Center for the Environment at Purdue University. He received his MS in biology from the University of Dayton and his PhD in zoology from Texas Tech University. He was on the faculty of Texas A&M University’s Department of Wildlife and Fisheries Sciences for thirty years. He has published more than two hundred articles in scientific journals in evolutionary genetics, including comparative cytogenetics, molecular systematics, molecular ecology, and ecotoxicology.

Charles H. Michler is the Fred M. van Eck Director of the Hardwood Tree Improvement and Regeneration Center at Purdue University and Site Director of the National Science Foundation Industry & University Cooperative Research Program’s Center for Advanced Forest Systems. He earned his MS and PhD in horticulture, physiology, and biochemistry from The Ohio State University. He has published more than eighty-five scholarly works and has edited nine books and proceedings. He is Editor of *Plant Breeding Reviews* and Associate Editor of the *Journal of Forest Research*.

Krista M. Nichols is Assistant Professor, Departments of Biological Sciences and Forestry and Natural Resources at Purdue University. She received her MS in fisheries and wildlife from Michigan State University and her PhD in zoology from Washington State University. She was a National Research Council postdoctoral Fellow at the National Marine Fisheries Services, Northwest Fisheries Science Center. Dr. Nichols has published in the fields of ecotoxicology, genetics, and ecology.

Olin E. Rhodes, Jr., is Professor in the FNR and Director of the Interdisciplinary Center for Ecological Sustainability at Purdue University. He received his MS in wildlife biology from Clemson University and his PhD in wildlife ecology from Texas Tech University. He was named a Purdue University Faculty Scholar in 2006. He has published more than 135 scholarly works in ecology and genetics and has recently served as Associate Editor of the *Journal of Wildlife Management*.

Keith E. Woeste is a research molecular geneticist for the USDA Forest Service Northern Research Station Hardwood Tree Improvement and Regeneration Center and Adjunct Assistant Professor at Purdue University’s FNR. He received an MDiv in theology from the Jesuit School of Theology at Berkeley, an MS in horticulture from the University of California–Davis, and his PhD in genetics from the University of California–Davis.

Molecular Approaches in Natural Resource Conservation and Management

Edited by

J. Andrew DeWoody

Purdue University

John W. Bickham

Purdue University

Charles H. Michler

Purdue University

Krista M. Nichols

Purdue University

Olin E. Rhodes, Jr.

Purdue University

Keith E. Woeste

Purdue University



CAMBRIDGE
UNIVERSITY PRESS

CAMBRIDGE UNIVERSITY PRESS
Cambridge, New York, Melbourne, Madrid, Cape Town, Singapore,
São Paulo, Delhi, Dubai, Tokyo, Mexico City

Cambridge University Press
32 Avenue of the Americas, New York, NY 10013-2473, USA
www.cambridge.org
Information on this title: www.cambridge.org/9780521731348

© Cambridge University Press 2010

This publication is in copyright. Subject to statutory exception
and to the provisions of relevant collective licensing agreements,
no reproduction of any part may take place without the written
permission of Cambridge University Press.

First published 2010

Printed in the United States of America

A catalog record for this publication is available from the British Library.

Library of Congress Cataloging in Publication data

Molecular approaches in natural resource conservation and management /
edited by J. Andrew DeWoody . . . [et al].
p. cm.

Includes bibliographical references and index.

ISBN 978-0-521-51564-1 (hardback) – ISBN 978-0-521-73134-8 (pbk.)

1. Biodiversity conservation. 2. Genetic resources conservation.

3. Molecular genetics. 4. Conservation of natural resources.

I. DeWoody, J. Andrew, 1969– II. Title.

QH75.M647 2010

333.95'16–dc22 2009050318

ISBN 978-0-521-51564-1 Hardback

ISBN 978-0-521-73134-8 Paperback

Cambridge University Press has no responsibility for the persistence or accuracy of URLs for
external or third-party Internet Web sites referred to in this publication and does not guarantee
that any content on such Web sites is, or will remain, accurate or appropriate.

Contents

Contributors	page ix
Preface	xv
1 Biodiversity discovery and its importance to conservation	1
Rodney L. Honeycutt, David M. Hillis, and John W. Bickham	
<i>Box 1: Genetic identification of cryptic species: An example in Rhogeessa</i>	22
Amy B. Baird	
2 Gene flow, biodiversity, and genetically modified crops: Weedy rice in Thailand	35
Barbara Schaal, Wesley J. Leverich, Sansanee Jamjod, Chanya Maneechote, Anbreen Bashir, Amena Prommin, Adirek Punyalue, Athitya Suta, Theerasak Sintukhiew, Anupong Wongtamee, Tonapha Pusadee, Sunisa Niruntrayakul, and Benjavan Rerkasem	
<i>Box 2: Environmental risk assessment of genetically engineered salmon</i>	37
Robert H. Devlin and Fredrik L. Sundström	
3 A community and ecosystem genetics approach to conservation biology and management	50
Thomas G. Whitham, Catherine A. Gehring, Luke M. Evans, Carri J. LeRoy, Randy K. Bangert, Jennifer A. Schweitzer, Gerard J. Allan, Robert C. Barbour, Dylan G. Fischer, Bradley M. Potts, and Joseph K. Bailey	
<i>Box 3: Landscape genetics of an American chestnut borer</i>	63
Jeffrey D. Holland	
4 Vertebrate sex-determining genes and their potential utility in conservation, with particular emphasis on fishes	74
J. Andrew DeWoody, Matthew C. Hale, and John C. Avise	
<i>Box 4: Sex identification and population size of grizzly bears by using noninvasive genetic sampling</i>	76
Lisette Waits	
5 Historical and contemporary dynamics of adaptive differentiation in European oaks	101
Antoine Kremer, Valérie Le Corre, Rémy J. Petit, and Alexis Ducousso	

	<i>Box 5: Adaptive shifts in natural populations of high dispersing species</i>	117
	Stephen R. Palumbi	
6	Association genetics, population genomics, and conservation: Revealing the genes underlying adaptation in natural populations of plants and animals	123
	Krista M. Nichols and David B. Neale	
	<i>Box 6: Unraveling counterintuitive evolutionary trends: Coat color in Soay sheep</i>	139
	Jake Gratten, Alastair J. Wilson, Allan F. McRae, Dario Beraldi, Peter M. Visscher, Josephine M. Pemberton, and Jon Slate	
7	Hybridization in threatened and endangered animal taxa: Implications for conservation and management of biodiversity	169
	Kelly R. Zamudio and Richard G. Harrison	
	<i>Box 7: Mating opportunities in animal hybrid zones</i>	171
	Marjorie Matocq	
8	Pollen and seed movement in disturbed tropical landscapes	190
	J. L. Hamrick	
	<i>Box 8–1: Effective population size</i>	192
	J. L. Hamrick	
	<i>Box 8–2: Allelic recharge in populations recovering from bottleneck events</i>	194
	Joseph D. Busch, Jennifer McCreight, and Peter M. Waser	
9	Implications of landscape alteration for the conservation of genetic diversity of endangered species	212
	Paul L. Leberg, Giridhar N. R. Athrey, Kelly R. Barr, Denise L. Lindsay, and Richard F. Lance	
	<i>Box 9: Dune restoration introduces genetically distinct American beachgrass, <i>Ammophila breviligulata</i>, into a threatened local population</i>	214
	Julie R. Etterson and Rebecca M. Holmstrom	
10	Integrating evolutionary considerations into recovery planning for Pacific salmon	239
	Robin S. Waples, Michelle M. McClure, Thomas C. Wainwright, Paul McElhany, and Peter W. Lawson	
	<i>Box 10: The Kermode bear: A swirl of scientific, management, and ethical values in British Columbia</i>	259
	Kermit Ritland	
11	Using molecular methods to improve the genetic management of captive breeding programs for threatened species	267
	Jamie A. Ivy and Robert C. Lacy	
	<i>Box 11: Pedigree reconstruction: An alternative to systematic breeding</i>	285
	Yousry A. El-Kassaby	

12 Wildlife reintroductions: The conceptual development and application of theory	296
Olin E. Rhodes, Jr., and Emily K. Latch	
<i>Box 12: Genetic ramifications of restoration of blight-resistant American chestnut</i>	307
Lisa Worthen, Charles H. Michler, and Keith E. Woeste	
13 Evolutionary toxicology	320
Lee R. Shugart, Chris W. Theodorakis, and John W. Bickham	
<i>Box 13: Microarrays and molecular phenotypes</i>	335
Stan D. Wullschleger and David J. Weston	
Index	363

Color plates follow page 174.

Contributors

Gerard J. Allan

Department of Biological Sciences
Environmental Genetics and
Genomics Facility
Northern Arizona University
Flagstaff, AZ

Giridhar N. R. Athrey

Department of Biology
University of Louisiana
Lafayette, LA

John C. Avise

Ecology and Evolutionary Biology
School of Biological Sciences
University of California
Irvine, CA

Joseph K. Bailey

Department of Biological Sciences and
the Merriam-Powell Center for
Environmental Research
Northern Arizona University
Flagstaff, AZ

Amy B. Baird

National Museum of Natural History –
Naturalis
Leiden, The Netherlands

Randy K. Bangert

Biological Sciences
Idaho State University
Pocatello, ID

Robert C. Barbour

Cooperative Research Centre for
Sustainable Production Forestry
School of Plant Science
University of Tasmania
Australia

Kelly R. Barr

Department of Biology
University of Louisiana
Lafayette, LA

Anbreen Bashir

Department of Biology
St. Louis University
St. Louis, MO

Dario Beraldi

Wild Evolution Group
Institute of Evolutionary Biology
School of Biological Sciences
University of Edinburgh
Edinburgh, UK

John W. Bickham

Department of Forestry and Natural
Resources and Center for the
Environment
Purdue University
West Lafayette, IN

Contributors**Joseph D. Busch**

Microbial Genetics and Genomics
Center
Northern Arizona University
Flagstaff, AZ

Robert H. Devlin

Fisheries and Oceans Canada
West Vancouver, BC
Canada

J. Andrew DeWoody

Departments of Forestry and
Natural Resources and Biological
Sciences
Purdue University
West Lafayette, IN

Alexis Ducousso

UMR Biodiversité Gènes et
Communautés
Institut National de la Recherche
Agronomique
Cestas, France

Yousry A. El-Kassaby

Faculty of Forestry
University of British Columbia
Vancouver, BC
Canada

Julie R. Etterson

Department of Biology
University of Minnesota Duluth
Duluth, MN

Luke M. Evans

Department of Biological Sciences
Northern Arizona University
Flagstaff, AZ

Dylan G. Fischer

The Evergreen State College
Olympia, WA

Catherine A. Gehring

Department of Biological Sciences
Northern Arizona University
Flagstaff, AZ

Jake Gratten

Department of Animal and Plant
Sciences
University of Sheffield
Sheffield, UK

Matthew C. Hale

Department of Biological Sciences
Purdue University
West Lafayette, IN

J. L. Hamrick

Department of Plant Biology
University of Georgia
Athens, GA

Richard G. Harrison

Department of Ecology and
Evolutionary Biology
Cornell University
Ithaca, NY

David M. Hillis

Section of Integrative Biology
University of Texas
Austin, TX

Jeffrey D. Holland

Department of Entomology
Purdue University
West Lafayette, IN

Rebecca M. Holmstrom

Department of Biology
University of Minnesota Duluth
Duluth, MN

Rodney L. Honeycutt

Natural Science Division
Pepperdine University, Seaver College
Malibu, CA

Jamie A. Ivy

Department of Collections
San Diego Zoo
San Diego, CA

Sansanee Jamjod

Faculty of Agriculture
Chiang Mai University
Chiang Mai, Thailand

Antoine Kremer

UMR Biodiversité Gènes et
Communautés
Institut National de la Recherche
Agronomique
Cestas, France

Robert C. Lacy

Department of Conservation Science
Chicago Zoological Society
Brookfield, IL

Richard F. Lance

Environmental Lab
U.S. Army Engineer Research and
Development Center
Vicksburg, MS

Emily K. Latch

Department of Biological Sciences
University of Wisconsin–Milwaukee
Milwaukee, WI

Peter W. Lawson

Conservation Biology Division
NOAA Fisheries
Northwest Fisheries Science Center
Newport, OR

Valérie Le Corre

UMR Biologie et Gestion des
Adventices
Institut National de la Recherche
Agronomique
Dijon, France

Paul L. Leberg

Department of Biology
University of Louisiana
Lafayette, LA

Carri J. LeRoy

The Evergreen State College
Olympia, WA

Wesley J. Leverich

Department of Biology
St. Louis University
St. Louis, MO

Denise L. Lindsay

Environmental Lab
U.S. Army Engineer Research and
Development Center
Vicksburg, MS

Chanya Maneechote

Faculty of Agriculture
Chiang Mai University
Chiang Mai, Thailand

Marjorie Matocq

Department of Natural Resources and
Environmental Science
University of Nevada
Reno, NV

Michelle M. McClure

Conservation Biology Division
NOAA Fisheries
Northwest Fisheries Science Center
Seattle, WA

Jennifer McCreight

Department of Forestry and Natural
Resources
Purdue University
West Lafayette, IN

Paul McElhany

Conservation Biology Division
NOAA Fisheries
Northwest Fisheries Science Center
Seattle, WA

Contributors**Allan F. McRae**

Genetic Epidemiology Group
Queensland Institute of Medical
Research
Herston, Australia

Charles H. Michler

Department of Forestry and Natural
Resources and Hardwood Tree
Improvement and Regeneration
Center
Purdue University
West Lafayette, IN

David B. Neale

Department of Plant Sciences
University of California at Davis
Davis, CA

Krista M. Nichols

Departments of Forestry and Natural
Resources and Biological Sciences
Purdue University
West Lafayette, IN

Sunisa Niruntrayakul

Faculty of Agriculture
Chiang Mai University
Chiang Mai, Thailand

Stephen R. Palumbi

Department of Biology
Hopkins Marine Station
Stanford University
Pacific Grove, CA

Josephine M. Pemberton

Wild Evolution Group
Institute of Evolutionary Biology
School of Biological Sciences
University of Edinburgh
Edinburgh, UK

Rémy J. Petit

UMR Biodiversité Gènes et
Communautés
Institut National de la Recherche
Agronomique
Cestas, France

Bradley M. Potts

Cooperative Research Centre for
Sustainable Production Forestry
School of Plant Science
University of Tasmania
Australia

Amena Prommin

Faculty of Agriculture
Chiang Mai University
Chiang Mai, Thailand

Adirek Punyalue

Faculty of Agriculture
Chiang Mai University
Chiang Mai, Thailand

Tonapha Pusadee

Faculty of Agriculture
Chiang Mai University
Chiang Mai, Thailand

Benjavan Rerkasem

Faculty of Agriculture
Chiang Mai University
Chiang Mai, Thailand

Olin E. Rhodes, Jr.

Department of Forestry and Natural
Resources
Purdue University
West Lafayette, IN

Kermit Ritland

Department of Forest Sciences
University of British Columbia
Vancouver, BC
Canada

Barbara Schaal

Department of Biology
Washington University
St. Louis, MO

Jennifer A. Schweitzer

Ecology and Evolutionary Biology
University of Tennessee
Knoxville, TN

Lee R. Shugart

LR Shugart and Associates, Inc.
Oak Ridge, TN

Theerasak Sintukhiew

Faculty of Agriculture
Chiang Mai University
Chiang Mai, Thailand

Jon Slate

Department of Animal and Plant
Sciences
University of Sheffield
Sheffield, UK

Fredrik L. Sundström

Fisheries and Oceans Canada
West Vancouver, BC
Canada

Athitya Suta

Faculty of Agriculture
Chiang Mai University
Chiang Mai, Thailand

Chris W. Theodorakis

Biology Department
Southern Illinois University at
Edwardsville
Edwardsville, IL

Peter M. Visscher

Queensland Institute of Medical
Research
Royal Brisbane Hospital
Queensland, Australia

Thomas C. Wainwright

Fish Ecology Division
NOAA Fisheries
Northwest Fisheries Science Center
Newport, OR

Lisette Waits

Fish and Wildlife Resources
University of Idaho
Moscow, ID

Robin S. Waples

Conservation Biology Division
NOAA Fisheries
Northwest Fisheries Science Center
Seattle, WA

Peter M. Waser

Department of Biological Sciences
Purdue University
West Lafayette, IN

David J. Weston

Environmental Sciences Division
Oak Ridge National Laboratory
Oak Ridge, TN

Thomas G. Whitham

Department of Biological Sciences and
Merriam-Powell Center for
Environmental Research
Northern Arizona University
Flagstaff, AZ

Alastair J. Wilson

Institute of Evolutionary Biology
School of Biological Sciences
University of Edinburgh
Edinburgh, UK

Keith E. Woeste

Department of Forestry and Natural
Resources and Hardwood Tree
Improvement and Regeneration
Center
Purdue University
West Lafayette, IN

Contributors**Anupong Wongtamee**

Faculty of Agriculture
Chiang Mai University
Chiang Mai, Thailand

Lisa Worthen

Department of Forestry and Natural
Resources
Purdue University
West Lafayette, IN

Stan D. Wullschleger

Environmental Sciences Division
Oak Ridge National Laboratory
Oak Ridge, TN

Kelly R. Zamudio

Department of Ecology and
Evolutionary Biology
Cornell University
Ithaca, NY

Preface

The world would be a wonderful place if our natural resources (e.g., forests, fish, and wildlife) needed no management and conservation was not a concern. In a world with a global human population approaching 7 billion and where most developed nations overconsume these resources, however, conservation is a concern and management is necessary for sustainable use. Historically, natural resource management strategies were determined by the collection and interpretation of basic field data. Today, as challenges to the sustainability and conservation of our natural resources arise, managers often need data that cannot be acquired using conventional methods. For example, a natural resource manager might want to know the number of successful breeders in a population or if genetic variation was being depleted because of a management practice. Traditional field craft alone cannot directly address such questions, but the answers can be determined with some precision if the field work is coupled with modern molecular genetic techniques.

Molecules can enlighten us about biological attributes that are virtually impossible to observe in the field (Awise 2004). Parentage analysis is one such arena in which genetic data can inform management practices (DeWoody 2005), but there are a host of others. For example, molecular data have revealed deep evolutionary splits in stocks at one time thought to be homogeneous. This finding has concomitant management implications (Hoffman et al. 2006). Similarly, molecules can enlighten us about biologies that are virtually impossible to observe in the field, such as pollen flow (Hamrick, this volume) or the physiology of migration (Nichols et al. 2008).

Recent advances in molecular genetics and genomics have been embraced by many scientists in natural resource conservation. Today, several major conservation and management journals (e.g., *Journal of Wildlife Management*, *North American Journal of Fisheries Management*, *Plant Breeding Reviews*) are now using “genetics” editors to deal solely with the influx of manuscripts that employ molecular data. We have attempted to synthesize some of the major uses of molecular markers in natural resource management in a book targeted not only at scientists but also at individuals actively making conservation and management decisions. To that end, we have identified contributors who are major figures in molecular ecology and evolution; many have published books of their own. Our aim has been to direct and distill the thoughts of these outstanding

scientists by compiling compelling case histories in molecular ecology as they apply to natural resource management.

Clearly, we hope this book will appeal to academics interested in conservation genetics, molecular ecology, and the quantitative genetics of wild organisms. We think this book could be used as an educational tool – as a text for graduate ecology/genetics courses but also, perhaps, in advanced undergraduate courses. Furthermore, we hope this book will be useful to audiences in natural resource management, education, and research by clarifying how genetic approaches can be used to answer resource-related questions.

ABOUT THE EDITORS

Our collective expertise spans from molecular population genetics in the wild to genomics and quantitative genetics of managed or cultured species. We all study the genetics of natural resources, however, and we find that similar issues arise in wildlife, forestry, and fisheries. For example, when the forest geneticists began asking how many sires contributed pollen to a nut-bearing hardwood tree, it turns out that fisheries geneticists had already studied this problem from the perspective of a male fish guarding a nest full of developing embryos, and they had created computer programs to estimate the number of parents contributing gametes to a nest (DeWoody et al. 2000). Another such intersection of research across disciplines lies in the study of genetic processes in small populations; the same conceptual and analytical approaches being used to elucidate the genetic consequences of wildlife reintroductions (Latch & Rhodes 2005) are employed to evaluate genetic diversity in hardwood tree species subjected to severe habitat fragmentation (Victory et al. 2006). Our desire to produce a book stems from our mutual interests in understanding how molecular genetics can be used to inform and improve natural resource management.

In addition to our research interests, we teach several courses that directly pertain to this book. These courses include *Conservation Genetics* (DeWoody), *Molecular Ecology and Evolution* (DeWoody), and *Evolutionary Quantitative Genetics* (Nichols). Furthermore, several of us (DeWoody, Michler, Rhodes) have served as “genetics” editors for conservation and management journals, including *Journal of Wildlife Management*, *North American Journal of Fisheries Management*, and *Plant Breeding Reviews*.

ACKNOWLEDGMENTS

In addition to the authors, most of whom also provided reviews on other chapters and/or boxes, we thank the following individuals for their invaluable feedback: Jean Beaulieu, Tasha Belfiore, John Burke, Dave Coltman, Tariq Ezaz, Ben Fitzpatrick, Anthony Fiumera, Mike Goodisman, Rick Howard, Irby Lovette, Bill Muir, Patty Parker, Devon Pearse, Joe Quattro, Kim Scribner, Ron Sederoff, and Rod Williams. All provided insightful comments that directly strengthened



Book contributors at an October 2008 meeting, held at the John S. Wright Forestry Center (Purdue University). Row 1: Krista Nichols, Kelly Zamudio, Charles Michler, Yousry El-Kassaby, Tom Whitham, Jamie Ivy, Emily Latch, Lisette Waits, and Marjorie Matocq. Row 2: Lee Shugart, Dave Neale, Dave Hillis, John Avise, Andrew DeWoody, Robin Waples, Rodney Honeycutt, Paul Leberg, and John Bickham. Row 3: Kermit Ritland, Antoine Kremer, Stan Wullschlegler, Keith Woeste, Peter Waser, Jim Hamrick, Gene Rhodes, and John Patton. Photo credit: Caleb D. Phillips. See *Color Plate 1*.

individual chapters and boxes, and we trust that this book has been enhanced by their efforts.

This volume was largely possible because of the financial and logistical support of the Department of Forestry and Natural Resources at Purdue University. In particular, the department sponsored an October 2008 meeting at Purdue where many of the book contributors congregated for three days of scientific discourse and fellowship before finalizing their respective chapters or boxes.

Our own research programs have been supported by a variety of organizations, including the National Science Foundation (DeWoody, Bickham, Michler, Nichols), the U.S. Department of Agriculture (DeWoody, Michler, Nichols, Rhodes, Woeste), the State of Indiana (DeWoody, Michler, Rhodes), the National Oceanic and Atmospheric Administration (Bickham), the Great Lakes Fishery Trust (DeWoody, Nichols), and the U.S. Forest Service (Michler, Woeste). We thank them all for investing in science.

REFERENCES

- Avise JC (2004) *Molecular Markers, Natural History, and Evolution*. Sinauer, Sunderland, MA.
- DeWoody JA (2005) Molecular approaches to the study of parentage, relatedness and fitness: practical applications for wild animals. *Journal of Wildlife Management*, **69**, 1400–1418.
- DeWoody JA, DeWoody YD, Fiumera A, Avise JC (2000) On the number of reproductives contributing to a half-sib progeny array. *Genetical Research* (Cambridge), **75**, 95–105.
- Hoffman JI, Matson CW, Amos W, Loughlin TR, Bickham JW (2006) Deep genetic subdivision within a continuously distributed and highly vagile marine mammal, the Steller's sea lion (*Eumetopias jubatus*). *Molecular Ecology*, **15**, 2821–2832.

Latch EK, Rhodes OE Jr (2005) The effects of gene flow and population isolation on the genetic structure of reintroduced wild turkey populations: are genetic signatures of source populations retained? *Conservation Genetics*, **6**, 981–997.

Nichols KM, Felip A, Wheeler P, Thorgaard GH (2008) The genetic basis of smoltification-related traits in *Oncorhynchus mykiss*. *Genetics*, **179**, 1559–1575.

Victory E, Glaubitz JC, Rhodes OE Jr, Woeste KE (2006) Genetic homogeneity in *Juglans nigra* (Juglandaceae) at nuclear microsatellites. *American Journal of Botany*, **93**, 118–126.

6 Association genetics, population genomics, and conservation: Revealing the genes underlying adaptation in natural populations of plants and animals

Krista M. Nichols and David B. Neale

INTRODUCTION

Understanding the genetic basis of complex adaptive traits is key to understanding how natural and anthropomorphic factors have influenced and will influence the shape of genetic diversity and trajectory of evolution in natural populations. Complex adaptive traits are quantitative traits – those that vary on a continuous scale, and even more generally, are sometimes defined as traits that are expressed as a function of products from multiple genes (Falconer & MacKay 1996; Roff 1997; Lynch & Walsh 1998). Although classical quantitative genetics has revealed the genetic basis to numerous morphological, physiological, and life history traits in plants and animals, the actual genes (loci) and allelic variation with loci underlying key functional differences among organisms remain unknown. Understanding the genes involved in species- and population-level diversity can provide important tools (i.e., genetic markers) for resource managers that are charged with conservation, management, and restoration of natural populations. In this chapter, our examples and review are focused on non-model, non-domesticated organisms as it is the diversity in natural populations, shaped by the natural processes of evolution, with which natural resource managers are most concerned.

Population genetics has undoubtedly been one of the most important fields in the conservation, management, and restoration of native plant and animal species. Together with ecological and life history information, “neutral” genetic markers, or those mirroring the neutral demographic processes of natural populations, are important tools for the delineation of management units or evolutionary significant units for conservation and management. Loci that have been shaped by natural selection, in the process of adaptive population divergence, can however exhibit levels of differentiation markedly different than neutral loci (Leinonen et al. 2008; Vali et al. 2008; Nosil et al. 2009). Until recently, understanding the genetic basis of complex traits has been limited to model

We acknowledge the input and comments from a variety of people in the writing of this chapter. KN thanks Ben Hecht, Sunnie McCalla, Garrett McKinney, Ashley Chin-Baarstad, and John Colletti for useful comments. We both thank Yue Chen and Alex Wong for assistance with literature review and the reference database (Table 6–1).



Figure 6–1: Schematic representation of LD among genetic markers, genes, and a causal mutation. Gray and white contiguous blocks represent haplotype blocks with significant LD, and within those blocks are genes. Detecting significant genotype–phenotype associations will depend on LD between genetic markers and the causal mutation. In this case, the causal mutation (gray star) is in LD with three markers (black stars). Note that the causal mutation is not itself surveyed in the study, but by linkage with markers, a significant genotype–phenotype association would be observed with the markers typed in the study.

organisms, which are easily reared in a laboratory or common garden environment, and for which genetic and genomic resources were available. With the expansion of genomics and statistical genetics in the last decade and numerous genetic tools capable of surveying large numbers of genetic markers or genes in the genome, the identification of candidate gene and genome regions underlying ecologically relevant traits is now possible. The identification of genes and allelic variation at genes functionally linked to ecologically variable phenotypes is tractable for even non-model species, and results from association genetics studies have great promise in providing added resolution in defining units for conservation and management. These studies, together with classical quantitative genetic approaches, reveal that genes or markers linked to genes underlying adaptive population divergence can give very different signatures of population divergence, and that, even in the face of low to moderate gene flow observed at neutral genetic markers, natural selection can maintain adaptive population divergence at genes underlying ecologically relevant traits (Leinonen et al. 2008).

In all cases, the ability to identify genes or genome regions associated with adaptive population differentiation or within population diversity relies on linkage disequilibrium (LD), also called gametic phase disequilibrium, between markers surveyed and the causal mutation(s) (Fig. 6–1). LD is the nonrandom association of alleles at different genes or loci (Slatkin 2008). LD can arise between loci that are physically unlinked as a consequence of population genetic processes such as genetic drift, population subdivision, population bottlenecks, inbreeding, and epistasis; the magnitude of LD among physically linked loci is a function of the amount of recombination among linked loci (see Slatkin 2008 for a review). The concept of LD is an extremely important one in association genetics as the extent of LD between observed markers and the causal genetic variant partially responsible for the observed phenotypic variation will largely dictate the power of different methods in revealing genes or genome regions associated with the trait of interest. If LD is high over long stretches of the genome, fewer markers are needed for association genetics, but the likelihood of identifying the genetic variant responsible for phenotypic variation is much lower. If LD is low across the genome or is found in only short haplotype blocks, many more markers will be needed to detect associations across the whole genome; however, with shorter blocks of LD across the genome, the task of identifying the causal genetic variant becomes much easier. In rare cases is the causal mutation responsible for the phenotypic variability surveyed or observed in initial analyses in non-model organisms.

Table 6–1. A sampling of major reviews of the methods and utility of association genetics

Topic	Phenotype? quantified?	Pedigree/ crosses?	References
Population genomics & neutrality tests Tests for signatures of natural selection	No	No	Nielsen 2001, 2005; Luikart et al. 2003; Schlotterer 2003; Storz 2005; Vasemagi & Primmer 2005; Thornton et al. 2007; Li et al. 2008; Stinchcombe & Hoekstra 2008
LD mapping Genotype–phenotype association studies in populations of unknown pedigree	Yes	No	Gupta et al. 2005; Stinchcombe & Hoekstra 2008; Weir 2008
QTL analysis Detection of genes or genome regions associated with phenotypes of interest in pedigreed populations	Yes	Yes	Wu et al. 2002; Erickson et al. 2004; Slate 2005; Stinchcombe & Hoekstra 2008

The literature is replete with reviews of the theoretical and statistical approaches and methods used for association genetics and the identification of genes or genome regions that have been shaped by natural selection (Table 6–1). We do not intend to exhaustively recapitulate prior reviews but rather provide a general overview with relevance to natural or free-living populations, paying special attention to the advantages and challenges of these methods in non-model, non-domesticated natural or free-living plant and animal populations. We take the definition of natural population in terms of the genetic dissection of ecologically relevant traits as defined by Slate (2005), who provides an excellent overview and review of quantitative trait loci (QTL) mapping methodologies and empirical results in natural populations of animals. Slate (2005) defines a *natural population* as one that is “descended from recently sampled individuals of a non-domesticated origin” excluding “model organisms that have been reared in the laboratory for many generations.” This definition is particularly important as we review the primary literature for the identification of QTL in natural populations as few association genetic studies have been conducted in un-manipulated, non-domesticated populations of organisms. Although we recognize that natural populations of model organisms have been explored, we limit our review to those species that are not long-standing model organisms (i.e., *Drosophila*, *Arabidopsis*, crops, and domesticated animals) and to those traits that have ecological significance in natural populations.

METHODS FOR DETECTING GENES FOR ECOLOGICALLY RELEVANT PHENOTYPES

Here, we detail methods that take two major approaches in the identification of genes or genome regions significantly associated with adaptive divergence

among individuals and populations. The first group of methods (quantitative genetic approaches), including LD or association mapping and QTL analyses, rely on surveys of molecular markers and measures of known phenotypes of interest. The second group of methods (population genetic approaches), called hitchhiking mapping, does not necessarily require measurement of phenotypes on all individuals but rather aims to identify molecular markers showing unusual patterns of population genetic differentiation (i.e., outliers) between populations of interest.

Quantitative genetic approaches

LD or association mapping

LD or association mapping reveals genes or genome regions that are significantly associated with specific phenotypes in natural populations of organisms of unknown relationship (see Neale & Ingvarsson 2008; Stinchcombe & Hoekstra 2008; Weir 2008 for review). LD is among the intuitively simplest of tests for genotype–phenotype associations; individuals sampled from natural populations are evaluated for their phenotype in some type of replicated genetic test, genotyped for polymorphisms in a subset of candidate genes or throughout the genome, and genotype–phenotype associations are tested in the absence of linkage mapping or known family relationships. Because family relationships and population subdivision alone can lead to false-positive associations between genotype and phenotype, ad hoc, multivariate methods are used to account for population subdivision and relatedness using a subset of “neutral” genetic markers (Pritchard et al. 2000; Yu et al. 2006; Zhao et al. 2007). These methods eliminate false-positive associations that arise simply because of population subdivision but can also eliminate true phenotype–genotype associations that covary with population subdivision. Because association mapping uses relatively simple linear mixed models, additional fixed and random effects can be incorporated into models testing for genotype–phenotype associations to account for phenotypic variation among environments, sexes, year classes, and so forth, in addition to variation occurring as a result of population subdivision (Yu et al. 2006; Stich et al. 2008; Yu et al. 2008). There are two main approaches for LD or association mapping, and these are categorized into tests for association with specific candidate genes (or candidate regions) of interest, or genome-wide tests for association.

Candidate gene approaches. For non-model organisms lacking a genome sequence or significant genomic resources, the candidate gene approach for association mapping offers more immediate and simple tests for association with phenotypes of interest. Originally devised for tests of association in complex human diseases, numerous statistical tests or approaches have been devised for tests for association between candidate gene polymorphisms and phenotypes (see Long & Langley 1999; Balding 2006 for reviews). Genes with known roles in particular suites of life history, physiological, behavioral, or morphological traits in model organisms or better-studied taxonomic groups may provide the best candidates

for similar traits in non-model organisms (Fitzpatrick et al. 2005). Even in the absence of significant genomic sequence resources, motifs in candidate genes that are conserved across taxa can be used to identify primers to isolate the homologous gene sequences in non-model organisms of interest (Krutovsky et al. 2007). Moreover, with massively parallel sequencing, candidate genes, whole transcriptomes, and whole genomes can be used for single nucleotide polymorphism (SNP) detection even in non-model organisms (Ellegren 2008). The candidate-gene approach has been particularly successful across taxonomic groups and offers the greatest promise for initial association mapping studies in non-model organisms. In some cases, genome regions identified from QTL mapping studies in controlled crosses of the same or related species would provide information on candidate regions for association studies. The disadvantage of the candidate-gene approach is that for some traits, a reasonably viable set of candidate genes is not available without pursuing genome-wide approaches such as whole genome expression or transcriptome studies.

Genome-wide association approaches. Genome-wide tests for genotype–phenotype associations are so far limited to model organisms for which significant genomic resources are available. For genome-wide tests of association, suites of markers distributed across the genome are tested for genotype–phenotype associations. In most cases, the position or order of these markers across the genome is known from linkage mapping or genome-sequencing efforts. A genome-wide scan, then, gives an overview of the patterns of genotype–phenotype associations along the chromosomes. Although deemed “genome-wide” approaches, a true whole genome approach would sample all polymorphisms at the genomic level, and this is a monumental task even in fully sequenced genomes. With LD among closely linked loci, it is not necessary to sample every polymorphism in the genome. In fully sequenced organisms, the extent of LD across the genome can be evaluated to determine, on average, the size of haplotype blocks in the genome, as depicted in Fig. 6–1. From this information, representative markers from those regions (sometimes called “tag SNPs”) can be used for whole-genome approaches in LD mapping (Carlson et al. 2004). In non-model organisms, obtaining information on the size and genomic distribution of haplotype blocks across the genome is a huge undertaking in itself. In non-model organisms, the most promising approach for genome-wide association studies may come in surveying associations in large numbers of candidate genes or expressed sequences identified from transcriptome sequencing (gene-space scan).

There are a number of advantages of LD mapping in natural populations when compared to QTL mapping and population genomics approaches. First, although LD mapping can account for relatedness among individuals using neutral markers, complete and known family relationships among individuals in the sampled population(s) are not necessary as they are for QTL studies in natural populations. In many organisms, pedigrees cannot be determined directly by observation and thus rely on time-consuming and expensive efforts to reconstruct pedigree information using molecular markers (Blouin 2003; Pemberton 2008). Compared to QTL mapping in the more traditional sense of one or a few

crosses, LD mapping has the advantage of surveying many more recombinants in the population, offering finer resolution for the possible detection of the causal mutation(s) responsible for variation in phenotype. For non-model organisms with few genomic resources available, candidate-gene association mapping offers the greatest promise for tests of phenotype–genotype associations. The major disadvantage of LD mapping in non-model organisms is the time and expense required to survey sequence polymorphisms for the development of SNP markers either in few candidate genes or on a genome-wide level.

Quantitative trait loci (QTL) analysis

QTL analyses seek to identify genes or genome regions significantly associated with phenotypes of interest in known crosses or pedigreed populations of plants and animals. The application, tools, and use of QTL analysis for natural populations are reviewed by Erickson and colleagues (2004) and Slate (2005); for a comprehensive overview of design and analysis of QTL, readers are referred to Doerge and coworkers (1997) and Lynch and Walsh (1998). Briefly, the tools required for this type of analysis include individuals produced in a known breeding scheme or of known relationships in a pedigreed population, molecular marker genotypes of these progeny for markers distributed across the genome, and phenotypes of interest measured in individuals from the breeding scheme or pedigree. The observed amount of recombination between markers used for genotyping is used to order markers into linkage groups, which are used as a framework for statistical tests of genotype–phenotype associations. By observing the cosegregation or inheritance of molecular marker genotypes with phenotypes of interest within the context of this linkage map, genome regions that are significantly associated with variation in the phenotypes are identified.

The type of breeding scheme used for QTL analysis in natural populations is largely related to the question(s) of interest. In model organisms, QTL analyses are commonly conducted in progeny produced from inbred line crosses, maximizing the amount of LD between marker genotype and phenotypes of interest. For outbred populations of interest, QTL analyses are conducted in crosses between individuals with divergent phenotypes or can be conducted in pedigreed populations. For questions regarding genes involved in speciation or reproductive isolation between divergent populations, crosses made between species or populations are necessary to dissect the architecture of quantitative traits, unless a natural hybrid zone can be identified. For questions regarding genes underlying phenotypic variation within populations, although crosses between individuals with divergent phenotypes can be made, analysis in the full or partial pedigree of the population would sample more of the genetic and phenotypic diversity within the population, taking into account the genetic relationships among all pairs of individuals (Slate et al. 1999; George et al. 2000; Pemberton 2008).

There are both advantages and disadvantages in using QTL analysis compared to other methods for association genetics. The advantage of the QTL approach in known, single-generation crosses is that LD between polymorphic markers and phenotypic traits are maximized as a result of observing many fewer recombination events in a single cross when compared to multiple generations and multiple crosses in a pedigree. Because LD is maximized (i.e., gray and white

contiguous blocks of LD are longer in Fig. 6–1), many fewer markers are needed to perform QTL analysis; however, because LD is maximized, the likelihood that a QTL analysis will identify the causal mutation responsible for a proportion of the phenotypic trait variation is low. Moreover, because few individuals are selected for crossing, mutations at some loci associated with phenotypic variation may go undetected if markers linked to or the actual causal mutation are not polymorphic in the few individuals that were drawn for crosses from the larger population. As a result, crosses may not capture some of the significant causal variants for phenotypic variation that may be found if the entire population or populations are sampled. Progeny from crosses manipulated by the experimenter are generally reared and phenotyped in a laboratory or common garden, where the effects of environment can be controlled. Controlling the environment is an advantage for the detection of QTL in that trait variance due to environmental effects is minimized, but for some traits, the environment-dependent expression of the trait is an important context for studies interesting to ecologists, evolutionary biologists, and conservation biologists. In contrast, QTL analyses in pedigree populations take advantage of the larger amount of recombination that has occurred among generations and families of individuals with different phenotypic trait values. Because of this reduced level of LD among phenotypic traits and causal mutations (i.e., gray and white contiguous blocks are shorter in Fig. 6–1) as a function of sampling more meioses in the population, QTL analyses in natural populations will require much larger sample sizes and many more markers to detect the same QTL that may have been observed in line crosses. In QTL analysis, pedigree information is directly included in tests for genotype–phenotype associations and is more accurate in defining shared coancestry among individuals than are methods used in LD mapping to account for kinship (Pemberton 2008). In both approaches, the power and precision to detect and localize loci underlying quantitative traits will depend on the number of markers chosen, the amount of recombination events or LD observed between markers, and the effect size of individual loci (Doerge et al. 1997; Lynch & Walsh 1998; Doerge 2002). Because recombination rates and LD are unique not only to species but also to specific regions of chromosomes, providing a magic number for the number of individuals and markers to choose for genome-wide approaches is not possible. Lynch and Walsh (1998) detail calculations for the numbers of individuals and markers to use in genome-wide QTL analysis with specific QTL effect sizes and desired accuracy of mapping QTL. QTL analyses in crosses made in non-model organisms in the laboratory or common garden environments are numerous, but the use of this approach in natural or free-living populations is limited to systems where the pedigree is known or can be estimated from parentage analysis using molecular markers.

Population genetic approaches

Hitchhiking mapping and outlier analysis

Population genomics is the assessment of population genetic parameters at large numbers of loci distributed across the genome, with the aim of identifying loci that have been shaped by natural selection (Schlotterer 2002, 2003; Luikart et al.

2003; Storz 2005; Thornton et al. 2007). Whereas much of the genome will reflect patterns of neutral genetic variation attributed to mutation and demographic processes, “outlier analysis” identifies loci in the genome showing unusually high or low patterns of variation among populations due to the effects of natural selection. This approach is also called hitchhiking mapping and rests on the idea that strong directional or divergent selection for an advantageous allele creates strong LD with closely linked loci, and that as an advantageous allele approaches fixation, a decrease in heterozygosity at closely linked loci will also be observed (Maynard Smith & Haigh 1974). LD around the beneficial mutation is strongest and more extensive when said mutation is a new mutation immediately acted upon by positive selection; when natural selection shapes standing genetic variation, the extent of LD of the beneficial mutation with unlinked loci will depend on the amount of neutral variation that has accumulated in the region (a function of the effective population size) and recombination (Przeworski et al. 2005). Several tests have been devised for tests of these signatures of natural selection in the genome. In all cases, population genomic tests are most powerful for detection of directional or divergent selection on new mutations, which instantly creates LD at linked neutral sites. Detecting signatures of selection on standing genetic variation is more difficult as diversity about the causal mutation is greater due to neutral evolution prior to the onset of directional selection.

Among all of the approaches reviewed herein, the tools required for population genomics are the simplest: Individuals from populations of interest are genotyped at polymorphic markers (amplified fragment length polymorphism [AFLP], microsatellite, or SNP) across the genome, population genetic parameters are calculated based on allele frequencies within and across sampled populations, and signatures of unusually high or low patterns of genetic diversity within and between populations are revealed with statistical tests. Population genetic parameters used for detection of outlier loci include: 1) F_{st} showing unusually large or small levels of population subdivision compared to most loci sampled (Lewontin & Krakauer 1973; Vitalis et al. 2001; Beaumont & Balding 2004; Beaumont 2005); 2) $\ln RV$, which captures the natural log of the ratio of variance in microsatellite repeat number or allele sizes between populations (Schlotterer 2002); 3) $\ln RH$, which captures the natural log of the ratio of expected heterozygosity between populations (Kauer et al. 2003); and 4) the Ewens–Watterson neutrality test, which tests for excess or deficits in expected homozygosity (Watterson 1977). Tests for outliers are made either empirically by the identification of outliers in the distributions of the population genetics parameters mentioned earlier in text, or by comparing the distribution of these test statistics to distributions of the same statistics generated by coalescent simulations under a model of neutral evolution and particular demographic scenarios (Teshima et al. 2006).

In non-model organisms, particularly organisms for which little or no genomic sequence information exists, the outlier analysis approach is among the easiest to perform as anonymous genetic markers such as AFLPs and microsatellites can readily be used. Moreover, as sequencing costs decline with the rapid development of new sequencing technologies, generation of genomic sequences in non-model organisms will become quite tractable (Ellegren 2008; see also Chapter 4 by DeWoody and colleagues). The outlier analysis approach does not require the

collection of phenotype data, a time-consuming and difficult task for particularly complex phenotypes. As with the LD mapping and QTL approaches, the ability to sample all loci in the genome for signatures of natural selection will depend on the extent of LD among closely linked loci. Unfortunately, because outliers can occur as false positives or false negatives owing to the large numbers of tests performed and possible violation of simple assumptions of demography (Simonsen et al. 1995; Teshima et al. 2006), it is necessary to follow up with candidate outliers with additional validation to determine if the region linked to the markers indeed shows patterns of sequence variation consistent with directional selection and is functionally linked to phenotypes or life history traits.

Neutrality tests with sequence or SNP data

For single or few loci, tests of neutrality are based on sequence or SNP data. In some cases, outliers identified in population genomic studies are followed up with tests for signatures of natural selection using sequence information in candidate regions, and, in others, candidate genes are used. These tests can be roughly broken down into three categories: 1) tests within and among populations of the same species (“polymorphism tests”); 2) tests among species (“divergence tests”); and 3) joint tests of population and species level variation (“joint polymorphism and divergence tests”) (Nielsen 2001, 2005; Walsh 2008). In all cases, the neutral model of evolution serves as the null hypothesis. For within-species analyses, site frequency spectrum of polymorphisms or haplotype diversity is compared against neutral expectations; examples of these types of tests include Tajima’s D and Fu and Li’s D and F tests (Nielsen 2001, 2005; Walsh 2008). Population genetic polymorphism tests are subject to strong assumptions about population demography and often have low power compared to divergence and joint tests (Simonsen et al. 1995; Nielsen 2001, 2005; Zhai et al. 2009). Many divergence tests and joint tests evaluate whether nonsynonymous-to-synonymous substitution rates (d_N/d_S) in genes deviate from those expected under neutrality and are not subject to false positives due to demographic processes (Nielsen 2001, 2005; Zhai et al. 2009). One popular joint test is called the McDonald–Kreitman test, which evaluates the d_N/d_S ratio within and between species. Another common joint test is the Hudson–Kreitman–Aguade test, which compares sequence variation within versus between species, with the idea that within- and between-species divergence under neutral expectations will depend only on mutation rate. In most cases, tests for signatures of natural selection using sequence data use multiple tests and approaches to verify whether the null hypothesis of neutrality can be rejected. Nielsen (2005) offers an excellent review of the effects of different scenarios of natural selection (directional and balancing selection, selective sweeps) on within- and between-species variability.

Tests for neutrality on one or few loci have an obvious advantage for non-model organisms and the same advantages as candidate-gene association tests. Sequence data are readily obtainable from non-model species for few candidate loci. One limitation of this approach, as mentioned earlier, includes false rejection of the null, neutrality hypothesis due to violation of assumptions of equilibrium demography when polymorphism-based tests are used. Tests based on divergence are inherently testing hypotheses about strong or repeated selection among species,

whereas polymorphism tests within species detect recent selection. Readers are directed to Zhai and colleagues (2009) and Teshima and coworkers (2006) for excellent reviews and simulations of the power of outlier and neutrality tests for testing for signatures of natural selection.

IDENTIFICATION OF GENES UNDERLYING ADAPTIVE TRAITS: EXAMPLES IN PLANTS AND ANIMALS

Although most association genetic studies have been conducted in model organisms, the transfer of these tools to related non-model, non-domesticated, natural or free-living populations has allowed the genetic dissection of ecologically relevant traits, with potentially important implications for conservation and management application. In many cases, the real power in the identification of genes associated with ecologically relevant traits comes from combining these approaches (Vasemagi & Primmer 2005; Neale & Ingvarsson 2008; Stinchcombe & Hoekstra 2008). In the next sections, we give some examples of how these different approaches have been successful in the identification of genes and, in some cases, the causal mutations, responsible for a large proportion of phenotypic or ecotypic variability in non-model or natural or free-living populations of animals and plants.

Genome-wide association and QTL studies in animals

No genome-wide association studies have been conducted in natural or free-living populations of animals, but a few QTL studies have been published for natural or free-living populations of animal species (Table 6–2). Published QTL studies in natural or free-living populations are limited to long-term data sets derived from carefully tracked pedigrees in populations of large mammal species, namely red deer (*Cervus elaphus*; Slate et al. 2002) and Soay sheep (*Ovis aries*; Beraldi et al. 2007a,b). Linkage maps have been developed for several other free-living or natural populations and will serve as an important resource for QTL and LD mapping in those species.

Most genome-wide studies of genotype–phenotype associations for ecologically relevant traits have occurred in crosses manipulated by researchers in the laboratory, using QTL analyses (Table 6–2). These studies have identified QTL for morphological variation, behavior phenotypes (including host preference–mediating ecological speciation and mate preference), disease resistance, and other physiological or life history traits. QTL mapping, as mentioned earlier in text, is not a means to an end and rarely identifies the causal mutation(s) underlying phenotypic variation, but it provides important information on genome regions to further test for associations with phenotypes of interest using LD mapping or in tests for signatures of natural selection. In fact, QTL studies provide an important top-down approach in the identification of candidate regions and gene sets for candidate gene association and tests for natural selection (Tables 6–3 and 6–4, respectively). For example, in lake whitefish, QTL identified for growth and morphological characters in manipulated crosses between pelagic and benthic forms

Table 6–2. Examples of QTL analyses in non-model, non-domesticated animal species of ecological significance

Species	Common name	Morphology	Physiology	Behavioral	Life history & fitness
Amphibians & reptiles					
<i>Ambystoma mexicanum</i>	Mexican axolotl		Voss & Shaffer 2000		
Fish					
<i>Astyanax mexicanus</i>	Cavefish	Protas et al. 2006, 2008; Gross et al. 2009	Protas et al. 2008		
<i>Coregonus clupeaformis</i>	Lake whitefish	Rogers & Bernatchez 2005			
<i>Gasterosteus aculeatus</i>	Three-spined stickleback	Peichel et al. 2001; Colosimo et al. 2004; Shapiro et al. 2004; Albert et al. 2008; Miller et al. 2007			
<i>Labeotropheus fuelleborni</i> × <i>Metriacclima zebra</i>	Cichlid spp.	Streelman et al. 2003			
<i>Oncorhynchus mykiss</i>	Rainbow trout	Nichols et al. 2004, 2008; Zimmerman et al. 2005	Jackson et al. 1998; Ozaki et al. 2001; Robison et al. 2001; Martyniuk et al. 2003; Nichols et al. 2003, 2007, 2008; O'Malley et al. 2003; Zimmerman et al. 2004; Perry et al. 2005; Sundin et al. 2005; Drew et al. 2007		Martyniuk et al. 2003; Haidle et al. 2008
<i>Oreochromis mossambicus</i> × <i>O. aureus</i>	Tilapia		Chanaani et al. 2004; Moen et al. 2004		
<i>Salmo salar</i>	Atlantic salmon		Houston et al. 2008; Moen et al. 2005; Ozaki et al. 2005; Reid et al. 2005; Moghaddam et al. 2007		Moghaddam et al. 2007

(continued)

Table 6-2 (continued)

Species	Common name	Morphology	Physiology	Behavioral	Life history & fitness
Insects					
<i>Acyrtosiphon pisum</i>	Pea aphid			Hawthorne & Via 2001; Via & Hawthorne 2002	Hawthorne & Via 2001; Via & Hawthorne 2002
<i>Aedes aegypti</i>	Mosquito		Zhong et al. 2006		
<i>Anopheles gambiae</i>	Mosquito		Menge et al. 2006		
<i>Anopheles gambiae</i> × <i>A. arabiensis</i>	Mosquito				Slotman et al. 2004
<i>Apis mellifera</i>	Honeybee			Rueppell et al. 2004, 2006; Hunt et al. 2007	
<i>Bombus terrestris</i>	Bumblebee				Wilfert et al. 2007b
<i>Culex pipiens</i> × <i>C. quinquefasciatus</i>	Mosquito		Wilfert et al. 2007a,b		Mori et al. 2007
<i>Heliconius cydno</i> × <i>H. pachinus</i>	Butterfly			Kronforst et al. 2006	
<i>Heliconius melpomene</i>	Butterfly	Baxter et al. 2009			
<i>Laupala paramigra</i> × <i>L. kohalensis</i>	Hawaiian cricket			Shaw et al. 2007	
<i>Tribolium castaneum</i>	Red flour beetle		Zhong et al. 2003, 2005		Zhong et al. 2005
Mammals					
<i>Cervus elaphus</i>	Red deer	Slate et al. 2002			Slate et al. 2002
<i>Ovis aries</i>	Soay sheep	Beraldi et al. 2007b	Beraldi et al., 2007a,b		Beraldi et al. 2007b

Table 6-3. Summary of selected candidate-gene association studies in non-model, non-domesticated animal species

Species	Common name	Trait	Candidate genes	Reference
Amphibians & reptiles				
<i>Ambystoma mexicanum</i>	Axolotl	Metamorphic timing	<i>THRα</i> , <i>THRβ</i>	Voss et al. 2003
<i>Aspidoscelis inornata</i>	Little striped whiptail	Body color	<i>MCTR</i>	Rosenblum et al. 2004
<i>Thamnophis sirtalis</i>	Garter snakes	Tetrodotoxin resistance	<i>tsNa(V)1.4</i>	Ceffney et al. 2005
Birds				
<i>Acrocephalus arundinaceus</i>	Great reed warbler	Parasite load	<i>MHCI</i>	Westerdahl et al. 2005
<i>Anser c. caerulescens</i>	Snow goose	Plumage color	<i>MCTR</i>	Mundy et al. 2004
<i>Coereba flaveola</i>	Bananaquit	Plumage color	<i>MCTR</i>	Theron et al. 2001
<i>Parus major</i>	Great tit	Personality	<i>DRD4α</i>	Fidler et al. 2007
<i>Passer domesticus</i>	House sparrow	Disease resistance	<i>MHCIIb</i>	Bonneaud et al. 2006
<i>Stercorarius parasiticus</i>	Arctic skuas	Plumage color	<i>MCTR</i>	Mundy et al. 2004
Insects				
<i>Bicyclus anynana</i>	Butterfly	Eyespot size	<i>Distal-less (Dll)</i>	Beidade et al. 2002
<i>Solenopsis invicta</i>	Fire ant	Social & mating system	<i>Gp-9</i>	Ross & Keller 1998; Krieger & Ross 2002
Fishes				
<i>Astyanax mexicanus</i>	Cavefish	Body coloration	<i>MCTR</i>	Gross et al. 2009
<i>Gadus morhua</i>	Atlantic cod	Muscle fiber number; growth and condition; migration behavior	<i>Pan1</i>	Johnston & Andersen 2008; Jonsdottir et al. 2008; Pampoulie et al. 2008
<i>Gasterosteus aculeatus</i>	Three-spined stickleback	Body armor plates	<i>Eda</i>	Cano et al. 2006; Kitano et al. 2008
<i>Metriacilima zebra</i>	Zebra mbuna cichlid	Body coloration	<i>c-ski^a</i>	Streelman et al. 2003
Mammals				
<i>Canis lupus</i>	Gray wolf	Coat color	<i>K locus</i>	Anderson et al. 2009
<i>Chaetodipus intermedius</i>	Pocket mice	Coat color	<i>MCTR</i> , <i>Agouti</i>	Nachman et al. 2003
<i>Ovis aries</i>	Sheep	Coat color	<i>MCTR</i> ; <i>TYRP1</i>	Deng et al. 2009; Gratten et al. 2007 ^b
<i>Peromyscus polionotus</i>	Oldfield mouse	Coat color	<i>MCTR</i> , <i>Agouti</i>	Mullen & Hoekstra 2008
Other invertebrates				
<i>Mya arenaria</i>	Soft shell clam	Paralytic shellfish poisoning resistance	<i>rNav 1.2a</i>	Bricej et al. 2005

^a Gene linked to causal mutation.

^b See also case study in this chapter.

Table 6-4. Examples of population genomics and tests for neutrality in natural populations of animals

Species	Common name	No. of loci or genes studied	Marker type	Reference
Amphibians & reptiles				
<i>Rana</i> spp.	Frogs	1	Candidate gene	Tennesen & Blouin 2008
<i>Rana temporaria</i>	Common frog	Many	AFLP	Bonin et al. 2006
Birds				
<i>Falco naumanni</i>	Lesser kestrel	1	Candidate gene (MHC)	Alcaide et al. 2008
<i>Rupicapra rupicapra</i>	Alpine chamois	1	Candidate gene (MHC)	Mona et al. 2008
Fishes				
Cichlid spp.	Cichlids	Many	SNPs	Loh et al. 2008
<i>Clupea harengus</i>	Atlantic herring	12	Microsatellites	Watts et al. 2008
<i>Coregonus clupeaformis</i>	Lake whitefish	Many	AFLP	Campbell & Bernatchez 2004
<i>Fundulus heteroclitus</i>	Mummichog	1	Candidate gene	Powers & Schulte 1998
<i>Gadus morhua</i>	Atlantic cod	Many, 11	SNPs; microsatellites	Nielsen et al. 2006; Moen et al. 2008
<i>Gasterosteus aculeatus</i>	Three-spined stickleback	15	Microsatellites	Raeymaekers et al. 2007; Makinen et al. 2008a,b; Barrett et al. 2008
		Many	Microsatellites, candidate genes	
		109	Microsatellites, candidate gene	
		1		
		82	Genes	Gerrard & Meyer 2007
		Many	Candidate genes	Gerrard & Meyer 2007
Haplochromine/Tilapiae spp.				
<i>Haplochromis</i> spp., <i>Oreochromis niloticus</i> , <i>Astatotilapia burtoni</i>	Cichlid spp. African cichlids	Many		
<i>Oncorhynchus tshawytscha</i>	Chinook salmon	11	Microsatellite, candidate gene	O'Malley et al. 2007
<i>Salmo salar</i>	Atlantic salmon	14	Microsatellites, candidate genes	Vasemagi et al. 2005a,b
		95	Microsatellites	
		573	AFLP	Herder et al. 2008
<i>Telmatherina prognatha</i>	Sailfin silversides			
<i>Telmatherina antoniae</i>				
<i>Theragra chalcogramma</i>	Walleye pollock	38	Microsatellites, allozymes, candidate gene	Canino et al. 2005

Insects						
<i>Acyrtosiphon pisum</i>	Pea aphid	45	AFLP, EST	Via & West 2008		
<i>Apis mellifera</i>	Honeybee	Many	SNPs	Zayed & Whitfield 2008		
<i>Colias eurytheme</i>	Butterfly	1	Candidate gene	Wheat et al. 2006		
		1	Candidate gene	Watt 1977		
<i>Melitaea cinxia</i>	Glanville fritillary butterfly	1	Candidate gene	Orsini et al. 2009		
<i>Neochlamisus bebbianae</i>	Leaf beetle	Many	AFLP	Egan et al. 2008		
<i>Timema cristinae</i>	Walking sticks	Many	AFLP	Nosil et al. 2008		
<i>Zeraphera diniana</i>	Larch budmoth	Many	AFLP	Emelianov et al. 2004		
Mammals						
<i>Arvicola terrestris</i>	Water vole	2	Candidate genes (MHC)	Bryja et al. 2007		
<i>Gracilinanus microtarsus</i> and <i>Marmosops incanus</i>	American mouse opossums	1	Candidate gene (MHC)	Meyer-Lucht et al. 2008		
<i>Oryctolagus cuniculus</i>	European rabbit	25	Allozymes	Campos et al. 2008		
<i>Ovis dalli</i>	Wild sheep	3	Candidate genes	Worley et al. 2006		
<i>Peromyscus maniculatus</i>	Deer mice	18	Allozymes	Storz & Dubach 2004		
<i>Peromyscus maniculatus</i>	Deer mice	2	Candidate genes	Storz & Kelly 2008		
<i>Peromyscus polionotus</i>	Oldfield mouse	2	Candidate genes	Mullen & Hoekstra 2008		
<i>Peromyscus spp.</i>	Mice	10–37	Allozymes	Storz & Nachman 2003		
<i>Peromyscus spp.</i>	Mice	1	Candidate gene	Gering et al. 2009		
Other invertebrates						
<i>Mytilus edulis</i>	Mussel	11	Microsatellite	Faure et al. 2008		
<i>Crassostrea virginica</i>	Oyster	Many	AFLP	Murray & Hare 2006		
<i>Littorina saxatilis</i>	Marine snail	Many	AFLP	Wilding et al. 2001		
		Many	AFLP	Galindo et al. 2009		
		14	Candidate regions	Wood et al. 2008		

colocalize with markers showing signatures of natural selection (i.e., “outlier” behavior) between sympatric pairs of these morphotypes found in several lakes in Quebec (Campbell & Bernatchez 2004; Rogers & Bernatchez 2005). In three-spined sticklebacks, the colocalization of QTL to the ectodysplasin gene provided the foundation for tests of *Eda* polymorphism and signatures of natural selection in natural populations exhibiting variation in lateral plate numbers (Colosimo et al. 2005).

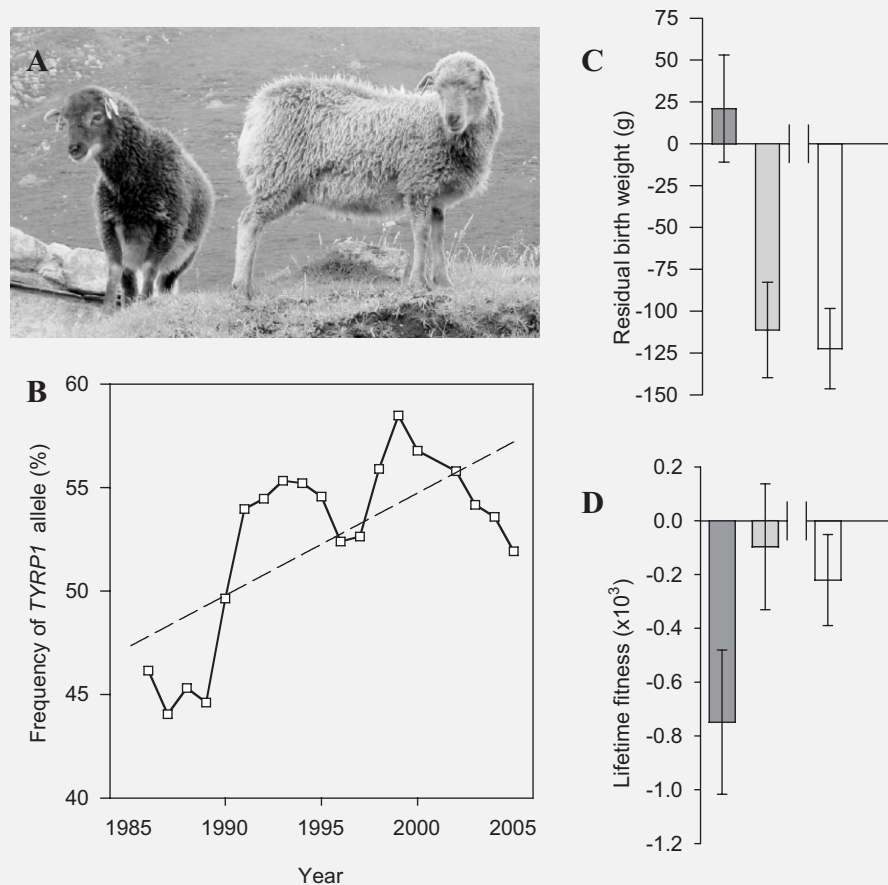
To our knowledge, no genome-wide LD or association mapping studies have yet been conducted in free-living or natural populations of animals. Important first steps for genome-wide association studies, however, include the generation of genome-wide sequence and SNP variation information, as well as examination of the extent of LD within species. In some non-model species, these resources are beginning to emerge; these resources include information on the extent of LD in wild mice (Laurie et al. 2007), red deer (Slate & Pemberton 2007), and collared flycatchers (Backstrom et al. 2006b), as well as linkage maps in wild bird populations including the great reed warbler (Akesson et al. 2007), collared flycatcher (Backstrom et al. 2006a), and zebra finch (Stapley et al. 2008).

Candidate-gene association studies in animals

The candidate-gene approach is by far the approach most used, and holds the most promise for use in non-model, natural populations of organisms. In most cases, candidate genes are chosen based on their known role for particularly morphological, behavioral, physiological, or life history traits in other taxa. Comparative genomics and identification of genes by whole-genome expression studies are also avenues for the identification of candidate genes. In non-model animal species, many candidate-gene studies have been focused on body-color polymorphism (see Protas & Patel 2008 for review) and disease resistance and mate choice as it relates to major histocompatibility complex (MHC) loci polymorphisms (Piertney & Oliver 2006) (Table 6–3). Examples include genetic polymorphism in coat color genes in mice species that are adapted to different environments (Nachman et al. 2003; Steiner et al. 2007), in hemoglobin genes in mice adapted to different altitudes (Storz et al. 2007), in color genes associated with albinism in cavefish (Protas et al. 2006), and in plumage coloration involved in mate choice (Mundy et al. 2004). Although the adaptive significance is not apparent, a gene associated with coat-color polymorphism in Soay sheep (Gratten et al. 2007) has also been identified and appears to segregate in the population with linked fitness-related traits (see Box 6 case study). In fewer cases, candidate genes are identified for further study based on whole-genome approaches such as QTL or association mapping. For example, polymorphism in the *Eda* gene found in QTL for plate morph in three-spined stickleback is associated with plate morphs in wild marine and freshwater populations (Colosimo et al. 2005; Barrett et al. 2008; Kitano et al. 2008). The fact that most candidate genes have been identified outside of whole-genome approaches is more likely due to the extensive resources and time needed to conduct a genome-wide study and to the extensive genomic resources needed to follow up with QTL studies to identify genes within QTL regions.

BOX 6: UNRAVELING COUNTERINTUITIVE EVOLUTIONARY TRENDS: COAT COLOR IN SOAY SHEEP

Jake Gratten, Alastair J. Wilson, Allan F. McRae, Dario Beraldi, Peter M. Visscher, Josephine M. Pemberton, and Jon Slate



Box Figure 6-1: (a) The two coat-color morphs in Soay sheep. (b) Increase in frequency of the *Tyrp1* T allele over a twenty-year period (linear regression, slope of +0.49%/year, $r^2 = 0.390$, $p = 0.004$). (c) Mean birth-weight differential of GG sheep (dark gray bar) and TT sheep (light gray bar), in each case relative to GT sheep, and of light sheep (white bar) relative to dark sheep. (d) Mean lifetime fitness differential of *Tyrp1* genotypes and coat-color phenotypes.

Background

Evolutionary biologists sometimes report that heritable traits under directional selection fail to evolve as predicted (Merila et al. 2001). A polymorphism for coat color in a wild population of Soay sheep (Box Fig. 6-1, a) is determined by a single nonsynonymous G → T substitution in the tyrosinase-related protein 1 gene (*Tyrp1*); GG homozygotes and GT heterozygotes have dark coats, whereas TT homozygotes are light (Gratten et al. 2007). Dark sheep are heavier than light sheep, and body size is positively correlated with fitness (Wilson et al. 2006). Therefore, it is surprising that the recessive light allele (T), which is not ancestral,

has reached a frequency of approximately 0.50 and has not declined in frequency during twenty years of intensive monitoring (Box Fig. 6–1, b). Why does coat color, which has a simple genetic basis, show a counterintuitive evolutionary trajectory?

Case Study

More than 2,500 Soay sheep living between 1985 and 2005 were typed at the *TYRP1* causative mutation, and genotype data were integrated with pedigree, life history, and body size data (Gratten et al. 2008). First, associations between *Tyrp1* and body size were analyzed using an “animal model” approach, whereby polygenic effects on body size were modeled as a random effect, independently of *Tyrp1* genotype (fixed effect). Similar models were constructed with coat-color phenotype instead of *Tyrp1* genotype. Both color ($F_{1,2201.5} = 26.03$, $p < .0001$, $n = 2,370$) and *Tyrp1* ($F_{2,1623.1} = 8.96$, $p = .0001$, $n = 1,757$) explained significant variation in birth weight (Box Fig. 6–1, c) and body size later in life. Dark sheep were heavier than light sheep, and the G allele was partially dominant for body weight (such that $GG \geq GT > TT$). These findings were supported by a transmission disequilibrium test (TDT: $F_{1,421} = 4.60$, $p = .034$), a form of combined association and linkage mapping that eliminates possible causes of spurious association such as undetected population structure or admixture. Thus, the relationship between body size and *Tyrp1* is due to genetic linkage, and dark sheep really are expected to be fitter than light sheep, all else being equal.

Next, associations between *Tyrp1*/coat color and fitness were analyzed using animal models and TDTs. Color was not associated with lifetime fitness, despite the fact that dark sheep were heavier than light sheep. *Tyrp1* genotype was associated, however, with lifetime fitness (Box Fig. 6–1, d; animal model: $F_{2,1336} = 4.03$, $p = .020$, $n = 1,355$). It is intriguing that fitness differences between *Tyrp1* genotypes were not those predicted by effects on body size. There was a cryptic difference between phenotypically indistinguishable homozygous (GG) and heterozygous (GT) dark sheep, with GG sheep being less fit than either GT dark sheep or TT light sheep. This association was also confirmed to be due to linkage (TDT; $F_{1,427} = 6.87$, $p = .010$, $n = 492$).

What do these results mean? The *Tyrp1* gene is associated with both body size and fitness, either directly or because it is in LD with tightly linked genes that affect the focal traits. These genes appear to act antagonistically because GG sheep are large but less fit, TT sheep carry alleles that confer small body size (but greater fitness), and GT sheep are relatively large and fit. Although body size is under directional selection, a localized negative genetic correlation in the vicinity of *Tyrp1* means that large body size alleles in this part of the genome are associated with decreased fitness. Overall, sheep carrying the T allele, irrespective of their size, are favored, which may explain why T has increased in frequency. These associations were able to be detected only when coat color genotype rather than phenotype was analyzed, due to the cryptic fitness difference between the two categories of dark sheep. The lessons from this study are that 1) an evolutionary response to selection can be modulated by local genetic correlations between linked genes, and 2) studying the underlying genotype of a trait may be

necessary to understand its evolutionary dynamics. Although the conservation genetic implications of this research are less immediate, the work does illustrate the fact that making management decisions on the basis of one trait may have unpredictable consequences on other genetically correlated traits.

REFERENCES

- Gratten J, Beraldi D, Lowder BV et al. (2007) Compelling evidence that a single nucleotide substitution in *TYRP1* is responsible for coat-colour polymorphism in a free-living population of Soay sheep. *Proceedings of the Royal Society of London-Series B: Biological Sciences*, **274**, 619–626.
- Gratten J, Wilson AJ, McRae R et al. (2008) A localized negative genetic correlation constrains microevolution of coat color in wild sheep. *Science*, **319**, 318–320.
- Merila J, Sheldon BC, Kruuk LEB (2001) Explaining stasis: microevolutionary studies in natural populations. *Genetica*, **112**, 199–222.
- Wilson AJ, Pemberton JM, Pilkington JG et al. (2006) Environmental coupling of selection and heritability limits evolution. *PLoS Biology*, **4**, 1270–1275.

Tests for signatures of natural selection in animals

In natural animal populations, tests for signatures of natural selection have identified outlier loci associated with ecological specialization, speciation, and adaptation in a wide range of species (Table 6–4). Tests for signatures of natural selection at loci throughout the genome (“population genomics”) have been one of the most rapidly developing areas for the identification of genes underlying adaptive population divergence. Because population genomics requires multiple testing and has the potential for the identification of false positives and negatives under certain selection and demographic scenarios (see *Hitchhiking mapping and outlier analysis*), the best supported evidence for true positives in outlier tests are those loci that can also be validated by linkage to QTL or by follow-up studies evaluating the identity of genes and nature of sequence variation functionally associated with traits of interest. For example, outliers identified by population genomics in sympatric ecotypes of lake whitefish are often colocalized to QTL regions for morphological and physiological differences among ecotypes (Campbell & Bernatchez 2004; Rogers & Bernatchez 2005). Outliers identifying footprints of selection in three-spined stickleback colocalize to QTL for morphotypic variation in that species (Makinen et al. 2008a). Anonymous AFLP marker loci identified as outliers among parapatric populations of *Littorina* gastropods (Wilding et al. 2001) have been used to isolate genomic sequence for finer-level sequence analysis of genes and genome regions under natural selection (Wood et al. 2008).

Genome-wide association and QTL studies in plants

Large-scale candidate gene or genome-wide association studies in plants have, until recently, been restricted to the model plant *Arabidopsis thaliana* (Zhao et al. 2007) or the domesticated plant *Zea mays* ssp. *mays* (Yu & Buckler 2006). There is an extensive literature on QTL mapping in forest trees, however (Table 6–5). We classify trees as plants from natural population versus domesticated plants because in just about every case, forest-tree QTL mapping studies begin with

Table 6-5. Summary of QTL analyses conducted in non-model, non-domesticated plant species

Scientific name	Common name	Growth	Phenology	Disease resistance	Cold hardiness	Drought tolerance	Wood property
<i>Castanea sativa</i>	Sweet chestnut	Casasoli et al. 2004, 2006	Casasoli et al. 2004				
<i>Cryptomeria japonica</i>	Japanese cryptomeria	Yoshimaru et al. 1998					Kuramoto et al. 2000
<i>Eucalyptus globulus</i>	Tasmanian blue gum	Marques et al. 2002; Kirst et al. 2004; Thamarus et al. 2004; Bundock et al. 2008	Bundock et al. 2008	Bundock et al. 2008			Bundock et al. 2008
<i>Eucalyptus grandis</i> × <i>Eucalyptus urophylla</i>	Grand eucalyptus × Timor mountain gum	Grattapaglia et al. 1995, 1996; Verhaegen et al. 1997; Marques et al. 2002; Missiaggia et al. 2005					Grattapaglia et al. 1996; Byrne et al. 1997a,b; Verhaegen et al. 1997; Kirst et al. 2005
<i>Eucalyptus nitens</i>	Shining gum	Byrne et al. 1997a			Byrne et al. 1997b		
<i>Eucalyptus tereticornis</i>	Forest red gum	Marques et al. 2002					
<i>Fagus sylvatica</i>	European beech	Scalfi et al. 2004					
<i>Larix decidua</i> × <i>Larix kaempferi</i>	European larch × Japanese larch						
<i>Pinus caribaea</i> × <i>Pinus elliotii</i>	Caribbean pine × Slash pine	Shepherd et al. 2006					Arcade et al. 2002
<i>Pinus elliotii</i> × <i>Pinus palustris</i>	Slash pine × Longleaf pine	Shepherd et al. 2006					Shepherd et al. 2003

Forest Trees

<i>Pinus pinaster</i>	Maritime pine	Plomion et al. 1996; Brendel et al. 2002; Chagne et al. 2003; Enebirri et al. 1997, 1998a,b	Plomion et al. 1996; Brendel et al. 2002; Chagne et al. 2003; Enebirri et al. 1997, 1998a,b	Markussen et al. 2003; Pot et al. 2006
<i>Pinus radiata</i>	Monterey pine	Lerceteau et al. 2000	Lerceteau et al. 2000	Kumar et al. 2000; Devey et al. 2004
<i>Pinus sylvestris</i>	Scots pine	Kaya et al. 1999; Chagne et al. 2003; Gwaze et al. 2003; Williams et al. 2007	Hurme et al. 1997, 2000	Hurme et al. 1997
<i>Pinus taeda</i>	Loblolly pine	Kim et al. 2004	Kim et al. 2004	Weng et al. 2002
<i>Populus davidiana</i>	Shan Yang	Zhang et al. 2006	Zhang et al. 2006	Zhang et al. 2006
<i>Populus tementosa</i>	Chinese white poplar	Wu & Stettler 1994;	Wu & Stettler 1994;	
<i>Populus trichocarpa</i>	Black cottonwood × Eastern cottonwood	Bradshaw & Stettler 1995; Wu et al. 1997, 1998; Wu 1998; Li et al. 1999; Ferris et al. 2002;	Bradshaw & Stettler 1995; Li et al. 1999; Chen et al. 2002; Frewen et al. 2000	Tschaplinski et al. 2006
<i>Pseudotsuga menziesii</i>	Douglas-fir	Wuilschleger et al. 2005; Rae et al. 2006, 2007, 2008	Jermstad et al. 2001a	Jermstad et al. 2001a; Wheeler et al. 2005
<i>Quercus petraea</i>	Sessile oak	Jermstad et al. 2003	Galling et al. 2005	Saintagne et al. 2004 (continued)

Table 6–5 (continued)

Forest Trees							
Scientific name	Common name	Growth	Phenology	Disease resistance	Cold hardiness	Drought tolerance	Wood property
<i>Quercus robur</i>	English oak	Scotti-Saintagne et al. 2004a, 2005; Casasoli et al. 2006	Scotti-Saintagne et al. 2004a; Galling et al. 2005			Parelle et al. 2007; Brendel et al. 2008	Saintagne et al. 2004
<i>Salix dasycladus</i> × <i>Salix viminalis</i>	Mao Zhi Liu × Basket willow	Ronnberg-Wastjung et al. 2005; Weih et al. 2006				Ronnberg-Wastjung et al. 2005	
<i>Salix viminalis</i> × <i>Salix schwerinii</i>	Basket willow × Common Osier	Tsarouhas et al. 2002, 2003, 2004				Tsarouhas et al. 2004	
Herbaceous Plants							
Scientific name	Common name	Fitness	Floral morphology	Herbivory	Heavy metal tolerance		
<i>Aquilegia formosa</i> × <i>Aquilegia pubescens</i>	Western columbine × Sierra columbine		Hodges et al. 2002				
<i>Arabis dopsis halleri</i>	N/A					Courbot et al. 2007; Willems et al. 2007	
<i>Arabis dopsis lyrata</i>	Lyre-leaved rock-cress			Heidel et al. 2006			
<i>Iris fulva</i> × <i>Iris brevicaulis</i>	Copper iris × Zigzag iris	Martin et al. 2005, 2006	Bouck et al. 2007				
<i>Mimulus</i>	Monkeyflower	Lin 2000; Hall et al. 2006	Lin & Ritland, 1997; Schemske & Bradshaw 1999; Lin 2000; Bleiweiss 2001; Fishman et al. 2002; Hall et al. 2006				

mapping population parent trees that have not resulted from any more than one generation of phenotypic selection from natural populations. The number of studies from herbaceous, natural plant populations is much less extensive (Table 6–5). The complex traits of study in forest-tree QTL mapping studies fall into six broad categories (growth, phenology, disease resistance, cold hardiness, drought, and wood property). All of these traits can be considered “adaptive,” although growth and wood property are generally considered “agronomic” and not specifically “adaptive.” Early-generation QTL mapping studies in trees often used rather small population sizes (~100), in which the number of QTLs detected was likely underestimated and the size of effects overestimated. Later studies using population sizes of 500 or more probably provide better estimates of QTL number and effect.

QTL mapping studies in forest trees share many of the same approaches and results. Mapping population parent trees are nearly always highly heterozygous and not inbred. Using a highly heterozygous, non-inbred population results in not all QTL loci segregating, and thus being detectable in individual crosses. Nevertheless, a large proportion of the total phenotypic variance for a trait can be accounted for from individual crosses, although the sizes of individual QTL effects are generally small (1–3%) (Wheeler et al. 2005). The QTL approach is rather powerful for identifying the number of QTLs, their chromosomal regions, and the sizes of their effects; however, the resolution of map position is generally quite crude (10–20 cM), so for large genomes lacking reference sequences, the path to positional cloning of QTLs is long, expensive, and not easily justified. Therefore, the genes underlying adaptive-trait QTLs in forest trees remain unknown.

The situation in herbaceous, natural plant QTL mapping is somewhat different (Table 6–5). Here, the traits of interest are often those leading to speciation events such as floral morphology, and thus hybrid crosses are used to maximize QTL segregation. The number of QTLs for such traits is generally quite few, and the sizes of their individual effects are high, justifying positional cloning of such QTLs that will now be greatly facilitated by the genome sequencing *Arabidopsis lyrata*, *Aquilegia*, and *Mimulus*. Species such as *A. lyrata* and *Boechera stricta* will be good systems for discovering individual genes underlying complex adaptive traits using combined population genetic, QTL mapping, and association approaches.

Candidate-gene association studies in plants

Association studies in natural plant systems are candidate-gene-based due to the lack of reference genome sequences. Studies have been published for four forest-tree species and two herbaceous species (Table 6–6). The studies in *Populus*, *Eucalyptus*, and *A. lyrata* included only one candidate gene each, whereas the *Pinus*, *Pseudotsuga*, and *Zea mays* ssp. *mays* included many candidate genes each. All species are characterized by a rapid decay of LD, particularly the conifer species (Neale & Savolainen 2004), so the search for associations is challenging, but when an association is found, it is quite likely that the polymorphism is within the gene determining the complex trait (or at least closely linked). Full gene-space candidate-gene association studies are experimentally and economically tractable

Table 6–6. Examples of candidate-gene association analyses in plant species

Species	Common name	Trait	Candidate genes	Reference
Trees				
<i>Eucalyptus nitens</i>	Shining gum	Wood properties	CCR	Thumma et al. 2005
<i>Pinus taeda</i>	Loblolly pine	Drought tolerance	<i>dhn-1, dhn-2, lp3-1, wrky-like, sod-chl</i>	Gonzalez-Martinez et al. 2008
		Wood properties	<i>cad, sams-2, comt-2, dhn-2, lp3-3, 4cl, ccr-1, α-tubulin, ccoaomt-1, agp-6, agp-like, c3h-1, c4h-1, c4h-2, cesA3β</i>	Gonzalez-Martinez et al. 2007
<i>Pseudotsuga menziesii</i>	Douglas-fir	Growth phenology cold-tolerance	<i>60s RPL31a</i> , CN639236.1 (guanine nucleotide-binding protein), ES421311.1 (hypothetical protein), Pm.CL783Contig1 (SOUL heme-binding family protein), <i>4CL1, LEA-EMB11</i> , CN637339.1 (hypothetical protein), CN638489.1 (α -expansin), sSPcDFD040B03103 (MADS-box transcription factor), CN637306.1 (MYB-like transcription factor), <i>f3h2</i> , Pm.CL234Contig1 (rab GTPase)	Eckert et al., 2009b
Herbaceous plants				
<i>Arabidopsis lyrata</i>	Lyre-leaved rock-cress	Herbivory	<i>GL1</i>	Kivimaki et al. 2007
<i>Zea mays ssp. parviglumis</i>	Balsas teosinte	Domestication	<i>d8, id1, tb1, te1, ts2, zap1, zen1, zf12, ba1, elm1, ids1, ra1, ra2, su1, tb1, te1, td1, zag11, zf1, zf12, ZmCIR1, ZmGI</i>	Weber et al. 2007, 2008

to perform with current generation sequencing and SNP genotyping technologies, and a large number of studies in a variety of forest-tree and herbaceous-plant species are now underway.

Tests for signatures of natural selection in plants

Population genetic approaches (i.e., tests of neutrality and outlier analysis) have been applied to large numbers of genes in the model plant *Arabidopsis thaliana* and in the domesticated crop (*Zea mays ssp. mays*). In a review by Wright and Gaut (2005), it is reported that as many as 20% of the genes may be under some form of selection, although that number is likely an overestimate. In natural plant populations, there are fewer studies and few genes have been evaluated (Table 6–7). Early resequencing studies in which tests of neutrality were performed included

Table 6–7. Examples of tests of neutrality or outlier analysis in natural plant populations

Species	Common name	No. of genes studied	Marker type	Reference
Trees				
<i>Abies kawakamii</i>	Kawakami fir	1	SNP, microsatellites, cDNA	Shih et al. 2007
<i>Betula pendula</i>	European white birch	2	Microsatellites	Jarvinen et al. 2003
<i>Cathaya argyrophylla</i>	Yin Shan	8	SNP, mitochondrial DNA	Wang & Ge 2006
<i>Cryptomeria japonica</i>	Sugi	7	SNP	Kado et al. 2003
<i>Cunninghamia konishii</i>	China fir	1	SNP	Hwang et al. 2003
<i>Cunninghamia lanceolata</i>	China fir	1	SNP	Hwang et al. 2003
<i>Picea abies</i>	Norway spruce	1, 22	SNP	Guillet-Claude et al. 2004; Heuertz et al. 2006
<i>Picea glauca</i>	White spruce	47	SNP	Namroud et al. 2008
<i>Picea mariana</i>	Black spruce	2	SNP	Guillet-Claude et al. 2004
<i>Pinus lambertiana</i>	Sugar pine	1	SNP	Jermstad et al. 2006
<i>Pinus pinaster</i>	Maritime pine	8	SNP	Pot et al. 2005
<i>Pinus radiata</i>	Monterey pine	8	SNP	Pot et al. 2005
<i>Pinus sylvestris</i>	Scots pine	1, 2, 14	SNP	Dvornyk et al. 2002; Garcia-Gil et al. 2003; Wachowiak et al. 2009
<i>Pinus taeda</i>	Loblolly pine	19, 18	SNP	Brown et al. 2004; Gonzalez-Martinez et al. 2006a
<i>Populus tremula</i>	European aspen	1, 5, 1	SNP	Ingvarsson 2005; Ingvarsson et al. 2006; Garcia & Ingvarsson 2007
<i>Pseudotsuga menziesii</i>	Douglas-fir	18, 121	SNP	Krutovsky & Neale 2005; Eckert et al. 2009a
<i>Quercus petraea</i>	Durmast oak	2	Microsatellites, SCARS, AFLP	Scotti-Saintagne et al. 2004b
<i>Quercus robur</i>	English oak	2	Microsatellites, SCARS, AFLP	Scotti-Saintagne et al. 2004b
<i>Taxodium distichum</i>	Bald cypress	4	SNP	Kado et al. 2006
Herbaceous plants				
<i>Helianthus annuus</i>	Sunflower	9	SNP	Liu & Burke 2006
<i>Hordeum vulgare</i> ssp. <i>spontaneum</i>	Barley	1, 9, 18, 877	SNP	Morrell et al. 2003, 2005; Rostoks et al. 2005; Jones et al. 2008
<i>Oryza rufipogon</i> and <i>Oryza nivara</i>	Rice	1, 10	SNP	Wang et al. 2007; Zhu et al. 2007
<i>Persea americana</i>	Avocado	4	SNP	Chen et al. 2008
<i>Solanum</i> ssp.	Tomato	8, 14	SNP	Roselius et al. 2005; Arunyawat et al. 2007

SCARS = sequence characterized amplified regions

one to no more than twenty genes. Based on the small sample of genes, it was not possible to gain an estimate of what proportion of these genomes might be under selection. Recent studies (Eckert et al. 2009a; Song et al. 2009) have reported neutrality tests for nearly 100 or more genes. These studies, combined with the earlier studies, suggest that approximately 10% of the genes may be under selection (Neale 2007). Thus, candidate-gene resequencing and tests of neutrality are efficient approaches toward identifying candidate genes for association studies that might underlie complex adaptive traits in natural plant populations. Furthermore, there is often a functional basis for candidate genes underlying a complex trait (Gonzalez-Martinez et al. 2006b; Eckert et al. 2009b). With the exception of *Populus trichocarpa* and *A. lyrata*, plants from natural populations lack a reference genome sequence to facilitate gene resequencing, although many have fairly rich expressed sequence tag (EST) databases. The newest generation of sequencing technologies makes it experimentally and economically possible to resequence large numbers of genes from natural plant systems.

The outlier approach has been applied to only a couple of natural plant populations to identify candidate genes (Scotti-Saintagne et al. 2004b; Namroud et al. 2008). The oak (Scotti-Saintagne et al. 2004b) and spruce (Namroud et al. 2008) studies identified 12% and 14% outlier loci, respectively. These percentages are consistent with estimates from neutrality testing of the proportion of genes under selection.

CASE STUDY: QTL, ASSOCIATION GENETICS, AND TESTS FOR NATURAL SELECTION IN A NATURAL FOREST-TREE POPULATION

As an animal example is provided in the boxed case study within this chapter, here we provide another example using the forest tree, Douglas-fir, as a case study for how combined population and quantitative genetic approaches can be used to discover the genes underlying a complex adaptive trait in a non-model and non-domesticated plant. Douglas-fir is a long-lived, woody perennial with limited genetic resources; it is not an organism that generally would be thought of as having attributes for easy identification of the genes underlying a complex adaptive trait. We show, however, that the combined population and quantitative genetic approaches we have outlined in this chapter can be applied to an organism such as Douglas-fir and how the knowledge derived can be applied in resource management strategies to help mitigate the impacts of climate change.

The adaptive complex traits of interest were bud phenology and cold-hardiness. Douglas-fir has a broad and ecologically diverse habitat in western North America. There is an extensive literature on the genetics of phenology and cold-hardiness in Douglas-fir based on a common garden approach (Campbell & Sorensen 1979; Aitken & Adams 1996, 1997; Rehfeldt 1997; Anekonda et al. 2000; St. Clair et al. 2005; St. Clair 2006). These studies clearly demonstrate the genetic control (high heritability) and adaptive patterns of variation across complex ecological landscapes. We surmised that phenology and cold-hardiness in Douglas-fir might then be good target complex adaptive traits to apply population and quantitative genetics approaches to finding the underlying genes.

The first step was to apply QTL mapping. A three-generation outbred pedigree was constructed, and the clonally propagated F₂ offspring were planted at two different test-site locations (Jermstad et al. 2001a,b). A restriction fragment length polymorphism (RFLP) linkage map was constructed (Jermstad et al. 1998), and the progeny were evaluated for bud phenology and cold-hardiness. Several QTLs for each of these traits were detected and mapped. Because the size of the segregating population was relatively small, however, it was likely that some QTLs were undetected and the sizes of individual QTL effects were overestimated. The parent trees were then re-mated to develop a much larger (~500) clonally replicated F₂ segregating population. In this experiment, however, the progeny were grown under experimental treatment conditions so that specific environmental cues (winter chill, spring heat sum, photoperiod, and moisture stress treatments) by QTL interactions could be estimated (Jermstad et al. 2003; Fig. 6–2). The goal of this aspect of the experiment was to identify QTLs interacting with specific cues from the environment and thus potentially giving clues as to the specific gene underlying the QTL. These QTL mapping experiments provided the first indications of the number of QTLs affecting bud phenology and cold-hardiness in Douglas-fir and their approximate locations in the genome, but the low-level resolution of their map position provided little indication of the specific genes underlying the QTL. A small number of candidate genes were mapped to the QTL maps, but again the resolution was rather crude (Wheeler et al. 2005).

In the next phase, the population-genomics approach was used to help identify candidate genes for cold-hardiness. In two studies, lists of 18 candidate genes (Krutovsky & Neale 2005) and 121 candidate genes (Eckert et al. 2009a) were developed based primarily on their function in *A. thaliana*. Amplicons from these candidate genes were resequenced in a small ($n = 24$) diversity panel to discover SNPs. The sequence polymorphism database developed from resequencing could then be used to estimate measures of nucleotide diversity and divergence and perform tests of neutrality. From these tests, six genes departed from neutrality and revealed signatures of selective sweeps (Table 6–8; Eckert et al. 2009a). In the next phase, these genes and others were tested for association with bud phenology and cold-hardiness to provide the quantitative genetic line of evidence that the genes underlying adaptive trait QTLs are now known.

An association mapping study was designed to test for association between SNPs in 117 candidate genes, including the 6 genes identified from the population-genomics approach (Table 6–8), and 21 adaptive-trait phenotypes, including bud phenology and cold-hardiness (Eckert et al. 2009b). An association population of 700 open-pollinated families from Douglas-fir trees sampled throughout the states of Washington and Oregon was assembled. Progeny from these families were grown in a randomized common garden, and all 21 phenotypes were evaluated. A maternal breeding value was estimated for each trait and each family. Next, an Illumina GoldenGate genotyping chip was designed that contained 384 SNPs from the 117 candidate genes. All 700 mother trees were genotyped for all 384 SNPs. The phenotype–genotype data set used included 21 traits and 228 high-quality SNP genotypes. A general linear model was used to test for associations between SNPs and the traits measured, and 30 significant associations were found (Eckert et al. 2009b). There were not, however, any

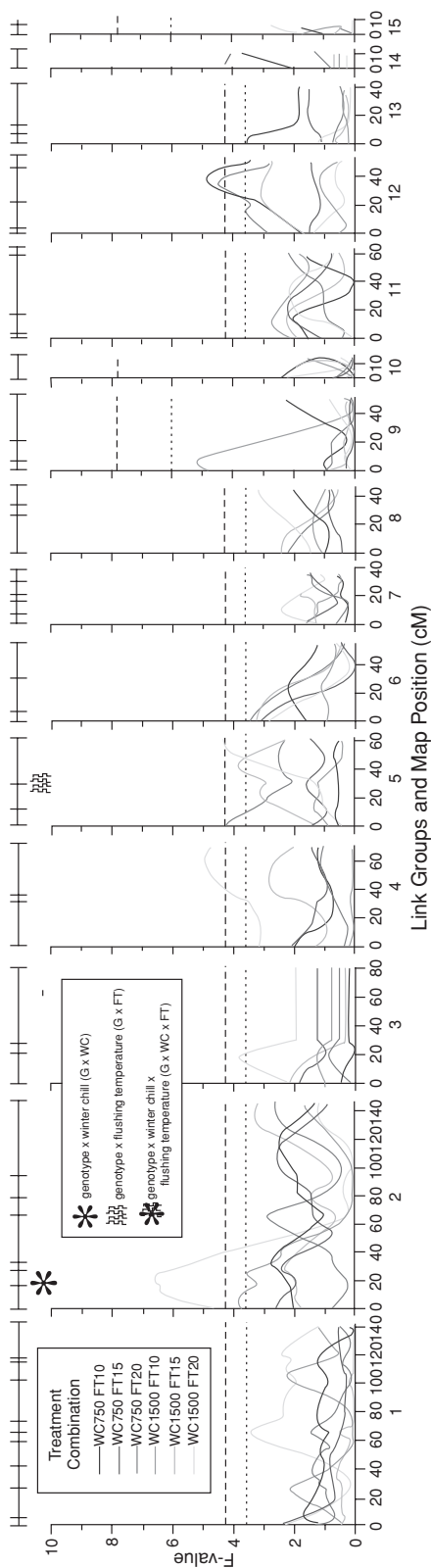


Figure 6-2: Terminal bud flush (TBF_{G1}) was used as a surrogate trait to measure growth initiation in the spring. The overwintering bud is released from dormancy and growth is initiated. Seven QTLs for TBF were detected in the growth initiation experiment (TBF_{G1}). QTLs were found on six linkage groups (LGs 2, 3, 4, 5, 12, and 14) and were detected in five of the six treatment (T) combinations. Only two QTL \times T interactions were found, one for winter chill on LG2 and one for flushing temperature on LG5. The interaction detected on LG5 is located at a marker that is intermediate between two QTLs detected by interval mapping (from Jermstad et al. 2003). See *Color Plate VIII*.

Table 6–8. A list of candidate genes putatively affected by directional natural selection (from Eckert et al. [2009a])

Locus	Gene product	Result ^a
Compound DHEW test		
Pm.CL908Contig1	GRAM-containing/ABA-responsive protein	$p_D = .001, p_H < .001, p_{EW} = .080$
ES420171.1	Cold-regulated plasma membrane protein	$p_D = .009, p_H = .050, p_{EW} = .035$
ES420250.1	Dehydrin-like protein	$p_D = .072, p_H = .083, p_{EW} = .042$
CN634517.1	Lumenal-binding protein	$p_D = .034, p_H = .148, p_{EW} = .076$
Polymorphism-to-divergence		
Pm.CL61Contig1	Cyclosporin A-binding protein	$k = 0.32$
Pm.CL908Contig1	GRAM-containing/ABA-responsive protein	$k = 0.58$
CN638556.1	Transcription regulation protein	$k = 0.41$
Synonymous-to-nonsynonymous divergence		
Pm.CL922Contig1	Thaumatin-like protein	$Ka/Ks = 14.48, \theta_\pi/D_{xy} = 0.087$
CN634677.1	LRR receptor-like protein kinase	$Ka/Ks = 10.78, \theta_\pi/D_{xy} = 0.066$

^a Results for the DHEW test are given as p values for each of the component tests (D = Tajima's D ; H = Fay and Wu's H ; EW = Ewen–Watterson test) comprising the joint test. Values for the EW test are one minus the left-tailed probabilities (cf.). Listed are p values for drift within a constant size population. Loci were significant when demographic models included in the simulations are bolded. For polymorphism-to-divergence tests, parameter estimates for a maximum likelihood implementation of the Hudson-Kreitman-Aguadé test are listed. Estimates of k are from a nested model where all three putative targets of selection are allowed to have free parameters. The parameter k specifies the level of elevation ($k > 1$) or reduction ($k < 1$) in diversity relative to divergence. Ka/Ks values were considered extreme when greater than 5.

genes in common between the population genomic approach and the association approach. This study was based on just 121 genes, so that when it was repeated with a large number of genes, one would expect to find many genes in common between approaches. These genes would be those most likely to be underlying complex adaptive traits and be under natural selection in populations of Douglas-fir.

THE GENES OF ADAPTIVE DIFFERENTIATION: UTILITY FOR CONSERVATION AND MANAGEMENT

Although genetics has historically been used to infer relationships among populations and species from “neutral” genetic information, adding information regarding the genetic architecture and genes involved in adaptive phenotypic diversification has great promise for conservation and management of natural, free-living populations. Bonin and colleagues (2007) describe a new index of population adaptation using results from population-genomic approaches and have found that diversity estimates from neutral and adaptive sets of loci are uncorrelated and tell different stories about the standing genetic diversity within and between populations. The idea that neutral and adaptive indices of diversity show different patterns is not new, however, and is an important consideration for the future of conservation genetics (Crandall et al. 2000; Merila & Crnokrak 2001; Reed & Frankham 2003; Kohn et al. 2006; Leinonen et al. 2008). The goal of most conservation programs for wild populations of organisms has been to maintain

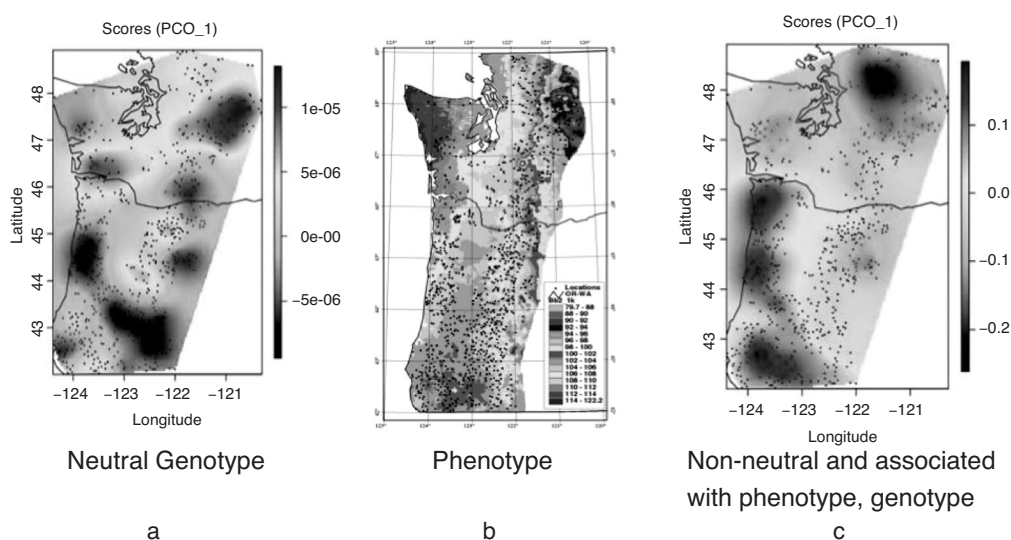


Figure 6-3: Patterns of neutral genetic diversity (a), phenotypic diversity (b), and adaptive genetic diversity (c). See Color Plate IX.

genetic diversity, while preserving local adaptations (Moritz 2002; Bonin et al. 2007). In other words, most conservation programs recognize both the phenotypic differences among populations and the demographic processes revealed by population genetic analysis in evaluating long-term population viability and delineating units for conservation (see Moritz 2002 for a review).

One of the key components required for the maintenance of genetic diversity is in obtaining baseline information about the genetic diversity in species and populations of interest so that in the face of anthropogenic impacts and environmental change, the influences of this change on genetic diversity may be monitored (Schwartz et al. 2007; Hoffmann & Willi 2008). Many natural plant and animal populations are threatened by the effects of environmental change. Populations that are currently adapted to a geographic region may no longer be adapted to that location due to changes in temperature, moisture availability, and other environmental factors. It is therefore important to develop detailed and precise descriptions of standing adaptive genetic variation in plant and animal populations so that monitoring activities can be implemented to detect genetic changes in populations. Incorporating genetic information from candidate regions associated with adaptive traits has been historically difficult, as the information has simply not been available for non-model species; however, this trend is changing as studies begin to reveal the genes and shifts in allele frequencies at those genes in response to environmental changes (Hoffmann & Willi 2008). Monitoring the changes in allele frequencies of genes underlying adaptive phenotypes, after being identified, is relatively straightforward. In an example from the Douglas-fir case study earlier in text, the patterns of diversity within non-neutral, phenotype-associated candidate genes show significant similarity to the patterns of phenotypic variation (Fig. 6-3). In contrast, there is little similarity in patterns of variation between neutral genetic variation and phenotypic variation in this system. It can be imagined how land managers might use

geographic information system (GIS)-type applications to lay standing patterns of adaptive genetic variation over predicted environmental patterns (*sensu* Joost et al. 2007, temperature, moisture, etc.) and to develop strategies for assisted migration of genotypes to ensure adaptation in the face of climate change. It is clear that the population and quantitative genomic approaches to understanding adaptive genetic variation in natural plant and animal populations will be of great value in genomically assisted gene-resource conservation and management strategies to mitigate the negative effects of environmental change.

The inclusion of genes underlying adaptive phenotypes will become imperative in conservation genetics, but much work remains on the details of which and how many “adaptive” loci to include in conservation genetic analyses. Hoffman and Willi (2008) review recent theoretical advances in this area and suggest that using loci that explain more than 5% of the phenotypic variation within and among populations will be useful in identifying shifts in allele frequencies in response to environmental change. Just as research on the number of loci and alleles per loci has been important in population genetics using “neutral” loci, the selection of genetic loci that contribute to a significant portion of the phenotypes describing differences among individuals within and across populations and species boundaries will be an active area of ongoing and future research.

REFERENCES

- Aitken SN, Adams WT (1996) Genetics of fall and winter cold hardiness of coastal Douglas-fir in Oregon. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **26**, 1828–1837.
- Aitken SN, Adams WT (1997) Spring cold hardiness under strong genetic control in Oregon populations of *Pseudotsuga menziesii* var. *menziesii*. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **27**, 1773–1780.
- Akesson M, Hansson B, Hasselquist D, Bensch S (2007) Linkage mapping of AFLP markers in a wild population of great reed warblers: importance of heterozygosity and number of genotyped individuals. *Molecular Ecology*, **16**, 2189–2202.
- Albert AYK, Sawaya S, Vines TH et al. (2008) The genetics of adaptive shape shift in stickleback: pleiotropy and effect size. *Evolution*, **62**, 76–85.
- Alcaide M, Edwards SV, Negro JJ, Serrano D, Tella JL (2008) Extensive polymorphism and geographical variation at a positively selected MHC class IIB gene of the lesser kestrel (*Falco naumanni*). *Molecular Ecology*, **17**, 2652–2665.
- Anderson TM, vonHoldt BM, Candille SI et al. (2009) Molecular and evolutionary history of melanism in North American gray wolves. *Science*, **323**, 1339–1343.
- Anekonda TS, Adams WT, Aitken SN et al. (2000) Genetics of cold hardiness in a cloned full-sib family of coastal Douglas-fir. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **30**, 837–840.
- Arcade A, Faivre-Rampant P, Paques LE, Prat D (2002) Localisation of genomic regions controlling microdensitometric parameters of wood characteristics in hybrid larches. *Annals of Forest Science*, **59**, 607–615.
- Arunyawat U, Stephan W, Stadler T (2007) Using multilocus sequence data to assess population structure, natural selection, and linkage disequilibrium in wild tomatoes. *Molecular Biology and Evolution*, **24**, 2310–2322.
- Backstrom N, Brandstrom M, Gustafsson L et al. (2006a) Genetic mapping in a natural population of collared flycatchers (*Ficedula albicollis*): conserved synteny but gene order rearrangements on the avian Z chromosome. *Genetics*, **174**, 377–386.
- Backstrom N, Ovarnstrom A, Gustafsson L, Ellegren H (2006b) Levels of linkage disequilibrium in a wild bird population. *Biology Letters*, **2**, 435–438.

- Balding DJ (2006) A tutorial on statistical methods for population association studies. *Nature Reviews Genetics*, **7**, 781–791.
- Barrett RDH, Rogers SM, Schluter D (2008) Natural selection on a major armor gene in threespine stickleback. *Science*, **322**, 255–257.
- Baxter SW, Johnston SE, Jiggins CD (2009) Butterfly speciation and the distribution of gene effect sizes fixed during adaptation. *Heredity*, **102**, 57–65.
- Beaumont MA (2005) Adaptation and speciation: what can F_{st} tell us? *Trends in Ecology & Evolution*, **20**, 435–440.
- Beaumont MA, Balding DJ (2004) Identifying adaptive genetic divergence among populations from genome scans. *Molecular Ecology*, **13**, 969–980.
- Beldade P, Brakefield PM, Long AD (2002) Contribution of distal-less to quantitative variation in butterfly eyespots. *Nature*, **415**, 315–318.
- Beraldi D, McRae AF, Gratten J et al. (2007a) Quantitative trait loci (QTL) mapping of resistance to strongyles and coccidia in the free-living Soay sheep (*Ovis aries*). *International Journal for Parasitology*, **37**, 121–129.
- Beraldi D, McRae AF, Gratten J et al. (2007b) Mapping quantitative trait loci underlying fitness-related traits in a free-living sheep population. *Evolution*, **61**, 1403–1416.
- Bleiweiss R (2001) Mimicry on the QT(L): genetics of speciation in *Mimulus*. *Evolution*, **55**, 1706–1709.
- Blouin MS (2003) DNA-based methods for pedigree reconstruction and kinship analysis in natural populations. *Trends in Ecology & Evolution*, **18**, 503–511.
- Bonin A, Nicole F, Pompanon F, Miaud C, Taberlet P (2007) Population adaptive index: a new method to help measure intraspecific genetic diversity and prioritize populations for conservation. *Conservation Biology*, **21**, 697–708.
- Bonin A, Taberlet P, Miaud C, Pompanon F (2006) Explorative genome scan to detect candidate loci for adaptation along a gradient of altitude in the common frog (*Rana temporaria*). *Molecular Biology and Evolution*, **23**, 773–783.
- Bonneaud C, Perez-Tris J, Federici P, Chastel O, Sorci G (2006) Major histocompatibility alleles associated with local resistance to malaria in a passerine. *Evolution*, **60**, 383–389.
- Bouck A, Wessler SR, Arnold ML (2007) Qtl analysis of floral traits in Louisiana Iris hybrids. *Evolution*, **61**, 2308–2319.
- Bradshaw HD Jr, Stettler RF (1995) Molecular genetics of growth and development in populus. IV. Mapping QTLs with large effects on growth, and phenology traits in a forest tree. *Genetics*, **139**, 963–973.
- Brendel O, Le Thiec D, Scotti-Saintagne C et al. (2008) Quantitative trait loci controlling water use efficiency and related traits in *Quercus robur* L. *Tree Genetics & Genomes*, **4**, 263–278.
- Brendel O, Pot D, Plomion C, Rozenberg P, Guehl JM (2002) Genetic parameters and QTL analysis of delta13C and ring width in maritime pine. *Plant Cell and Environment*, **25**, 945–953.
- Bricelj VM, Connell L, Konoki K et al. (2005) Sodium channel mutation leading to saxitoxin resistance in clams increases risk of PSP. *Nature*, **434**, 763–767.
- Brown GR, Gill GP, Kuntz RJ, Langley CH, Neale DB (2004) Nucleotide diversity and linkage disequilibrium in loblolly pine. *Proceedings of the National Academy of Sciences USA*, **101**, 15255–15260.
- Bryja J, Charbonnel N, Berthier K, Galan M, Cosson JF (2007) Density-related changes in selection pattern for major histocompatibility complex genes in fluctuating populations of voles. *Molecular Ecology*, **16**, 5084–5097.
- Bundock PC, Potts BM, Vaillancourt RE (2008) Detection and stability of quantitative trait loci (QTL) in *Eucalyptus globulus*. *Tree Genetics & Genomes*, **4**, 85–95.
- Byrne M, Murrell JC, Owen JV et al. (1997a) Identification and mode of action of quantitative trait loci affecting seedling height and leaf area in *Eucalyptus nitens*. *Theoretical and Applied Genetics*, **94**, 674–681.
- Byrne M, Murrell JC, Owen JV, Williams ER, Moran GF (1997b) Mapping of quantitative trait loci influencing frost tolerance in *Eucalyptus nitens*. *Theoretical and Applied Genetics*, **95**, 975–979.

- Campbell D, Bernatchez L (2004) Generic scan using AFLP markers as a means to assess the role of directional selection in the divergence of sympatric whitefish ecotypes. *Molecular Biology and Evolution*, **21**, 945–956.
- Campbell RK, Sorensen FC (1979) New basis for characterizing germination. *Journal of Seed Technology*, **4**, 24–34.
- Campos R, Storz JF, Ferrand N (2008) Evidence for contrasting modes of selection at interacting globin genes in the European rabbit (*Oryctolagus cuniculus*). *Heredity*, **100**, 602–609.
- Canino MF, O'Reilly PT, Hauser L, Bentzen P (2005) Genetic differentiation in walleye pollock (*Theragra chalcogramma*) in response to selection at the pantophysin (PanI) locus. *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 2519–2529.
- Cano JM, Matsuba C, Makinen H, Merila J (2006) The utility of QTL-linked markers to detect selective sweeps in natural populations – a case study of the EDA gene and a linked marker in threespine stickleback. *Molecular Ecology*, **15**, 4613–4621.
- Carlson CS, Eberle MA, Rieder MJ et al. (2004) Selecting a maximally informative set of single-nucleotide polymorphisms for association analyses using linkage disequilibrium. *American Journal of Human Genetics*, **74**, 106–120.
- Casasoli M, Derory J, Morera-Dutrey C et al. (2006) Comparison of quantitative trait loci for adaptive traits between oak and chestnut based on an expressed sequence tag consensus map. *Genetics*, **172**, 533–546.
- Casasoli M, Pot D, Plomion C et al. (2004) Identification of QTLs affecting adaptive traits in *Castanea sativa* Mill. *Plant Cell and Environment*, **27**, 1088–1101.
- Chagne D, Brown G, Lalanne C et al. (2003) Comparative genome and QTL mapping between maritime and loblolly pines. *Molecular Breeding*, **12**, 185–195.
- Chen H, Morrell PL, de la Cruz M, Clegg MT (2008) Nucleotide diversity and linkage disequilibrium in wild avocado (*Persea americana* mill.). *Journal of Heredity*, **99**, 382–389.
- Chen THH, Howe GT, Bradshaw HD (2002) Molecular genetic analysis of dormancy-related traits in poplars. *Weed Science*, **50**, 232–240.
- Cnaani A, Zilberman N, Tinman S, Hulata G, Ron M (2004) Genome-scan analysis for quantitative trait loci in an F-2 tilapia hybrid. *Molecular Genetics and Genomics*, **272**, 162–172.
- Colosimo PF, Hosemann KE, Balabhadra S et al. (2005) Widespread parallel evolution in sticklebacks by repeated fixation of ectodysplasin alleles. *Science*, **307**, 1928–1933.
- Colosimo PF, Peichel CL, Nereng K et al. (2004) The genetic architecture of parallel armor plate reduction in threespine sticklebacks. *PLoS Biology*, **2**, 635–641.
- Courbot M, Willems G, Motte P et al. (2007) A major quantitative trait locus for cadmium tolerance in *Arabidopsis halleri* colocalizes with HMA4, a gene encoding a heavy metal ATPase. *Plant Physiology*, **144**, 1052–1065.
- Crandall KA, Bininda-Emonds OR, Mace GM, Wayne RK (2000) Considering evolutionary processes in conservation biology. *Trends in Ecology and Evolution*, **15**, 290–295.
- Deng WD, Shu W, Yang SL, Shi XW, Mao HM (2009) Pigmentation in black-boned sheep (*Ovis aries*): association with polymorphism of the MC1R gene. *Molecular Biology Reports*, **36**, 431–436.
- Devey ME, Carson SD, Nolan MF et al. (2004) QTL associations for density and diameter in *Pinus radiata* and the potential for marker-aided selection. *Theoretical and Applied Genetics*, **108**, 516–524.
- Doerge RW (2002) Mapping and analysis of quantitative trait loci in experimental populations. *Nature Reviews Genetics*, **3**, 43–52.
- Doerge RW, Zeng ZB, Weir BS (1997) Statistical issues in the search for genes affecting quantitative traits in experimental populations. *Statistical Science*, **12**, 195–219.
- Drew RE, Schwabl H, Wheeler PA, Thorgaard GH (2007) Detection of QTL influencing cortisol levels in rainbow trout (*Oncorhynchus mykiss*). *Aquaculture*, **272**, S183–S194.
- Dvornyk V, Sirvio A, Mikkonen M, Savolainen O (2002) Low nucleotide diversity at the pal1 locus in the widely distributed *Pinus sylvestris*. *Molecular Biology and Evolution*, **19**, 179–188.
- Eckert A, Wegrzyn J, Pande B et al. (2009a) Multilocus patterns of nucleotide diversity and divergence reveal positive selection at candidate genes related to cold-hardiness in coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*). *Genetics*, **183**, 289–298.

- Eckert AJ, Bower AD, Wegrzyn JL et al. (2009b) Association genetics of coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*, Pinaceae). I. Cold-hardiness related traits. *Genetics*, **182**, 1289–1302.
- Egan SP, Nosil P, Funk DJ (2008) Selection and genomic differentiation during ecological speciation: isolating the contributions of host association via a comparative genome scan of *Neochlamisus bebbianae* leaf beetles. *Evolution*, **62**, 1162–1181.
- Ellegren H (2008) Sequencing goes 454 and takes large-scale genomics into the wild. *Molecular Ecology*, **17**, 1629–1631.
- Emebiri LC, Devey ME, Matheson AC, Slee MU (1997) Linkage of RAPD markers to NESTUR, a stem growth index in *radiata* pine seedlings. *Theoretical and Applied Genetics*, **95**, 119–124.
- Emebiri LC, Devey ME, Matheson AC, Slee MU (1998a) Age-related changes in the expression of QTLs for growth in *radiata* pine seedlings. *Theoretical and Applied Genetics*, **97**, 1053–1061.
- Emebiri LC, Devey ME, Matheson AC, Slee MU (1998b) Interval mapping of quantitative trait loci affecting NESTUR, a stem growth efficiency index of *radiata* pine seedlings. *Theoretical and Applied Genetics*, **97**, 1062–1068.
- Emelianov I, Marec F, Mallet J (2004) Genomic evidence for divergence with gene flow in host races of the larch budmoth. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **271**, 97–105.
- Erickson DL, Fenster CB, Stenoien HK, Price D (2004) Quantitative trait locus analyses and the study of evolutionary process. *Molecular Ecology*, **13**, 2505–2522.
- Falconer D, MacKay T (1996) *Introduction to Quantitative Genetics*, 4th edn. Longman Group Ltd., Essex, England.
- Faure MF, David P, Bonhomme F, Bierne N (2008) Genetic hitchhiking in a subdivided population of *Mytilus edulis*. *BMC Evolutionary Biology*, **8**, 164.
- Ferris R, Long L, Bunn SM et al. (2002) Leaf stomatal and epidermal cell development: identification of putative quantitative trait loci in relation to elevated carbon dioxide concentration in poplar. *Tree Physiology*, **22**, 633–640.
- Fidler AE, van Oers K, Drent PJ et al. (2007) Drd4 gene polymorphisms are associated with personality variation in a passerine bird. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **274**, 1685–1691.
- Fishman L, Kelly AJ, Willis JH (2002) Minor quantitative trait loci underlie floral traits associated with mating system divergence in *Mimulus*. *Evolution*, **56**, 2138–2155.
- Fitzpatrick MJ, Ben-Shahar Y, Smid HM et al. (2005) Candidate genes for behavioural ecology. *Trends in Ecology & Evolution*, **20**, 96–104.
- Frewen BE, Chen THH, Howe GT et al. (2000) Quantitative trait loci and candidate gene mapping of bud set and bud flush in Populus. *Genetics*, **154**, 837–845.
- Gailing O, Kremer W, Steiner W, Hattamer HH, Finkeldey R (2005) Results on quantitative trait loci for flushing date in oaks can be transferred to different segregating progenies. *Plant Biology (Stuttgart)*, **7**, 516–525.
- Galindo J, Moran P, Rolan-Alvarez E (2009) Comparing geographical genetic differentiation between candidate and noncandidate loci for adaptation strengthens support for parallel ecological divergence in the marine snail *Littorina saxatilis*. *Molecular Ecology*, **18**, 919–930.
- Garcia MV, Ingvarsson PK (2007) An excess of nonsynonymous polymorphism and extensive haplotype structure at the PtABI1B locus in European aspen (*Populus tremula*): a case of balancing selection in an obligately outcrossing plant? *Heredity*, **99**, 381–388.
- Garcia-Gil MR, Mikkonen M, Savolainen O (2003) Nucleotide diversity at two phytochrome loci along a latitudinal cline in *Pinus sylvestris*. *Molecular Ecology*, **12**, 1195–1206.
- Geffeney SL, Fujimoto E, Brodie ED, Brodie ED, Ruben PC (2005) Evolutionary diversification of TTX-resistant sodium channels in a predator–prey interaction. *Nature*, **434**, 759–763.
- George AW, Visscher PM, Haley CS (2000) Mapping quantitative trait loci in complex pedigrees: a two-step variance component approach. *Genetics*, **156**, 2081–2092.
- Gering EJ, Opazo JC, Storz JF (2009) Molecular evolution of cytochrome b in high- and low-altitude deer mice (genus *Peromyscus*). *Heredity*, **102**, 226–235.

- Gerrard DT, Meyer A (2007) Positive selection and gene conversion in SPP120, a fertilization-related gene, during the east African Cichlid fish radiation. *Molecular Biology and Evolution*, **24**, 2286–2297.
- Gonzalez-Martinez SC, Ersoz E, Brown GR, Wheeler NC, Neale DB (2006a) DNA sequence variation and selection of tag single-nucleotide polymorphisms at candidate genes for drought-stress response in *Pinus taeda* L. *Genetics*, **172**, 1915–1926.
- Gonzalez-Martinez SC, Huber D, Ersoz E, Davis JM, Neale DB (2008) Association genetics in *Pinus taeda* L. II. Carbon isotope discrimination. *Heredity*, **101**, 19–26.
- Gonzalez-Martinez SC, Krutovsky KV, Neale DB (2006b) Forest-tree population genomics and adaptive evolution. *New Phytologist*, **170**, 227–238.
- Gonzalez-Martinez SC, Wheeler NC, Ersoz E, Nelson CD, Neale DB (2007) Association genetics in *Pinus taeda* L. I. Wood property traits. *Genetics*, **175**, 399–409.
- Grattapaglia D, Bertolucci FLG, Penchel R, Sederoff RR (1996) Genetic mapping of quantitative trait loci controlling growth and wood quality traits in *Eucalyptus grandis* using a maternal half-sib family and RAPD markers. *Genetics*, **144**, 1205–1214.
- Grattapaglia D, Bertolucci FL, Sederoff RR (1995) Genetic mapping of QTLs controlling vegetative propagation in *Eucalyptus grandis* and *E. urophylla* using a pseudo-testcross strategy and RAPD markers. *Theoretical and Applied Genetics*, **90**, 933–947.
- Gratten J, Beraldi D, Lowder BV et al. (2007) Compelling evidence that a single nucleotide substitution in TYRP1 is responsible for coat-colour polymorphism in a free-living population of Soay sheep. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **274**, 619–626.
- Gross JB, Borowsky R, Tabin CJ (2009) A novel role for Mc1r in the parallel evolution of depigmentation in independent populations of the cavefish *Astyanax mexicanus*. *PLoS Genetics*, **5**(1), e1000326.
- Guillet-Claude C, Isabel N, Pelgas B, Bousquet J (2004) The evolutionary implications of knox-I gene duplications in conifers: correlated evidence from phylogeny, gene mapping, and analysis of functional divergence. *Molecular Biology and Evolution*, **21**, 2232–2245.
- Gupta PK, Rustgi S, Kulwal PL (2005) Linkage disequilibrium and association studies in higher plants: present status and future prospects. *Plant Molecular Biology*, **57**, 461–485.
- Gwaze DP, Zhou Y, Reyes-Valdes MH, Al-Rababah MA, Williams CG (2003) Haplotypic QTL mapping in an outbred pedigree. *Genetical Research*, **81**, 43–50.
- Haidle L, Janssen JE, Gharbi K et al. (2008) Determination of quantitative trait loci (QTL) for early maturation in rainbow trout (*Oncorhynchus mykiss*). *Marine Biotechnology*, **10**, 579–592.
- Hall MC, Basten CJ, Willis JH (2006) Pleiotropic quantitative trait loci contribute to population divergence in traits associated with life-history variation in *Mimulus guttatus*. *Genetics*, **172**, 1829–1844.
- Hawthorne DJ, Via S (2001) Genetic linkage of ecological specialization and reproductive isolation in pea aphids. *Nature*, **412**, 904–907.
- Heidel AJ, Clauss MJ, Kroymann J, Savolainen O, Mitchell-Olds T (2006) Natural variation in MAM within and between populations of *Arabidopsis lyrata* determines glucosinolate phenotype. *Genetics*, **173**, 1629–1636.
- Herder F, Pfaender J, Schliewen UK (2008) Adaptive sympatric speciation of polychromatic “roundfin” sailfin silverside fish in Lake Matano (Sulawesi). *Evolution*, **62**, 2178–2195.
- Heuertz M, De Paoli E, Kallman T et al. (2006) Multilocus patterns of nucleotide diversity, linkage disequilibrium and demographic history of Norway spruce [*Picea abies* (L.) Karst]. *Genetics*, **174**, 2095–2105.
- Hodges SA, Whittall JB, Fulton M, Yang JY (2002) Genetics of floral traits influencing reproductive isolation between *Aquilegia formosa* and *Aquilegia pubescens*. *American Naturalist*, **159**, S51–S60.
- Hoffmann AA, Willi Y (2008) Detecting genetic responses to environmental change. *Nature Reviews Genetics*, **9**, 421–432.
- Houston RD, Haley CS, Hamilton A et al. (2008) Major quantitative trait loci affect resistance to infectious pancreatic necrosis in Atlantic salmon (*Salmo salar*). *Genetics*, **178**, 1109–1115.
- Hunt GJ, Amdam GV, Schlipalius D et al. (2007) Behavioral genomics of honeybee foraging and nest defense. *Naturwissenschaften*, **94**, 247–267.

- Hurme P, Repo T, Savolainen O, Paakkonen T (1997) Climatic adaptation of bud set and frost hardiness in Scots pine (*Pinus sylvestris*). *Canadian Journal of Forest Research – Revue Canadienne de Recherche Forestiere*, **27**, 716–723.
- Hurme P, Sillanpää MJ, Arjas E, Repo T, Savolainen O (2000) Genetic basis of climatic adaptation in Scots pine by Bayesian quantitative trait locus analysis. *Genetics*, **156**, 1309–1322.
- Hwang SY, Lin TP, Ma CS et al. (2003) Postglacial population growth of *Cunninghamia konishii* (*Cupressaceae*) inferred from phylogeographical and mismatch analysis of chloroplast DNA variation. *Molecular Ecology*, **12**, 2689–2695.
- Ingvarsson PK (2005) Nucleotide polymorphism and linkage disequilibrium within and among natural populations of European Aspen (*Populus tremula* L., *Salicaceae*). *Genetics*, **169**, 945–953.
- Ingvarsson PK, Garcia MV, Hall D, Luquez V, Jansson S (2006) Clinal variation in phyB2, a candidate gene for day-length-induced growth cessation and bud set, across a latitudinal gradient in European aspen (*Populus tremula*). *Genetics*, **172**, 1845–1853.
- Jackson TR, Ferguson MM, Danzmann RG et al. (1998) Identification of two QTL influencing upper temperature tolerance in three rainbow trout (*Oncorhynchus mykiss*) half-sib families. *Heredity*, **80**, 143–151.
- Jarvinen P, Lemmetyinen J, Savolainen O, Sopanen T (2003) DNA sequence variation in BpMADS2 gene in two populations of *Betula pendula*. *Molecular Ecology*, **12**, 369–384.
- Jermstad KD, Bassoni DL, Jech KS et al. (2003) Mapping of quantitative trait loci controlling adaptive traits in coastal Douglas fir. III. Quantitative trait loci-by-environment interactions. *Genetics*, **165**, 1489–1506.
- Jermstad KD, Bassoni DL, Jech KS, Wheeler NC, Neale DB (2001a) Mapping of quantitative trait loci controlling adaptive traits in coastal Douglas-fir. I. Timing of vegetative bud flush. *Theoretical and Applied Genetics*, **102**, 1142–1151.
- Jermstad KD, Bassoni DL, Wheeler NC et al. (2001b) Mapping of quantitative trait loci controlling adaptive traits in coastal Douglas-fir. II. Spring and fall cold-hardiness. *Theoretical and Applied Genetics*, **102**, 1152–1158.
- Jermstad KD, Bassoni DL, Wheeler NC, Neale DB (1998) A sex-averaged genetic linkage map in coastal Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var 'menziesii') based on RFLP and RAPD markers. *Theoretical and Applied Genetics*, **97**, 762–770.
- Jermstad KD, Sheppard LA, Kinloch BB et al. (2006) Isolation of a full-length CC-NBS-LRR resistance gene analog candidate from sugar pine showing low nucleotide diversity. *Tree Genetics & Genomes*, **2**, 76–85.
- Johnston IA, Andersen O (2008) Number of muscle fibres in adult Atlantic cod varies with temperature during embryonic development and pantophysin (PanI) genotype. *Aquatic Biology*, **4**, 167–173.
- Jones H, Leigh FJ, Mackay I et al. (2008) Population-based resequencing reveals that the flowering time adaptation of cultivated barley originated east of the fertile crescent. *Molecular Biology and Evolution*, **25**, 2211–2219.
- Jonsdóttir IG, Marteinsdóttir G, Pampoulié C (2008) Relation of growth and condition with the Pan I locus in Atlantic cod (*Gadus morhua* L.) around Iceland. *Marine Biology*, **154**, 867–874.
- Joost S, Bonin A, Bruford MW et al. (2007) A spatial analysis method (SAM) to detect candidate loci for selection: towards a landscape genomics approach to adaptation. *Molecular Ecology*, **16**, 3955–3969.
- Jorge V, Dowkiw A, Faivre-Rampant P, Bastien C (2005) Genetic architecture of qualitative and quantitative *Melampsora larici-populina* leaf rust resistance in hybrid poplar: genetic mapping and QTL detection. *New Phytologist*, **167**, 113–127.
- Kado T, Ushio Y, Yoshimaru H, Tsumura Y, Tachida H (2006) Contrasting patterns of DNA variation in natural populations of two related conifers, *Cryptomeria japonica* and *Taxodium distichum* (*Cupressaceae sensu lato*). *Genes & Genetic Systems*, **81**, 103–113.
- Kado T, Yoshimaru H, Tsumura Y, Tachida H (2003) DNA variation in a conifer, *Cryptomeria japonica* (*Cupressaceae sensu lato*). *Genetics*, **164**, 1547–1559.

- Kauer MO, Dieringer D, Schlotterer C (2003) A microsatellite variability screen for positive selection associated with the "Out of Africa" habitat expansion of *Drosophila melanogaster*. *Genetics*, **165**, 1137–1148.
- Kaya Z, Sewell MM, Neale DB (1999) Identification of quantitative trait loci influencing annual height- and diameter-increment growth in loblolly pine (*Pinus taeda* L.). *Theoretical and Applied Genetics*, **98**, 586–592.
- Kim YY, Kang BY, Choi HS et al. (2004) Identification of QTL (quantitative trait loci) associated with 2-year growth traits of full-sib progenies in *Populus davidiana* dode based on composite interval mapping. *Journal of Korean Forestry Society*, **93**, 251–264.
- Kirst M, Basten CJ, Myburg AA, Zeng Z-B, Sederoff RR (2005) Genetic architecture of transcript-level variation in differentiating xylem of a eucalyptus hybrid. *Genetics*, **169**, 2295–2303.
- Kirst M, Myburg AA, De Leon JPG et al. (2004) Coordinated genetic regulation of growth and lignin revealed by quantitative trait locus analysis of cDNA microarray data in an interspecific backcross of eucalyptus. *Plant Physiology (Rockville)*, **135**, 2368–2378.
- Kitano J, Bolnick DI, Beauchamp DA et al. (2008) Reverse evolution of armor plates in the threespine stickleback. *Current Biology*, **18**, 769–774.
- Kivimäki M, Karkkainen K, Gaudeul M, Loe G, Agren J (2007) Gene, phenotype and function: GLABROUS1 and resistance to herbivory in natural populations of *Arabidopsis lyrata*. *Molecular Ecology*, **16**, 453–462.
- Kohn MH, Murphy WJ, Ostrander EA, Wayne RK (2006) Genomics and conservation genetics. *Trends in Ecology & Evolution*, **21**, 629–637.
- Krieger MJB, Ross KG (2002) Identification of a major gene regulating complex social behavior. *Science*, **295**, 328–332.
- Kronforst MR, Young LG, Kapan DD et al. (2006) Linkage of butterfly mate preference and wing color preference cue at the genomic location of wingless. *Proceedings of the National Academy of Sciences USA*, **103**, 6575–6580.
- Krutovsky KV, Elisk CG, Matvienko M, Kozik A, Neale DB (2007) Conserved ortholog sets in forest trees. *Tree Genetics & Genomes*, **3**, 61–70.
- Krutovsky KV, Neale DB (2005) Nucleotide diversity and linkage disequilibrium in cold-hardiness- and wood quality-related candidate genes in Douglas fir. *Genetics*, **171**, 2029–2041.
- Kumar S, Spelman RJ, Garrick DJ et al. (2000) Multiple-marker mapping of wood density loci in an outbred pedigree of *radiata* pine. *Theoretical and Applied Genetics*, **100**, 926–933.
- Kuramoto N, Kondo T, Fujisawa Y et al. (2000) Detection of quantitative trait loci for wood strength in *Cryptomeria japonica*. *Canadian Journal of Forest Research*, **30**, 1525–1533.
- Laurie CC, Nickerson DA, Anderson AD et al. (2007) Linkage disequilibrium in wild mice. *PLoS Genetics*, **3**, 1487–1495.
- Leinonen T, O'Hara RB, Cano JM, Merila J (2008) Comparative studies of quantitative trait and neutral marker divergence: a meta-analysis. *Journal of Evolutionary Biology*, **21**, 1–17.
- Lerceteau E, Plomion C, Andersson B (2000) AFLP mapping and detection of quantitative trait loci (QTLs) for economically important traits in *Pinus sylvestris*: a preliminary study. *Molecular Breeding*, **6**, 451–458.
- Lewontin RC, Krakauer J (1973) Distribution of gene frequency as a test of theory of selective neutrality of polymorphisms. *Genetics*, **74**, 175–195.
- Li J, Su X, Zhang Q, Louis Z (1999) Detection of QTLs for growth and phenology traits of poplar using RAPD markers. *Forest Research*, **12**, 111–117.
- Li YF, Costello JC, Holloway AK, Hahn MW (2008) "Reverse ecology" and the power of population genomics. *Evolution*, **62**, 2984–2994.
- Lin JZ (2000) The relationship between loci for mating system and fitness-related traits in *Mimulus (Scrophulariaceae)*: a test for deleterious pleiotropy of QTLs with large effects. *Genome*, **43**, 628–633.
- Lin JZ, Ritland K (1997) Quantitative trait loci differentiating the outbreeding *Mimulus guttatus* from the inbreeding *M. platycalyx*. *Genetics*, **146**, 1115–1121.

- Lind M, Dalman K, Stenlid J, Karlsson B, Olson A (2007) Identification of quantitative trait loci affecting virulence in the basidiomycete *Heterobasidion annosum* s.l. *Current Genetics*, **52**, 35–44.
- Liu AZ, Burke JM (2006) Patterns of nucleotide diversity in wild and cultivated sunflower. *Genetics*, **173**, 321–330.
- Loh YHE, Katz LS, Mims MC et al. (2008) Comparative analysis reveals signatures of differentiation amid genomic polymorphism in Lake Malawi cichlids. *Genome Biology*, **9**(7), R113.
- Long AD, Langley CH (1999) The power of association studies to detect the contribution of candidate genetic loci to variation in complex traits. *Genome Research*, **9**, 720–731.
- Luikart G, England PR, Tallmon D, Jordan S, Taberlet P (2003) The power and promise of population genomics: from genotyping to genome typing. *Nature Reviews Genetics*, **4**, 981–994.
- Lynch M, Walsh B (1998) *Genetics and Analysis of Quantitative Traits*. Sinauer Associates, Sunderland, MA.
- Makinen HS, Cano M, Merila J (2008a) Identifying footprints of directional and balancing selection in marine and freshwater three-spined stickleback (*Gasterosteus aculeatus*) populations. *Molecular Ecology*, **17**, 3565–3582.
- Makinen HS, Shikano T, Cano JM, Merila J (2008b) Hitchhiking mapping reveals a candidate genomic region for natural selection in three-spined stickleback chromosome VIII. *Genetics*, **178**, 453–465.
- Markussen T, Fladung M, Achere V et al. (2003) Identification of QTLs controlling growth, chemical and physical wood property traits in *Pinus pinaster* (Ait.). *Silvae Genetica*, **52**, 8–15.
- Marques CM, Brondani RPV, Grattapaglia D, Sederoff R (2002) Conservation and synteny of SSR loci and QTLs for vegetative propagation in four Eucalyptus species. *Theoretical and Applied Genetics*, **105**, 474–478.
- Martin NH, Bouck AC, Arnold ML (2005) Loci affecting long-term hybrid survivorship in Louisiana irises: implications for reproductive isolation and introgression. *Evolution*, **59**, 2116–2124.
- Martin NH, Bouck AC, Arnold ML (2006) Detecting adaptive trait introgression between *Iris fulva* and *I. brevicaulis* in highly selective field conditions. *Genetics*, **172**, 2481–2489.
- Martyniuk CJ, Perry GML, Mogahadam HK, Ferguson MM, Danzmann RG (2003) The genetic architecture of correlations among growth-related traits and male age at maturation in rainbow trout. *Journal of Fish Biology*, **63**(3), 746–764.
- Maynard Smith J, Haigh J (1974) The hitch-hiking effect of a favourable gene. *Genetical Research*, **23**, 23–35.
- Menge DM, Zhong DB, Guda T et al. (2006) Quantitative trait loci controlling refractoriness to *Plasmodium falciparum* in natural *Anopheles gambiae* mosquitoes from a malaria-endemic region in western Kenya. *Genetics*, **173**, 235–241.
- Merila J, Crnokrak P (2001) Comparison of genetic differentiation at marker loci and quantitative traits. *Journal of Evolutionary Biology*, **14**, 892–903.
- Meyer-Lucht Y, Otten C, Puttker T, Sommer S (2008) Selection, diversity and evolutionary patterns of the MHC class II DAB in free-ranging neotropical marsupials. *BMC Genetics*, **9**, 39.
- Miller CT, Beleza S, Pollen AA et al. (2007) Cis-regulatory changes in kit ligand expression and parallel evolution of pigmentation in sticklebacks and humans. *Cell*, **131**, 1179–1189.
- Missiaggia AA, Piacuzzi AL, Grattapaglia D (2005) Genetic mapping of Eef1, a major effect QTL for early flowering in *Eucalyptus grandis*. *Tree Genetics & Genomes*, **1**, 79–84.
- Moen T, Agresti JJ, Cnaani A et al. (2004) A genome scan of a four-way tilapia cross supports the existence of a quantitative trait locus for cold tolerance on linkage group 23. *Aquaculture Research*, **35**, 893–904.
- Moen T, Hayes B, Nilsen F et al. (2008) Identification and characterisation of novel SNP markers in Atlantic cod: evidence for directional selection. *BMC Genetics*, **9**, 18.

- Moen T, Munck H, Raya LG (2005) A genome scan reveals a QTL for resistance to infectious salmon anaemia in Atlantic salmon (*Salmo salar*). *Aquaculture*, **247**, 25–26.
- Moghadam HK, Poissant J, Fotherby H et al. (2007) Quantitative trait loci for body weight, condition factor and age at sexual maturation in Arctic charr (*Salvelinus alpinus*): comparative analysis with rainbow trout (*Oncorhynchus mykiss*) and Atlantic salmon (*Salmo salar*). *Molecular Genetics and Genomics*, **277**, 647–661.
- Mona S, Crestanello B, Bankhead-Dronnet S et al. (2008) Disentangling the effects of recombination, selection, and demography on the genetic variation at a major histocompatibility complex class II gene in the alpine chamois. *Molecular Ecology*, **17**, 4053–4067.
- Mori A, Romero-Severson J, Severson DW (2007) Genetic basis for reproductive diapause is correlated with life history traits within the *Culex pipiens* complex. *Insect Molecular Biology*, **16**, 515–524.
- Moritz C (2002) Strategies to protect biological diversity and the evolutionary processes that sustain it. *Systematic Biology*, **51**, 238–254.
- Morrell PL, Lundy KE, Clegg MT (2003) Distinct geographic patterns of genetic diversity are maintained in wild barley (*Hordeum vulgare ssp spontaneum*) despite migration. *Proceedings of the National Academy of Sciences USA* **100**, 10812–10817.
- Morrell PL, Toleno DM, Lundy KE, Clegg MT (2005) Low levels of linkage disequilibrium in wild barley (*Hordeum vulgare ssp spontaneum*) despite high rates of self-fertilization. *Proceedings of the National Academy of Sciences USA*, **102**, 2442–2447.
- Mullen LM, Hoekstra HE (2008) Natural selection along an environmental gradient: a classic cline in mouse pigmentation. *Evolution*, **62**, 1555–1569.
- Mundy NI, Badcock NS, Hart T et al. (2004) Conserved genetic basis of a quantitative plumage trait involved in mate choice. *Science*, **303**, 1870–1873.
- Murray MC, Hare MP (2006) A genomic scan for divergent selection in a secondary contact zone between Atlantic and Gulf of Mexico oysters, *Crassostrea virginica*. *Molecular Ecology*, **15**, 4229–4242.
- Nachman MW, Hoekstra HE, D'Agostino SL (2003) The genetic basis of adaptive melanism in pocket mice. *Proceedings of the National Academy of Sciences USA*, **100**, 5268–5273.
- Namroud MC, Beaulieu J, Juge N, Laroche J, Bousquet J (2008) Scanning the genome for gene single nucleotide polymorphisms involved in adaptive population differentiation in white spruce. *Molecular Ecology*, **17**, 3599–3613.
- Neale DB (2007) Genomics to tree breeding and forest health. *Current Opinion in Genetics & Development*, **17**, 539–544.
- Neale DB, Ingvarsson PK (2008) Population, quantitative and comparative genomics of adaptation in forest trees. *Current Opinion in Plant Biology*, **11**, 149–155.
- Neale DB, Savolainen O (2004) Association genetics of complex traits in conifers. *Trends in Plant Science*, **9**, 325–330.
- Newcombe G, Bradshaw HD Jr (1996) Quantitative trait loci conferring resistance in hybrid poplar to *Septoria populicola*, the cause of leaf spot. *Canadian Journal of Forest Research*, **26**, 1943–1950.
- Newcombe G, Bradshaw HD Jr, Chastagner GA, Stettler RF (1996) A major gene for resistance to *Melampsora medusae f. sp. deltoidea* in a hybrid poplar pedigree. *Phytopathology*, **86**, 87–94.
- Nichols KM, Bartholomew J, Thorgaard GH (2003) Mapping multiple genetic loci associated with *Ceratomyxa shasta* resistance in *Oncorhynchus mykiss*. *Diseases of Aquatic Organisms*, **56**, 145–154.
- Nichols KM, Broman KW, Sundin K et al. (2007) Quantitative trait loci x maternal cytoplasmic environment interaction for development rate in *Oncorhynchus mykiss*. *Genetics*, **175**, 335–347.
- Nichols KM, Felip A, Wheeler PA, Thorgaard GH (2008) The genetic basis of smoltification-related traits in *Oncorhynchus mykiss*. *Genetics*, **179**, 1559–1575.
- Nichols KM, Wheeler PA, Thorgaard GH (2004) Quantitative trait loci analyses for meristic traits in *Oncorhynchus mykiss*. *Environmental Biology of Fishes*, **69**, 317–331.
- Nielsen R (2001) Statistical tests of selective neutrality in the age of genomics. *Heredity*, **86**, 641–647.

- Nielsen R (2005) Molecular signatures of natural selection. *Annual Review of Genetics*, **39**, 197–218.
- Nielsen EE, Hansen MM, Meldrup D (2006) Evidence of microsatellite hitch-hiking selection in Atlantic cod (*Gadus morhua* L.): implications for inferring population structure in nonmodel organisms. *Molecular Ecology*, **15**, 3219–3229.
- Nosil P, Egan SP, Funk DJ (2008) Heterogeneous genomic differentiation between walking-stick ecotypes: “isolation by adaptation” and multiple roles for divergent selection. *Evolution*, **62**, 316–336.
- Nosil P, Funk DJ, Ortiz-Barrientos D (2009) Divergent selection and heterogeneous genomic divergence. *Molecular Ecology*, **18**, 375–402.
- O’Malley KG, Camara MD, Banks MA (2007) Candidate loci reveal genetic differentiation between temporally divergent migratory runs of Chinook salmon (*Oncorhynchus tshawytscha*). *Molecular Ecology*, **16**, 4930–4941.
- O’Malley KG, Sakamoto T, Danzmann RG, Ferguson MM (2003) Quantitative trait loci for spawning date and body weight in rainbow trout: testing for conserved effects across ancestrally duplicated chromosomes. *Journal of Heredity*, **94**, 273–284.
- Orsini L, Wheat CW, Haag CR et al. (2009) Fitness differences associated with Pgi SNP genotypes in the Glanville fritillary butterfly (*Melitaea cinxia*). *Journal of Evolutionary Biology*, **22**, 367–375.
- Ozaki A, de Leon FG, Glebe B et al. (2005) Identification of QTL for resistance to *Cryptobia salmositica* infection in Atlantic salmon (*Salmo salar*): a model for pathogen disease resistance QTL? *Aquaculture*, **247**, 27–27.
- Ozaki A, Sakamoto T, Khoo S et al. (2001) Quantitative trait loci (QTLs) associated with resistance/susceptibility to infectious pancreatic necrosis virus (IPNV) in rainbow trout (*Oncorhynchus mykiss*). *Molecular Genetics and Genomics*, **265**, 23–31.
- Pampoulie C, Jakobsdottir KB, Marteinsdottir G, Thorsteinsson V (2008) Are vertical behaviour patterns related to the pantophysin locus in the Atlantic cod (*Gadus morhua* L.)? *Behavior Genetics*, **38**, 76–81.
- Parelle J, Zapater M, Scotti-Saintagne C et al. (2007) Quantitative trait loci of tolerance to waterlogging in a European oak (*Quercus robur* L.): physiological relevance and temporal effect patterns. *Plant Cell and Environment*, **30**, 422–434.
- Peichel CL, Nereng KS, Ohgi KA et al. (2001) The genetic architecture of divergence between threespine stickleback species. *Nature*, **414**, 901–905.
- Pemberton JM (2008) Wild pedigrees: the way forward. *Proceedings of the Royal Society of London-Series B: Biological Sciences*, **275**, 613–621.
- Perry GML, Ferguson MM, Sakamoto T, Danzmann RG (2005) Sex-linked quantitative trait loci for thermotolerance and length in the rainbow trout. *Journal of Heredity*, **96**, 97–107.
- Piertney SB, Oliver MK (2006) The evolutionary ecology of the major histocompatibility complex. *Heredity*, **96**, 7–21.
- Plomion C, Durel CE, O’Malley DM (1996) Genetic dissection of height in maritime pine seedlings raised under accelerated growth conditions. *Theoretical and Applied Genetics*, **93**, 849–858.
- Pot D, McMillan L, Echt C et al. (2005) Nucleotide variation in genes involved in wood formation in two pine species. *New Phytologist*, **167**, 101–112.
- Pot D, Rodrigues J-C, Rozenberg P et al. (2006) QTLs and candidate genes for wood properties in maritime pine (*Pinus pinaster* Ait.). *Tree Genetics & Genomes*, **2**, 10–24.
- Powers DA, Schulte PM (1998) Evolutionary adaptations of gene structure and expression in natural populations in relation to a changing environment: a multidisciplinary approach to address the million-year saga of a small fish. *Journal of Experimental Zoology*, **282**, 71–94.
- Pritchard JK, Stephens M, Rosenberg NA, Donnelly P (2000) Association mapping in structured populations. *American Journal of Human Genetics*, **67**, 170–181.
- Protas M, Tabansky I, Conrad M et al. (2008) Multi-trait evolution in a cave fish, *Astyanax mexicanus*. *Evolution & Development*, **10**, 196–209.
- Protas ME, Hersey C, Kochanek D et al. (2006) Genetic analysis of cavefish reveals molecular convergence in the evolution of albinism. *Nature Genetics*, **38**, 107–111.
- Protas ME, Patel NH (2008) Evolution of coloration patterns. *Annual Review of Cell and Developmental Biology*, **24**, 425–446.

- Przeworski M, Coop G, Wall JD (2005) The signature of positive selection on standing genetic variation. *Evolution*, **59**, 2312–2323.
- Rae AM, Ferris R, Tallis MJ, Taylor G (2006) Elucidating genomic regions determining enhanced leaf growth and delayed senescence in elevated CO₂. *Plant Cell and Environment*, **29**, 1730–1741.
- Rae AM, Pinel MPC, Bastien C et al. (2008) QTL for yield in bioenergy *Populus*: identifying GxE interactions from growth at three contrasting sites. *Tree Genetics & Genomes*, **4**, 97–112.
- Rae AM, Tricker PJ, Bunn SM, Taylor G (2007) Adaptation of tree growth to elevated CO₂: quantitative trait loci for biomass in *Populus*. *New Phytologist*, **175**, 59–69.
- Raeymaekers JAM, Van Houdt JKJ, Larmuseau MHD, Geldof S, Volckaert FAM (2007) Divergent selection as revealed by P-ST and QTL-based F-ST in three-spined stickleback (*Gasterosteus aculeatus*) populations along a coastal-inland gradient. *Molecular Ecology*, **16**, 891–905.
- Reed DH, Frankham R (2003) Correlation between fitness and genetic diversity. *Conservation Biology*, **17**, 230–237.
- Rehfeldt GE (1997) Quantitative analyses of the genetic structure of closely related conifers with disparate distributions and demographics: the *Cupressus arizonica* (*Cupressaceae*) complex. *American Journal of Botany*, **84**, 190–200.
- Reid DP, Szanto A, Glebe B, Danzmann RG, Ferguson MM (2005) QTL for body weight and condition factor in Atlantic salmon (*Salmo salar*): comparative analysis with rainbow trout (*Oncorhynchus mykiss*) and Arctic charr (*Salvelinus alpinus*). *Heredity*, **94**, 166–172.
- Robison BD, Wheeler PA, Sundin K, Sikka P, Thorgaard GH (2001) Composite interval mapping reveals a major locus influencing embryonic development rate in rainbow trout (*Oncorhynchus mykiss*). *Journal of Heredity*, **92**, 16–22.
- Roff DA (1997) *Evolutionary Quantitative Genetics*. Chapman & Hall, New York.
- Rogers SM, Bernatchez L (2005) Integrating QTL mapping and genome scans towards the characterization of candidate loci under parallel selection in the lake whitefish (*Coregonus clupeaformis*). *Molecular Ecology*, **14**, 351–361.
- Ronnberg-Wastljung AC, Glynn C, Weih M (2005) QTL analyses of drought tolerance and growth for a *Salix dasyclados* x *Salix viminalis* hybrid in contrasting water regimes. *Theoretical and Applied Genetics*, **110**, 537–549.
- Roselius K, Stephan W, Stadler T (2005) The relationship of nucleotide polymorphism, recombination rate and selection in wild tomato species. *Genetics*, **171**, 753–763.
- Rosenblum EB, Hoekstra HE, Nachman MW (2004) Adaptive reptile color variation and the evolution of the Mc1r gene. *Evolution*, **58**, 1794–1808.
- Ross KG, Keller L (1998) Genetic control of social organization in an ant. *Proceedings of the National Academy of Sciences USA*, **95**, 14232–14237.
- Rostoks N, Mudie S, Cardle L et al. (2005) Genome-wide SNP discovery and linkage analysis in barley based on genes responsive to abiotic stress. *Molecular Genetics and Genomics*, **274**, 515–527.
- Rueppell O, Chandra SBC, Pankiw T et al. (2006) The genetic architecture of sucrose responsiveness in the honeybee (*Apis mellifera* L.). *Genetics*, **172**, 243–251.
- Rueppell O, Pankiw T, Nielsen DI et al. (2004) The genetic architecture of the behavioral ontogeny of foraging in honeybee workers. *Genetics*, **167**, 1767–1779.
- Saintagne C, Bodenes C, Barreneche T et al. (2004) Distribution of genomic regions differentiating oak species assessed by QTL detection. *Heredity*, **92**, 20–30.
- Scalfi M, Troglio M, Piovani P et al. (2004) A RAPD, AFLP and SSR linkage map, and QTL analysis in European beech (*Fagus sylvatica* L.). *Theoretical and Applied Genetics*, **108**, 433–441.
- Schemske DW, Bradshaw HD Jr (1999) Pollinator preference and the evolution of floral traits in monkeyflowers (*Mimulus*). *Proceedings of the National Academy of Sciences USA*, **96**, 11910–11915.
- Schlotterer C (2002) A microsatellite-based multilocus screen for the identification of local selective sweeps. *Genetics*, **160**, 753–763.
- Schlotterer C (2003) Hitchhiking mapping – functional genomics from the population genetics perspective. *Trends in Genetics*, **19**, 32–38.

- Schwartz MK, Luikart G, Waples RS (2007) Genetic monitoring as a promising tool for conservation and management. *Trends in Ecology & Evolution*, **22**, 25–33.
- Scotti-Saintagne C, Bertocchi E, Barreneche T (2005) Quantitative trait loci mapping for vegetative propagation in pedunculate oak. *Annals of Forest Science*, **62**, 369–374.
- Scotti-Saintagne C, Bodenes C, Barreneche T et al. (2004a) Detection of quantitative trait loci controlling bud burst and height growth in *Quercus robur* L. *Theoretical and Applied Genetics*, **109**, 1648–1659.
- Scotti-Saintagne C, Mariette S, Porth I et al. (2004b) Genome scanning for interspecific differentiation between two closely related oak species (*Quercus robur* L. and *Q. petraea* (Matt.) Liebl.). *Genetics*, **168**, 1615–1626.
- Shapiro MD, Marks ME, Peichel CL et al. (2004) Genetic and developmental basis of evolutionary pelvic reduction in threespine sticklebacks. *Nature*, **428**, 717–723.
- Shaw KL, Parsons YM, Lesnick SC (2007) QTL analysis of a rapidly evolving speciation phenotype in the Hawaiian cricket *Laupala*. *Molecular Ecology*, **16**, 2879–2892.
- Shepherd M, Cross M, Dieters MJ et al. (2003) Genetics of physical wood properties and early growth in a tropical pine hybrid. *Canadian Journal of Forest Research*, **33**, 1923–1932.
- Shepherd M, Huang S, Eggler P et al. (2006) Congruence in QTL for adventitious rooting in *Pinus elliottii* x *Pinus caribaea* hybrids resolves between and within-species effects. *Molecular Breeding*, **18**, 11–28.
- Shih FL, Hwang SY, Cheng YP, Lee PF, Lin TP (2007) Uniform genetic diversity, low differentiation, and neutral evolution characterize contemporary refuge populations of Taiwan fir (*Abies kawakamii*, Pinaceae). *American Journal of Botany*, **94**, 194–202.
- Simonsen KL, Churchill GA, Aquadro CF (1995) Properties of statistical tests of neutrality for DNA polymorphism data. *Genetics*, **141**, 413–429.
- Slate J (2005) Quantitative trait locus mapping in natural populations: progress, caveats and future directions. *Molecular Ecology*, **14**, 363–379.
- Slate J, Pemberton JM (2007) Admixture and patterns of linkage disequilibrium in a free-living vertebrate population. *Journal of Evolutionary Biology*, **20**, 1415–1427.
- Slate J, Pemberton JM, Visscher PM (1999) Power to detect QTL in a free-living polygynous population. *Heredity*, **83**, 327–336.
- Slate J, Visscher PM, MacGregor S et al. (2002) A genome scan for quantitative trait loci in a wild population of red deer (*Cervus elaphus*). *Genetics*, **162**, 1863–1873.
- Slatkin M (2008) Linkage disequilibrium – understanding the evolutionary past and mapping the medical future. *Nature Reviews Genetics*, **9**, 477–485.
- Slotman M, della Torre A, Powell JR (2004) The genetics of inviability and male sterility in hybrids between *Anopheles gambiae* and *An. arabiensis*. *Genetics*, **167**, 275–287.
- Song BH, Winsor AJ, Schmid KJ et al. (2009) Multilocus patterns of nucleotide diversity, population structure and linkage disequilibrium in *Boeckhera stricta*, a wild relative of *Arabidopsis*. *Genetics*, **181**, 1021–1033.
- St. Clair JB (2006) Genetic variation in fall cold hardiness in coastal Douglas-fir in western Oregon and Washington. *Canadian Journal of Botany-Revue Canadienne De Botanique*, **84**, 1110–1121.
- St. Clair JB, Mandel NL, Vance-Boland KW (2005) Geneecology of Douglas-fir in western Oregon and Washington. *Annals of Botany*, **96**, 1199–1214.
- Stapley J, Birkhead TR, Burke T, Slate J (2008) A linkage map of the zebra finch *Taeniopygia guttata* provides new insights into avian genome evolution. *Genetics*, **179**, 651–667.
- Steiner CC, Weber JN, Hoekstra HE (2007) Adaptive variation in beach mice produced by two interacting pigmentation genes. *PLoS Biology*, **5**, 1880–1889.
- Stich B, Moring J, Piepho HP et al. (2008) Comparison of mixed-model approaches for association mapping. *Genetics*, **178**, 1745–1754.
- Stinchcombe JR, Hoekstra HE (2008) Combining population genomics and quantitative genetics: finding the genes underlying ecologically important traits. *Heredity*, **100**, 158–170.
- Storz JF (2005) Using genome scans of DNA polymorphism to infer adaptive population divergence. *Molecular Ecology*, **14**, 671–688.

- Storz JF, Dubach JM (2004) Natural selection drives altitudinal divergence at the albumin locus in deer mice, *Peromyscus maniculatus*. *Evolution*, **58**, 1342–1352.
- Storz JF, Kelly JK (2008) Effects of spatially varying selection on nucleotide diversity and linkage disequilibrium: insights from deer mouse globin genes. *Genetics*, **180**, 367–379.
- Storz JF, Nachman MW (2003) Natural selection on protein polymorphism in the rodent genus *Peromyscus*: evidence from interlocus contrasts. *Evolution*, **57**, 2628–2635.
- Storz JF, Sabatino SJ, Hoffmann FG et al. (2007) The molecular basis of high-altitude adaptation in deer mice. *PLoS Genetics*, **3**, 448–459.
- Streelman JT, Albertson RC, Kocher TD (2003) Genome mapping of the orange blotch colour pattern in cichlid fishes. *Molecular Ecology*, **12**, 2465–2471.
- Sundin K, Brown KH, Drew RE et al. (2005) Genetic analysis of a development rate QTL in backcrosses of clonal rainbow trout, *Oncorhynchus mykiss*. *Aquaculture*, **247**, 75–83.
- Tagu D, Bastien C, Faivre-Rampant P et al. (2005) Genetic analysis of phenotypic variation for ectomycorrhiza formation in an interspecific F1 poplar full-sib family. *Mycorrhiza*, **15**, 87–91.
- Tennessen JA, Blouin MS (2008) Balancing selection at a frog antimicrobial peptide locus: fluctuating immune effector alleles? *Molecular Biology and Evolution*, **25**, 2669–2680.
- Teshima KM, Coop G, Przeworski M (2006) How reliable are empirical genomic scans for selective sweeps? *Genome Research*, **16**, 702–712.
- Thamarus K, Groom K, Bradley A et al. (2004) Identification of quantitative trait loci for wood and fibre properties in two full-sib pedigrees of *Eucalyptus globulus*. *Theoretical and Applied Genetics*, **109**, 856–864.
- Theron E, Hawkins K, Birmingham E, Ricklefs RE, Mundy NI (2001) The molecular basis of an avian plumage polymorphism in the wild: a melanocortin-1-receptor point mutation is perfectly associated with the melanic plumage morph of the bananaquit, *Coereba flaveola*. *Current Biology*, **11**, 550–557.
- Thornton KR, Jensen JD, Becquet C, Andolfatto P (2007) Progress and prospects in mapping recent selection in the genome. *Heredity*, **98**, 340–348.
- Thumma BR, Nolan MF, Evans R, Moran GF (2005) Polymorphisms in cinnamoyl CoA reductase (CCR) are associated with variation in microfibril angle in *Eucalyptus* spp. *Genetics*, **171**, 1257–1265.
- Tsarouhas V, Gullberg U, Lagercrantz U (2002) An AFLP and RFLP linkage map and quantitative trait locus (QTL) analysis of growth traits in *Salix*. *Theoretical and Applied Genetics*, **105**, 277–288.
- Tsarouhas V, Gullberg U, Lagercrantz U (2003) Mapping of quantitative trait loci controlling timing of bud flush in *Salix*. *Hereditas (Lund)*, **138**, 172–178.
- Tsarouhas V, Gullberg U, Lagercrantz U (2004) Mapping of quantitative trait loci (QTLs) affecting autumn freezing resistance and phenology in *Salix*. *Theoretical and Applied Genetics*, **108**, 1335–1342.
- Tschaplinski TJ, Tuskan GA, Sewell MM et al. (2006) Phenotypic variation and quantitative trait locus identification for osmotic potential in an interspecific hybrid inbred F-2 poplar pedigree grown in contrasting environments. *Tree Physiology*, **26**, 595–604.
- Vali U, Einarsson A, Waits L, Ellegren H (2008) To what extent do microsatellite markers reflect genome-wide genetic diversity in natural populations? *Molecular Ecology*, **17**, 3808–3817.
- Vasemagi A, Gross R, Paaver T et al. (2005a) Analysis of gene associated tandem repeat markers in Atlantic salmon (*Salmo salar* L.) populations: implications for restoration and conservation in the Baltic Sea. *Conservation Genetics*, **6**, 385–397.
- Vasemagi A, Nilsson J, Primmer CR (2005b) Expressed sequence tag-linked microsatellites as a source of gene-associated polymorphisms for detecting signatures of divergent selection in Atlantic salmon (*Salmo salar* L.). *Molecular Biology and Evolution*, **22**, 1067–1076.
- Vasemagi A, Primmer CR (2005) Challenges for identifying functionally important genetic variation: the promise of combining complementary research strategies. *Molecular Ecology*, **14**, 3623–3642.

- Verhaegen D, Plomion C, Gion JM et al. (1997) Quantitative trait dissection analysis in Eucalyptus using RAPD markers: 1. Detection of QTL in interspecific hybrid progeny, stability of QTL expression across different ages. *Theoretical and Applied Genetics*, **95**, 597–608.
- Via S, Hawthorne DJ (2002) The genetic architecture of ecological specialization: correlated gene effects on host use and habitat choice in pea aphids. *American Naturalist*, **159**, S76–S88.
- Via S, West J (2008) The genetic mosaic suggests a new role for hitchhiking in ecological speciation. *Molecular Ecology*, **17**, 4334–4345.
- Vitalis R, Dawson K, Boursot P (2001) Interpretation of variation across marker loci as evidence of selection. *Genetics*, **158**, 1811–1823.
- Voss SR, Prudic KL, Oliver JC, Shaffer HB (2003) Candidate gene analysis of metamorphic timing in ambystomatid salamanders. *Molecular Ecology*, **12**, 1217–1223.
- Voss SR, Shaffer HB (2000) Evolutionary genetics of metamorphic failure using wild-caught vs. laboratory axolotls (*Ambystoma mexicanum*). *Molecular Ecology*, **9**, 1401–1407.
- Wachowiak W, Balk PA, Savolainen O (2009) Search for nucleotide diversity patterns of local adaptation in dehydrins and other cold-related candidate genes in Scots pine (*Pinus sylvestris* L.). *Tree Genetics & Genomes*, **5**, 117–132.
- Walsh B (2008) Using molecular markers for detecting domestication, improvement, and adaptation genes. *Euphytica*, **161**, 1–17.
- Wang HW, Ge S (2006) Phylogeography of the endangered *Cathaya argyrophylla* (Pinaceae) inferred from sequence variation of mitochondrial and nuclear DNA. *Molecular Ecology*, **15**, 4109–4122.
- Wang S, Zhu QH, Guo XY et al. (2007) Molecular evolution and selection of a gene encoding two tandem microRNAs in rice. *FEBS Letters*, **581**, 4789–4793.
- Watt WB (1977) Adaptation at specific loci. 1. Natural selection on phosphoglucose isomerase of *Colias* butterflies – biochemical and population aspects. *Genetics*, **87**, 177–194.
- Watterson GA (1977) Heterosis or neutrality? *Genetics*, **85**, 789–814.
- Watts PC, O’Leary D, Cross MC et al. (2008) Contrasting levels of genetic differentiation among putative neutral microsatellite loci in Atlantic herring *Clupea harengus* populations and the implications for assessing stock structure. *Hydrobiologia*, **606**, 27–33.
- Weber A, Clark RM, Vaughn L et al. (2007) Major regulatory genes in maize contribute to standing variation in teosinte (*Zea mays ssp parviglumis*). *Genetics*, **177**, 2349–2359.
- Weber AL, Briggs WH, Rucker J et al. (2008) The genetic architecture of complex traits in teosinte (*Zea mays ssp parviglumis*): new evidence from association mapping. *Genetics*, **180**, 1221–1232.
- Weih M, Ronnberg-Wastljug AC, Glynn C (2006) Genetic basis of phenotypic correlations among growth traits in hybrid willow (*Salix dasyclados* x *S-viminalis*) grown under two water regimes. *New Phytologist*, **170**, 467–477.
- Weir BS (2008) Linkage disequilibrium and association mapping. *Annual Review of Genomics and Human Genetics*, **9**, 129–142.
- Weng C, Kubisiak TL, Nelson CD, Stine M (2002) Mapping quantitative trait loci controlling early growth in a (longleaf pine x slash pine) x slash pine BC1 family. *Theoretical and Applied Genetics*, **104**, 852–859.
- Westerdahl H, Waldenstrom J, Hansson B et al. (2005) Associations between malaria and MHC genes in a migratory songbird. *Proceedings of the Royal Society of London – Series B: Biological Sciences*, **272**, 1511–1518.
- Wheat CW, Watt WB, Pollock DD, Schulte PM (2006) From DNA to fitness differences: sequences and structures of adaptive variants of *Colias* phosphoglucose isomerase (PGI). *Molecular Biology and Evolution*, **23**, 499–512.
- Wheeler NC, Jermstad KD, Krutovsky K et al. (2005) Mapping of quantitative trait loci controlling adaptive traits in coastal Douglas-fir. IV. Cold-hardiness QTL verification and candidate gene mapping. *Molecular Breeding*, **15**, 145–156.
- Wilding CS, Butlin RK, Grahame J (2001) Differential gene exchange between parapatric morphs of *Littorina saxatilis* detected using AFLP markers. *Journal of Evolutionary Biology*, **14**, 611–619.

- Wilfert L, Gadau J, Baer B, Schmid-Hempel P (2007a) Natural variation in the genetic architecture of a host-parasite interaction in the bumblebee *Bombus terrestris*. *Molecular Ecology*, **16**, 1327–1339.
- Wilfert L, Gadau J, Schmid-Hempel P (2007b) The genetic architecture of immune defense and reproduction in male *Bombus terrestris* bumblebees. *Evolution*, **61**, 804–815.
- Willems G, Drager DB, Courbot M et al. (2007) The genetic basis of zinc tolerance in the metallophyte *Arabidopsis halleri* ssp. *halleri* (Brassicaceae): an analysis of quantitative trait loci. *Genetics*, **176**, 659–674.
- Williams CG, Reyes-Valdes MH, Huber DA (2007) Validating a QTL region characterized by multiple haplotypes. *Theoretical and Applied Genetics*, **116**, 87–94.
- Wood HM, Grahame JW, Humphray S, Rogers J, Butlin RK (2008) Sequence differentiation in regions identified by a genome scan for local adaptation. *Molecular Ecology*, **17**, 3123–3135.
- Worley K, Carey J, Veitch A, Coltman DW (2006) Detecting the signature of selection on immune genes in highly structured populations of wild sheep (*Ovis dalli*). *Molecular Ecology*, **15**, 623–637.
- Wright SI, Gaut BS (2005) Molecular population genetics and the search for adaptive evolution in plants. *Molecular Biology and Evolution*, **22**, 506–519.
- Wu R, Bradshaw HD, Jr., Stettler RF (1997) Molecular genetics of growth and development in *Populus* (Salicaceae). V. Mapping quantitative trait loci affecting leaf variation. *American Journal of Botany*, **84**, 143–153.
- Wu R, Bradshaw HD, Jr., Stettler RF (1998) Developmental quantitative genetics of growth in *Populus*. *Theoretical and Applied Genetics*, **97**, 1110–1119.
- Wu R, Stettler RF (1994) Quantitative genetics of growth and development in *Populus*. I. A three-generation comparison of tree architecture during the first 2 years of growth. *Theoretical and Applied Genetics*, **89**, 1046–1054.
- Wu RL (1998) Genetic mapping of QTLs affecting tree growth and architecture in *Populus*: implication for ideotype breeding. *Theoretical and Applied Genetics*, **96**, 447–457.
- Wu RL, Ma CX, Casella G (2002) Joint linkage and linkage disequilibrium mapping of quantitative trait loci in natural populations. *Genetics*, **160**, 779–792.
- Wullschlegel SD, Yin TM, DiFazio SP et al. (2005) Phenotypic variation in growth and biomass distribution for two advanced-generation pedigrees of hybrid poplar. *Canadian Journal of Forest Research*, **35**, 1779–1789.
- Yoshimaru H, Ohba K, Tsurumi K et al. (1998) Detection of quantitative trait loci for juvenile growth, flower bearing and rooting ability based on a linkage map of sugi (*Cryptomeria japonica* D. Don). *Theoretical and Applied Genetics*, **97**, 45–50.
- Yu JM, Buckler ES (2006) Genetic association mapping and genome organization of maize. *Current Opinion in Biotechnology*, **17**, 155–160.
- Yu JM, Holland JB, McMullen MD, Buckler ES (2008) Genetic design and statistical power of nested association mapping in maize. *Genetics*, **178**, 539–551.
- Yu JM, Pressoir G, Briggs WH et al. (2006) A unified mixed-model method for association mapping that accounts for multiple levels of relatedness. *Nature Genetics*, **38**, 203–208.
- Zayed A, Whitfield CW (2008) A genome-wide signature of positive selection in ancient and recent invasive expansions of the honey bee *Apis mellifera*. *Proceedings of the National Academy of Sciences USA*, **105**, 3421–3426.
- Zhai WW, Nielsen R, Slatkin M (2009) An investigation of the statistical power of neutrality tests based on comparative and population genetic data. *Molecular Biology and Evolution*, **26**, 273–283.
- Zhang D, Zhang Z, Yang K (2006) QTL analysis of growth and wood chemical content traits in an interspecific backcross family of white poplar (*Populus tomentosa* × *P-bolleana*) × *P-tomentosa*. *Canadian Journal of Forest Research*, **36**, 2015–2023.
- Zhao KY, Aranzana MJ, Kim S et al. (2007) An *Arabidopsis* example of association mapping in structured samples. *PLoS Genetics*, **3**, 71–82.
- Zhong DB, Menge DM, Temu EA, Chen H, Yan GY (2006) Amplified fragment length polymorphism mapping of quantitative trait loci for malaria parasite susceptibility in the yellow fever mosquito *Aedes aegypti*. *Genetics*, **173**, 1337–1345.
- Zhong DB, Pai A, Yan GY (2003) Quantitative trait loci for susceptibility to tapeworm infection in the red flour beetle. *Genetics*, **165**, 1307–1315.

- Zhong DB, Pai A, Yan GY (2005) Costly resistance to parasitism: evidence from simultaneous quantitative trait loci mapping for resistance and fitness in *Tribolium castaneum*. *Genetics*, **169**, 2127–2135.
- Zhu QH, Zheng XM, Luo JC, Gaut BS, Ge S (2007) Multilocus analysis of nucleotide variation of *Oryza sativa* and its wild relatives: severe bottleneck during domestication of rice. *Molecular Biology and Evolution*, **24**, 875–888.
- Zimmerman AM, Evenhuis JP, Thorgaard GH, Ristow SS (2004) A single major chromosomal region controls natural killer cell-like activity in rainbow trout. *Immunogenetics*, **55**, 825–835.
- Zimmerman AM, Wheeler PA, Ristow SS, Thorgaard GH (2005) Composite interval mapping reveals three QTL associated with pyloric caeca number in rainbow trout, *Oncorhynchus mykiss*. *Aquaculture*, **247**, 85–95.

Index

- acorn barnacle, active differentiation for, 117–119
 - gene-frequency shifts for, 117–119
- Acropora*, hybridization among, 182–183
- adaptation, genetic. *See* genetic adaptation
- adaptive differentiation
 - in European white oaks, 101–120
 - ancient examples of, 102–105, 107
 - Bulmer effect in, 112–115
 - components of, 110–111
 - contemporary dynamics of, 109–116
 - dynamics of, 112–115
 - erasure of, migration as influence on, 105–107
 - gene flow and, 115–116
 - historical dynamics of, 102–109
 - LDD in, 105, 107
 - LND in, 107
 - minimal genetic markers for, 104–105
 - pollen flow as influence on, 105–107
 - provenance tests for, 102
 - recent examples of, 107–109
 - for refugial populations, 103–104
 - as transient, during colonization, 105
 - among high-dispersing species, 117–119
 - for acorn barnacle, 117–119
- AFLP. *See* amplified fragment length polymorphism
- agriculture
 - biodiversity and, 35–47
 - development of, 35–36
- allelic recharge, among mammals, 194–196
 - among banner-tailed kangaroo rats, 194–196
 - in bottleneck events, 194–195
 - emigration rates as influence on, 195
- allozymes, 330
- American chestnut trees, 63–64
 - mortality factors for, 63
 - reintroduction efforts for, 63, 307–309
 - disease resistance and, 308–309
 - molecular scatology for, 63–64
- Ammophila breviligulata*, dune restoration and, 213–215
 - molecular and phenotypic data for, 215
- AMOVA analysis, for evolutionary toxicology, 352
- amphibians. *See also* spadefoot toads, hybridization among
 - cryptic species of, phylogenetics for, 21
 - extinction rates for, 5–6
 - sex-determining genes in, 78–79
 - evolution from TSD, 80
 - evolutionary plasticity of, 80
 - GSD and, 80
 - species discovery rates for, 9
- amplified fragment length polymorphism (AFLP), 20
 - evolutionary toxicology and, in detection methods, 331–332
 - in fishes, for sex-determining genes, 88
 - for heritable phenotypes, 56
- anthropogenic hybridization, 174–177
- arthropods, heritable phenotypes for, 54–55
- association genetics, 132–148
 - in animals, 132–141
 - body-color polymorphism and, 138
 - candidate gene approach to, 135, 138
 - genome-wide, 132–138
 - natural selection signature tests in, 141
 - neutrality tests for, 136
 - QTL studies for, 132–138
 - methodology for, 125
 - natural selection in
 - in animals, 141
 - in candidate genes, 136
 - in plants, 146–148
 - in plants, 141–151
 - candidate gene approach to, 145–146
 - in Douglas-firs, 148–151
 - genome wide, 141–145
 - natural selection signature tests in, 146–148
 - neutrality tests for, 147
 - QTL studies in, 141–145
- association mapping, 126
 - for Douglas-firs, 149–151
- Azerbaijan, evolutionary toxicology in, 347–350

- bacteria, species discovery rates for, 9
- banner-tailed kangaroo rats, allelic recharge among, 194–196
- bar coding, 18–20
for DNA, 18–19
mitochondrial markers in, 20
phylogenetic derivation from, 19–20
species identification from, 19
- bears. *See* grizzly bears, sex identification and population sampling for; Kermode bears, conservation strategies for
- biodiversity, 2–24
advances in medicine as result of, 2
for PCR, 2
agriculture and, 35–47
allelic recharge and, 194–196
cryptic species and, 24
definition of, 2
discovery of, 1–28
distribution of, 3–4
patterns of, 3
enumeration of, 8–13
status of species discovery and description, 8–11
extinction of species and, 4–8
increased rates of, 5
IUCN listings for, 5–6
mass, 5
patterns of, 4–5
risks of, 5–6
future inventory of, 13–24
phylogenetics in, 13
taxonomy in, 13
gene flow and, 35–47
in plants, 36
for GM crops, 35–47
environmental hazards as result of, 36
gene flow in, 36–41
non-GM crops v., 35
production methods for, 35
“hot spots,” 4
hybridization and, 169–170
importance of, 2–3
indirect benefits of, 2–3
after landscape fragmentation
for endangered species, 212–234
immediate consequences on, 190–191
“living dead” species and, 208
long-term effects of, 192–193
polymorphism and, 190–191
predictions for, 193, 208
short-term effects of, 191–192
spatial genetic structure and, 191
from weedy rice, 45
from gene flow, 47
- Biological Dynamics of Forest Fragments Project, 202
- biomarkers, evolutionary toxicology and, 322
- birds. *See also* black-capped vireo, landscape fragmentation and; golden-cheeked warbler, landscape fragmentation and
extinction rates for, 7–8
heritable phenotypes for, 55
landscape fragmentation as influence on, 217–226
for black-capped vireo, 222–226
for golden-cheeked warbler, 218–222
sex-determining genes in, 77–79
molecular assays for, 79
- black-capped vireo, landscape fragmentation and, 222–226
bottleneck events and, 223
case study assessment for, 226
conservation management factors for, 225
gene flow and, 225
genetic variations among, 222–224
Mantel tests for, 224–225
golden-cheeked warbler and, biogenetic comparison with, 219
habitat requirements for, 222, 225–226
- body-color polymorphism, 138
among Kermode bears, 260
among Soay sheep, 139–141
- bottleneck events, 194–195
black-capped vireo and, 223
wildlife reintroduction during, 312–313
- Bulmer effect, 112–115
- California tiger salamanders, hybridization of, 180–181
- captive breeding programs, for conservation of species, 267–291
coefficient of relatedness for, 270
founding populations in, 273
gene diversity, 270–271
goals of, 267, 272–273
inbreeding coefficient in, 269–270
incomplete pedigrees in, application of concepts to, 271–272
kinship in, 269
mean, 269
molecular methods for, 267–268, 276–291
for allele identification, 288–289
with animal models, 291
for estimating relatedness, 279–284
for gene diversity, 287–288
for genetic management, 289–290
inbreeding and, 287
markers in, 283–284
for organisms living in groups, 284–288
pedigree issues and, resolution of, 276–279
for quantitative genetic analysis, 290–291
for relationship categories identification, 282–284
studies on, 268
for unresolved needs, 289–291
for variation in selection, 290
population growth in, 273–274
population maintenance in, 274–275
successes as result of, 267
terms for, 269–272

- chromosomes, sex-determining genes and, 77
- in fishes, 85, 86
 - in reptiles, 79
- climate change
- community genetics and, 66–68
 - in deserts, 66
 - in mountain forests, 66
 - prediction models for, 67–68
 - conservation and, 66
 - hybridization of species as result of, 180
 - Pacific salmon recovery planning and, 262
- community genetics, 50
- case studies for, 51
 - climate change and, 66–68
 - in deserts, 66
 - in mountain forests, 66
 - prediction models for, 67–68
 - conservation and management in, 52–53
 - population analysis for, 52–53
 - three-way interactions in, 52
 - for foundation species, 50
 - as community drivers, 50
 - definition of, 55–56
 - dependent communities influenced by, 51–52
 - heritable phenotypes in, 56–57
 - for GEOs, 61–66
 - ecological consequences of, 62, 65–66
 - ecosystem phenotypes in, 62
 - fitness of, 62
 - as foundation species, 61–62
 - native species hybridization by, 62
 - nontarget phenotypes in, 62
 - heritable phenotypes, 53–59
 - AFLP molecular markers for, 56
 - for arthropods, 54–55
 - for birds, 55
 - conservation consequences for, 56–59
 - in foundation species, 56–57
 - for insects, 55
 - Mantel tests for, 56
 - for microbes, 55
 - with species-area relationships, 58–59
 - species differentiation from, 57–58
 - support for similar genotypes, 56
 - management applications for, 68–69
 - donor tagging as part of, 69
 - for MVIPs, 60–61
 - for MVPs, 59–61
 - for generalist species, 60
 - population size as factor in, 60
 - transfer experiments for, 60
 - terms for, 51
 - variation in, 50
- conservation, of species
- for black-capped vireo, management factors for, 225
 - with captive breeding programs, 267–291
 - coefficient of relatedness in, 270
 - founding populations in, 273
 - gene diversity, 270–271
 - goals of, 267, 272–273
 - inbreeding coefficient in, 269–270
 - incomplete pedigrees in, application of concepts to, 271–272
 - kinship in, 269
 - molecular methods for, 267–268, 276–291
 - population growth in, 273–274
 - population maintenance in, 274–275
 - successes as result of, 267
 - terms for, 269–272
- climate change and, 66
- community genetics and, 52–53
- population analysis for, 52–53
 - three-way interactions in, 52
- in dune restoration, 214–215
- for *Ammophila breviligulata*, 214–215
- EDGE scores for, 15
- genetic adaptation for, 123–153
- association genetics and, 132–148
 - detection methods for, 125–132
 - natural populations in, 125
 - population genetics and, 123–124, 129–132
- genetic markers in, 74–77
- DNA fingerprinting, 74, 75
 - individual identification in, 74
 - sexing assays, with DNA, 74–77
- for golden-cheeked warbler, landscape fragmentation and, 220
- hybridization and, 169–185
- among *Acropora*, 182–183
 - anthropogenic, 174–177
 - with applied studies, 184–185
 - biodiversity and, 169–170
 - case studies for, 173–174, 175
 - categorization of, 170
 - correlates for, 176
 - disease resilience as result of, 183
 - ecological correlates of, 177
 - extinction and, 169
 - habitat specialization as correlate for, 180–181
 - mating issues, for original species, 171–172
 - natural, 174–177
 - predictors of, 178–181
 - selective removal of nonendangered species and, 179
 - among spadefoot toads, 183
 - species fitness as result of, 169
 - zone dynamics for, 177, 181–182
- hybridization and applied studies for, 184–185
- for Kermode bear, 259–261
- landscape fragmentation as influence on, literature survey of, 229–230
- for Pacific salmon, 244–262
- abundance and productivity assessments in, 248–250
 - climate change as influence on, 262

- conservation, of species (*cont.*)
 ESU viability and, 240, 254–257, 258
 future applications of, 257–262
 integration strategies for, 241
 methodologies for, 247–248
 molecular approaches to, 262
 population identification in, 246–248
 population viability and, 248–254
 Recovery Domains in, 244–245
 risk factor integration in, 252–254
 spatial structure and diversity
 assessments in, 251–252
 terms for, 240
 TRTs in, 244
 VSP and, 246, 254, 257, 258
 with pedigree reconstruction, 285–286
 phylogenetics and, 13–17
 delimiting species and, 14–15
 PSC and, 14
 pollen and seed movement and, with
 landscape fragmentation, 206–207
 management strategies for, 207
 promotion of, from hybridization,
 182–184
 with wildlife reintroduction, 296–314
 development of, 296
 founding event phase of, 303–305
 genetic consequences of, 299–303
 population establishment phase of,
 305–310
 population growth phase of, 310–313
 population theory and, 297–298, 299
 variation predictions for, 298
 conspecific sperm precedence (CSP),
 181–182
 crustaceans. *See* rusty crayfish, hybridization
 among, zone dynamics as factor in
 CSP. *See* conspecific sperm precedence
- Darwin, Charles, 1
 geological study by, 1
- DDT. *See* dichlorodiphenyltrichloroethane
- deoxyribonucleic acid (DNA)
 bar coding for, 18–19
 evolutionary toxicology as influence on,
 evidence of, 321
 adduct studies in, 324–325
 in anonymous markers, 331–332
 detection methods for, 331–337
 marker selection criteria for, 336–337
 in MHC, 333
 with microarrays, 334
 in organelles, 332–333
 with sequencing, 333–334
 in SNPs, 333–334
 fingerprinting from, in conservation
 management, 74, 75
 RAPD and, 90
 sexing assays with, 74–77
- deserts, climate change in, community
 genetics and, 66
 drought-adaptive genotypes in, 66
- dichlorodiphenyltrichloroethane (DDT), 327
Dinizia excelsa, pollen movement for,
 202–203
 discovery of species. *See* species discovery,
 rates of
- disease resistance
 in American chestnut trees, 308–309
 in GM crops, 36
 “distinct population segments” (DPS),
 243–244
- DNA. *See* deoxyribonucleic acid
- DNA adduct studies, 324–325
 measurement methods in, 325
 phases of, 324–325
- Douglas-firs, association genetics in, 148–151
 mapping studies for, 149–151
 population genomics in, 149
 QTL mapping for, 149
- DPS. *See* “distinct population segments”
- dune restoration, 214–215
Ammophila breviligulata and, 214–215
 molecular and phenotypic data for,
 215
- E. cyclocarpum*, pollen movement for,
 204–206
 mean parameters for, 205
 study sites for, 204–205
- ecosystem genetics, 50
 case studies for, 51
 climate change and, 66–68
 in deserts, 66
 in mountain forests, 66
 prediction models for, 67–68
 conservation and management in, 52–53
 population analysis for, 52–53
 three-way interactions in, 52
 for foundation species, 50
 as community drivers, 50
 definition of, 55–56
 dependent communities influenced by,
 51–52
 heritable phenotypes in, 56–57
 for GEOs, 61–62, 66
 ecological consequences of, 62, 65–66
 ecosystem phenotypes in, 62
 fitness of, 62
 as foundation species, 61–62
 native species hybridization by, 62
 nontarget phenotypes in, 62
 heritable phenotypes, 53–59
 AFLP molecular markers for, 56
 for arthropods, 54–55
 for birds, 55
 conservation consequences for, 56–59
 in foundation species, 56–57
 for insects, 55
 Mantel tests for, 56
 for microbes, 55
 with species-area relationships, 58–59
 species differentiation from, 57–58
 support for similar genotypes, 56

- management applications for, 68–69
 - donor tagging as part of, 69
- for MVIPs, 60–61
- for MVPs, 59–61
 - for generalist species, 60
 - population size as factor in, 60
 - transfer experiments for, 60
- variation in, 50
- ED. *See* evolutionary distinctiveness
- EDGE score. *See* evolutionary distinct and globally endangered score
- EE. *See* environmental effects (EE), on sex-determining genes in fishes
- EMBL. *See* European Molecular Biology Laboratory
- emigration rates, allelic recharge among mammals and, 195
- Endangered Species Act (ESA)
 - Pacific salmon under, 239, 244–246
 - delisting of, 255
 - population identification for, 246–248
 - Recovery Domains in, 244–245
 - strategy mandates for, 245–246
 - protection criteria for, 243–244
 - DPS in, 243–244
- endangered species, landscape
 - fragmentation as influence on, 212–234. *See also* black-capped vireo, landscape fragmentation and; golden-cheeked warbler, landscape fragmentation and; Pacific salmon among birds, 217–226
 - for black-capped vireo, 222–226
 - for golden-cheeked warbler, 218–222
 - genetic consequences of, 212–213
 - literature survey of, 226–233
 - for conservation status, 229–230
 - for genetic responses to fragmentation, 228–229
 - for habitat structure, 232–233
 - for species vagility, 230–232
 - population fragmentation among, 213–216
 - in structurally complex habitats, 217
 - vagility of, 217
- environmental effects (EE), on
 - sex-determining genes in fishes, 81
- environmental sex determination (ESD), 79–80
 - behavior as influence on, in fishes, 81–82
 - social structure as factor in, 82
 - in fishes, 81–83
 - behavior as influence on, 81–82
 - in protogynous species, 82
 - temperature as influence on, 82–83
 - TSD and, 83
- ESA. *See* Endangered Species Act
- ESD. *See* environmental sex determination
- ESU. *See* evolutionarily significant unit
- eukaryotes, phylogenetics of, 18–20
 - with bar coding, 18–20
 - with mitochondrial markers, 20
 - species identification from, 19
- European Molecular Biology Laboratory (EMBL), 19
- European white oaks
 - adaptive differentiation in, 101–120
 - ancient examples of, 102–105, 107
 - Bulmer effect in, 112–115
 - components of, 110–111
 - contemporary dynamics of, 109–116
 - dynamics of, 112–115
 - erasure of, migration as influence on, 105–107
 - gene flow and, 115–116
 - historical dynamics of, 102–109
 - LDD in, 105, 107
 - LND in, 107
 - minimal genetic markers for, 104–105
 - pollen flow as influence on, 105–107
 - provenance tests for, 102
 - recent examples of, 107–109
 - for refugial populations, 103–104
 - as transient, during colonization, 105
 - genetic differentiation among, 106, 109
 - evolutionarily significant unit (ESU), 15
 - categorization of, 15–16
 - criteria for, 15
 - NOAA guidelines for, 244
 - Pacific salmon as, in recovery planning, 240, 254–257, 258
 - risk integration for, 256–257
 - phylogeographic concordance for, 15
 - evolutionary distinct and globally endangered (EDGE) score, 16
 - for conservation of species, 15
 - ED criteria for, 16
 - evolutionary distinctiveness (ED), 16
 - evolutionary toxicology, 320–355
 - case studies for, 347–352
 - in Azerbaijan, 347–350
 - in Pigeon River region, 351–352
 - causality assessment for, 337–347
 - by biological gradient, 344
 - by consistency of association, 339–340
 - with experimental evidence, 344–346
 - plausibility as factor in, 346–347
 - by specificity of association, 340–342
 - by strength of association, 338–339
 - by time order, 342–344
 - from DDT, 327
 - definition of, 320
 - with microsatellites, 330–331
 - detection methods, 329–347
 - with AFLP, 331–332
 - with allozymes, 330
 - through DNA, 331–337
 - for genotoxicants, 329–330
 - genetic ecotoxicology, 322–325
 - DNA adduct studies in, 324–325
 - future applications for, 325
 - historical background of, 322–324

- evolutionary toxicology (*cont.*)
 genetic systems influenced by, 321–329
 allele frequency in, 328–329
 AMOVA analysis for, 352
 assignment tests for, 354
 Bayesian analysis for, 353–354
 in biomarkers, 322
 coalescent-based analysis for, 352–353
 within DNA, 321
 history of, 321–322
 MLE analysis for, 353
 multivariate analysis for, 352
 population-level consequences in,
 325–329
 reproduction effects, 321
 response categories for, 327–328
 statistical assessment methods for,
 352–354
 transgenerational inheritance in, 327
 mutations from, 320–321, 329
 toxicogenomics, 335–336
 workshops and symposia for, 323
- Ewens-Watterson neutrality test, 130
- extinction, of species, 1
 biodiversity and, 4–8
 hybridization and, 169
 increased rates of, 5
 for amphibians, 5–6
 for birds, 7–8
 for fishes, 8
 for mammals, 6–7
 for reptiles, 8
 IUCN listings for, 5–6
 mass, 5
 patterns of, 4–5
Rhogeesa tumida, 22–23
 risks of, 5–6
 Tree of Life and, 1
- female-heterogametic systems, in fishes, 81
- fishes. *See also* lake sturgeon, sex-
 determining genes in; Pacific salmon
 ESD in, 81–83
 behavior as influence on, 81–82
 in protogynous species, 82
 temperature as influence on, 82–83
 TSD and, 83
 extinction rates for, 8
 genetically engineered, 38, 47
 case study for, 37–39
 QTLs for, 37–38
 GSD in, 83–86
 sex-determining genes in, 81–94
 with AFLPs, 88
 as autosomal, 86
 chromosomal influences on, 85, 86
 EE as influence on, 81
 ESD and, 81–83
 female-heterogametic systems and, 81
 GSD and, 83–86
 hermaphroditism and, 81
 isolation of markers for, 86–88
 in lake sturgeon, 88–94
 loci for, 84
 male-heterogametic systems and, 81
 in monosex cultures, 86–87
 for population structure studies, 87
 transcriptome analysis for, 88
 unisexuality and, 81
 TSD and, 83
- forests. *See* American chestnut trees; pollen
 and seed movement, with landscape
 fragmentation
- foundation species
 community genetics for, 50
 as community drivers, 50
 definition of, 55–56
 dependent communities influenced by,
 51–52
 heritable phenotypes in, 56–57
 GEOs as, 61–62
 heritable phenotypes in, 56–57
- gene(s), sex-determining, in vertebrates, 74
 genetic markers, in conservation, 74–77
- gene flow
 adaptive differentiation and, 115–116
 biodiversity and, 35–47
 in plants, 36
 among black-capped vireo, 225
 definition of, 36
 in GM crops, 36–41
 aggressive weed formation from, 41
 community-wide changes from, 40–41
 plant fitness as factor for, 40
 population genetics as factor for, 39–40
 selective advantages from, 40
 studies on, 39
 from pollen and seed movement, with
 landscape fragmentation, 203
 for weedy rice, 43, 46
 genetic evidence of, 44
- genetic adaptation, 123–153. *See also*
 association genetics
 association genetics, 132–148
 in animals, 132–141
 methodology for, 125
 in plants, 141–151
 detection methods for, 125–132
 association mapping, 126
 candidate gene approaches in, 126–127
 genome-wide association approaches in,
 127–129
 with LD, 126, 127–128
 population genetic approaches in,
 129–132
 quantitative approaches in, 126
- natural populations in, 125
 definitions of, 125
 QTL methodologies for, 125, 128–129
 population genetics and, 123–124,
 129–132
 hitchhiking mapping in, 129–131
 LD in, 124, 126

- neutrality tests for, 131–132
 - in nonmodel organisms, 130–131
 - outlier analysis in, 129–131
- for species conservation and management, 151–153
- genetic ecotoxicology, 322–325
 - DNA adduct studies in, 324–325
 - future applications for, 325
 - historical background of, 322–324
- genetic sex determination (GSD)
 - in amphibians, 80
 - evolution from TSD, 80
 - in fishes, 83–86
 - chromosomal influence on, 85
 - in lake sturgeon, 89
- genetically engineered organisms (GEOs),
 - community genetics for, 61–66
 - ecological consequences of, 62, 65–66
 - ecosystem phenotypes in, 62
 - fitness of, 62
 - as foundation species, 61–62
 - native species hybridization by, 62
 - nontarget phenotypes in, 62
- genetically modified (GM) crops, 35–36
 - biodiversity and, 35–47
 - environmental hazards as result of, 36
 - disease resistance as, 36
 - to nontarget organisms, 36
 - transgene movements as, 36
- gene flow in, 36–41
 - aggressive weed formation from, 41
 - community-wide changes from, 40–41
 - plant fitness as factor for, 40
 - population genetics as factor for, 39–40
 - selective advantages from, 40
 - studies on, 39
- non-GM crops v., 35
- production methods for, 35
- genetics. *See also* association genetics; community genetics; ecosystem genetics; genetic adaptation; genetic sex determination; population genetics
 - association, 132–148
 - in animals, 132–141
 - methodology for, 125
 - in plants, 141–151
 - community and ecosystem, 50
 - case studies for, 51
 - climate change and, 66–68
 - conservation and management in, 52–53
 - for foundation species, 50
 - for GEOs, 61–66
 - heritable phenotypes, 53–59
 - management applications for, 68–69
 - for MVPs, 60–61
 - for MVPs, 59–61
 - terms for, 51
 - variation in, 50
 - phylogenetics
 - bar coding and, 19–20
 - biodiversity and, 13
 - conservation of species and, 13–17
 - for cryptic species, 20–24
 - databases for, 27–28
 - ESU and, 15
 - of eukaryotes, 18–20
 - lineage divergence and, 16
 - MU and, 15
 - PD and, 16–17
 - of prokaryotes, 17–18
 - species discovery rates with, 26
 - population, 123–124, 129–132
 - hitchhiking mapping in, 129–131
 - LD in, 124, 126
 - neutrality tests for, 131–132
 - in nonmodel organisms, 130–131
 - outlier analysis in, 129–131
 - quantitative, 123
- GEOs. *See* genetically engineered organisms
- GM crops. *See* genetically modified crops
- golden-cheeked warbler, landscape fragmentation and, 218–222
 - black-capped vireo and, biogenetic comparison with, 219
 - case study assessment for, 226
 - conservation and recovery efforts for, 220
 - genetic variation among, 220–222
 - Mantel tests for, 221–222
 - habitat specificity for, 219–220
 - vagility of, 232
- Gorman, George, 299
- grizzly bears, sex identification and population sampling for, 76–77
- GSD. *See* genetic sex determination
- Guaiaacum sanctum*, pollen movement for, 206
- habitat restoration. *See* dune restoration
- Hacienda Solimar, pollen movement in, 204–205
- heritable phenotypes
 - AFLP molecular markers for, 56
 - for arthropods, 54–55
 - for birds, 55
 - community genetics and, 53–59
 - conservation consequences for, 56–59
 - in foundation species, 56–57
 - Mantel tests for, 56
 - with species-area relationships, 58–59
 - species differentiation from, 57–58
 - support for similar genotypes, 56
 - for insects, 55
 - for microbes, 55
- hermaphroditism, in fishes, 81
- high-yielding varieties (HYVs), of weedy rice, 41–42
 - first observation of, 42
- hitchhiking mapping, 129–131
- “hot spots,” of biodiversity, 4
 - establishment of, 4
 - PD and, 16–17
 - plant diversity and, 4

- Hudson-Kreitman-Aguade test, 131
- hybridization, in endangered taxa, 169–185
 - among *Acropora*, 182–183
 - anthropogenic, 174–177
 - applied studies for, 184–185
 - biodiversity and, 169–170
 - case studies for, 173–174, 175
 - missing data for, 178
 - categorization of, 170
 - correlates for, 176
 - habitat specialization as, 180–181
 - disease resilience as result of, 183
 - ecological correlates of, 177
 - extinction and, 169
 - habitat specialization as correlate for, 180–181
 - for California tiger salamanders, 180–181
 - climate change as influence on, 180
 - mating issues
 - for original species, 171–172
 - for rusty crayfish, 171–172
 - natural, 174–177
 - predictors of, 178–181
 - demography as, 178–179
 - habitat modification as, 178
 - population size as, 179
 - promotion of conservation as result of, 182–184
 - with applied studies, 184–185
 - selective removal of nonendangered species and, 179
 - among spadefoot toads, 183
 - species fitness as result of, 169
 - zone dynamics for, 177, 181–182
 - CSP and, 181–182
 - for rusty crayfish, 171–172
- HYVs. *See* high-yielding varieties
- insects
 - heritable phenotypes for, 55
 - species evaluation of, shortcomings for, 9
- International Union for Conservation of Nature (IUCN)
 - species life span listings, 5–6
 - threatened species compilation, 7
- IUCN. *See* International Union for Conservation of Nature
- Kermode bears, conservation strategies for, 259–261
 - color polymorphism among, 260
 - logging as factor in, 260–261
 - genetic consequences from, 261
- lake sturgeon, sex-determining genes in, 88–94
 - candidate genes, 89
 - GSD and, 89
 - random markers in, 90
 - alternatives to, 90
 - with RAPD, 90
 - RDA for, 90
 - sexual maturity for, 89
 - subtractive hybridization for, 90
 - transcriptome pyrosequencing for, 90–93
- landscape fragmentation
 - allelic recharge and, among mammals, 194–196
 - for banner-tailed kangaroo rats, 194–196
 - in bottleneck events, 194–195
 - emigration rates as influence on, 195
 - biodiversity and
 - for endangered species, 212–234
 - immediate consequences on, 190–191
 - long-term effects of, 192–193
 - polymorphism and, 190–191
 - predictions for, 193
 - short-term effects of, 191–192
 - spatial genetic structure and, 191
 - endangered species and, 212–234
 - among birds, 217–226
 - genetic consequences of, 212–213
 - literature survey of, 226–233
 - population fragmentation among, 213–216
 - in structurally complex habitats, 217
 - vagility of, 217
 - pollen and seed movement and, 190–208
 - biodiversity after, 190–191
 - case studies for, 201–206
 - conservation and, 206–207
 - estimates of, 193–200
 - gene flow with, 203
 - genetic relatedness and, 201
 - seed dispersal, 200–201
 - among tropical plant species, 197
- LD. *See* linkage disequilibrium
- LDD. *See* long-distance dispersal
- linkage disequilibrium (LD)
 - in genetic adaptation, 124, 126, 127–128
 - QTL mapping v., 127–128
- “living dead” species, 208
- LND. *See* Local Neighborhood Diffusion
- Local Neighborhood Diffusion (LND), 107
- long-distance dispersal (LDD), 105, 107
- major histocompatibility complex (MHC), 333
- male-heterogametic systems, in fishes, 81
- mammals. *See also* banner-tailed kangaroo rats, allelic recharge among; grizzly bears, sex identification and population sampling for; Kermode bears, conservation strategies for; Soay sheep, body-color polymorphism among
 - allelic recharge among, 194–196
 - among banner-tailed kangaroo rats, 194–196
 - in bottleneck events, 194–195
 - emigration rates as influence on, 195
 - association genetics in, 132–141

- body-color polymorphism and, 138
- candidate gene approach to, 135, 138
- genome-wide, 132–138
- natural selection signature tests in, 141
- neutrality tests for, 136
- QTL studies for, 132–138
- cryptic species of, phylogenetics for, 24
- extinction rates for, 6–7
 - Rhogeesa tumida*, 22–23
- sex-determining genes in, 77–79
 - exceptions for, 77–78
 - molecular assays for, 78
 - primary products in, 78
- sex identification and population sampling for, 76–77
 - among grizzly bears, 76–77
- species discovery rates for, 9
- management unit (MU), 15
- Mantel tests, 56
 - for black-capped vireo, for genetic variation, 224–225
 - for golden-cheeked warbler, for genetic variation, 221–222
- McDonald-Kreitman test, 131
- MHC. *See* major histocompatibility complex
- microbes
 - heritable phenotypes for, 55
 - species discovery rates for, 9, 25
- microsatellites, 330–331
- minimum viable interacting populations (MVIPs), community genetics for, 60–61
- minimum viable populations (MVPs), community genetics for, 59–61
 - for generalist species, 60
 - population size as factor in, 60
 - transfer experiments for, 60
- mitochondrial markers, 20
- MLSA. *See* multilocus sequence analysis
- molecular taxonomy, 17–18
 - of eukaryotes, 18–20
 - with bar coding, 18–20
 - with mitochondrial markers, 20
 - species identification from, 19
 - of prokaryotes, 17–18
 - distance-based approaches to, 17
 - MLSA for, 18
 - sequencing for, 18
 - species recognition in, 18
- mountain forests, climate change in, community genetics and, 66
- MU. *See* management unit
- multilocus sequence analysis (MLSA), 18
- mutations, from evolutionary toxicology, 320–321, 329
- MVIPs. *See* minimum viable interacting populations
- MVPs. *See* minimum viable populations
- National Oceanic and Atmospheric Administration (NOAA), 244
 - ESU criteria under, 244
- National Science Foundation, 1
- natural hybridization, 174–177
- natural selection, in association genetics
 - in animals, 141
 - among candidate genes, 145–146
 - in plants, 146–148
- naturalists. *See* Darwin, Charles; Wallace, Alfred Russel
- neutrality tests, for population genetics, 131–132
 - in animals, 136
 - Ewens-Watterson test, 130
 - Hudson-Kreitman-Aguade test, 131
 - limitations of, 131
 - McDonald-Kreitman test, 131
 - in plants, 147
- NOAA. *See* National Oceanic and Atmospheric Administration
- outlier analysis, in population genetics, 129–131
 - Ewens-Watterson neutrality test and, 130
 - testing parameters in, 130
- Pacific salmon, 239–262
 - ecological role of, 239
 - under ESA, 239, 244–246
 - delisting of, 255
 - Recovery Domains in, 244–245
 - strategy mandates for, 245–246
 - evolution history as factor in, 241–243
 - diversity patterns in, 242
 - dynamic adaptations in, 243
 - replaceable populations within, 243
 - transplant limitations in, 242–243
 - federal protection for, 243–244
 - under ESA, 244–246
 - recovery planning for, 244–262
 - abundance and productivity assessments in, 248–250
 - climate change as influence on, 262
 - ESU viability and, 240, 254–257, 258
 - future applications of, 257–262
 - integration strategies for, 241
 - methodologies for, 247–248
 - molecular approaches to, 262
 - population identification in, 246–248
 - population viability and, 248–254
 - Recovery Domains in, 244–245
 - risk factor integration in, 252–254
 - spatial structure and diversity assessments in, 251–252
 - terms for, 240
 - TRTs in, 244
 - VSP and, 246, 254, 257, 258
- Palo Verde National Park, pollen movement in, 204–205
- PCR. *See* polymerase chain reaction
- PD. *See* phylogenetic diversity
- pedigree reconstruction, 285–286
 - for western larch, 285–286

- phylogenetic diversity (PD), 16–17
 - biodiversity “hot spots” and, 16–17
- phylogenetic species concept (PSC), 14
 - delimiting species and, 14–15
- phylogenetics
 - bar coding and, 19–20
 - biodiversity and, 13
 - conservation of species and, 13–17
 - delimiting species and, 14–15
 - EDGE scores for, 16
 - PSC, 14
 - for cryptic species, 20–24
 - from AFLP, 20
 - amphibians, 21
 - mammals, 24
 - sorting of, 21–24
 - databases for, 27–28
 - systematic development of, 27
 - ESU and, 15
 - categorization of, 15–16
 - criteria for, 15
 - phylogeographic concordance for, 15
 - of eukaryotes, 18–20
 - with bar coding, 18–20
 - with mitochondrial markers, 20
 - species identification from, 19
 - lineage divergence and, 16
 - MU and, 15
 - PD and, 16–17
 - of prokaryotes, 17–18
 - distance-based approaches to, 17
 - MLSA for, 18
 - sequencing for, 18
 - species recognition for, 18
 - species discovery rates with, 26
 - phylogeographic concordance, 15
- Pigeon River region, evolutionary toxicology
 - in, 351–352
- plants, biodiversity of. *See also* American chestnut trees; Douglas-firs, association genetics in; European white oaks; pollen and seed movement, with landscape fragmentation; weedy rice
 - association genetics and, 141–151
 - candidate gene approach to, 145–146
 - in Douglas-firs, 148–151
 - genome wide, 141–145
 - natural selection signature tests in, 146–148
 - neutrality tests for, 147
 - QTL studies in, 141–145
 - gene flow and, 36
 - in GM crops, 36–41
 - for weedy rice, 43, 46
 - in GM crops, 35–41
 - environmental hazards as result of, 36
 - gene flow in, 36–41
 - non-GM crops v., 35
 - production methods for, 35
 - as “hot spots,” 4
- pedigree reconstruction for, 285–286
 - for western larch, 285–286
- weeds, 41
 - for weedy rice, 41–45
 - biodiversity effects of, 45
 - first observations of, 42
 - fitness of, 43–44, 45–46
 - gene flow for, 43, 46
 - HYVs for, 41–42
 - molecular markers for, 47
 - morphology of, 42
 - origin of, 41
 - population spread of, 44–45
 - wild, 42
 - wildlife reintroduction of, 307–309
 - for American chestnut tree, 307–309
- pollen and seed movement, with landscape fragmentation, 190–208
 - biodiversity after
 - immediate consequences on, 190–191
 - “living dead” species and, 208
 - long-term effects of, 192–193
 - polymorphism and, 190–191
 - predictions for, 193, 208
 - short-term effects of, 191–192
 - spatial genetic structure and, 191
 - case studies for, 201–206
 - Dinizia excelsa*, 202–203
 - E. cyclocarpum*, 204–206
 - flow rates in, 198
 - Guaiaacum sanctum*, 206
 - S. globulifera*, 203–204
 - S. humilis*, 202
 - conservation and, 206–207
 - management strategies for, 207
 - estimates of, 193–200
 - factors as influence on, 193–196
 - for mean/maximum distances, 201
 - studies for, 197–200
 - gene flow with, 203
 - genetic relatedness and, 201
 - seed dispersal, 200–201
 - new populations as result of, 200–201
 - among tropical plant species, 197
- pollen flow, 105–107
- pollutants. *See* evolutionary toxicology
- polymerase chain reaction (PCR), 2
- polymorphism. *See also* body-color polymorphism
 - landscape fragmentation and, as influence on, 190–191
- population genetics, 123–124, 129–132
 - hitchhiking mapping in, 129–131
 - LD in, 124, 126
 - neutrality tests for, 131–132, 136
 - Ewens-Watterson test, 130
 - Hudson-Kreitman-Aguade test, 131
 - limitations of, 131
 - McDonald-Kreitman test, 131
 - in nonmodel organisms, 130–131
 - outlier analysis in, 129–131
 - testing parameters in, 130

- population theory, wildlife reintroduction and, 297–298
- prokaryotes, phylogenetics of, 17–18
 distance-based approaches to, 17
 MLSA for, 18
 sequencing for, 18
 species recognition in, 18
- provenance tests, 102
- PSC. *See* phylogenetic species concept
- QTLs. *See* quantitative trait locis
- quantitative genetics, 123
- quantitative trait locis (QTLs)
 in association genetics
 in animals, 132–138
 for Douglas-firs, 149
 in plants, 141–145
 for genetic adaptations, 125, 128–129
 for genetically engineered salmon, 37–38
 LD mapping v., 127–128
- randomly applied polymorphic DNA (RAPD), in lake sturgeon, 90
 alternatives to, 90
- RAPD. *See* randomly applied polymorphic DNA
- RDA. *See* representational difference analysis
- Recovery Domains, 244–245
- representational difference analysis (RDA), 90
- reptiles. *See also* California tiger salamanders, hybridization of
 extinction rates for, 8
 sex-determining genes in, 79–80
 chromosomal influence on, 79
 ESD and, 79–80
 TSD and, 80
- resistance to disease. *See* disease resistance
- restriction fragment length polymorphisms (RFLP), 331–332
- RFLP. *See* restriction fragment length polymorphisms
- Rhogeesa tumida*, 22–23
 DNA sequencing for, 22
 genetic variation within, 22–23
- rice. *See* weedy rice
- rusty crayfish, hybridization among, zone dynamics as factor in, 171–172
- S. globulifera*, pollen movement for, 203–204
- S. humilis*, pollen movement for, 202
 flow rates, 198
- SARST. *See* serial analysis of ribosomal sequence tags
- SBH. *See* sequencing by hybridization
- seed movement. *See* pollen and seed movement, with landscape fragmentation
- sequencing by hybridization (SBH), 26
- serial analysis of ribosomal sequence tags (SARST), 26
- sex-determining genes, 77–94
 in amphibians, 79–80
 evolution from TSD, 80
 evolutionary plasticity of, 80
 GSD and, 80
 in birds, 77–79
 molecular assays for, 79
 chromosomes and, 77
 in fishes, 81–94
 with AFLP's, 88
 as autosomal, 86
 chromosomal influences on, 85, 86
 EE as influence on, 81
 ESD and, 81–83
 female-heterogametic systems and, 81
 hermaphroditism and, 81
 isolation of markers for, 86–88
 in lake sturgeon, 88–94
 loci for, 84
 male-heterogametic systems and, 81
 in monosex cultures, 86–87
 for population structure studies, 87
 transcriptome analysis for, 88
 TSD and, 83
 unisexuality and, 81
- genetic markers in
 assays as, with DNA, 74–77
 DNA fingerprinting, 74
 individual identification in, 74
- in mammals, 77–79
 exceptions for, 77–78
 molecular assays for, 78
 primary products in, 78
- in reptiles, 79–80
 ESD and, 79–80
 TSD and, 80
- in vertebrates, 74
 in amphibians, 79–80
 in birds, 77–79
 diversity of, 78
 in fishes, 81–94
 in mammals, 77–79
 in reptiles, 79–80
- single nucleotide polymorphisms (SNPs), 333–334
- SNPs. *See* single nucleotide polymorphisms
- Soay sheep, body-color polymorphism among, 139–141
 with animal model approach, 140
 genotypic fitness and, 140
- spadefoot toads, hybridization among, 183
- species discovery, rates of, 8–11
 for amphibians, 9
 for bacteria and microbes, 9, 25
 for cryptic species, 20–24
 from AFLP, 20
 amphibians, 21
 mammals, 24
 sorting of, 21–24

- species discovery, rates of (*cont.*)
 enhancement of, 24–27
 for microbes, 25
 with phylogenetics, 26
 with SARST, 26
 with SBH, 26
 from T-RFLP, 25
 from taxonomic databases, 25
 limitation factors for, 11–13
 inventory assessment, rates of, 12–13
 regional inventories, lack of, 12
 taxonomic experts, shortage of, 12
 for mammals, 9
- T-RFLP. *See* terminal restriction fragment
 length polymorphism
- taxonomy
 biodiversity and, 13
 molecular, 17–18
 of eukaryotes, 18–20
 of prokaryotes, 17–18
- Technical Recovery Teams (TRTs), 244
- temperature-dependent sex determination
 (TSD), 80
 in fishes, 83
- terminal restriction fragment length
 polymorphism (T-RFLP), 25
- toxicogenomics, 335–336
- transgenerational inheritance, 327
- Tree of Life, 1
- tropical landscapes. *See also* pollen and seed
 movement, with landscape
 fragmentation
 pollen and seed movement in, 197
- TRTs. *See* Technical Recovery Teams
- TSD. *See* temperature-dependent sex
 determination
- unisexuality, in fishes, 81
- vertebrates. *See also* amphibians; birds;
 fishes; mammals; reptiles
 sex-determining genes in, 74
 in amphibians, 79–80
 in birds, 77–79
 diversity of, 78
 in fishes, 81–94
 in mammals, 77–79
 in reptiles, 79–80
- viable salmonid population (VSP), 246, 254,
 257, 258
- VSP. *See* viable salmonid population
- Wallace, Alfred Russel, 1
 geological study by, 1
- weeds
 from GM crops, aggressive formation of,
 41
 rice as, 41–45
- weedy rice, 41–45
 biodiversity effects of, 45
 from gene flow, 47
 cross-fertilization of, 43
 first observations of, 42
 fitness of, 43–44, 45–46
 gene flow for, 43, 46
 biodiversity influenced by, 47
 genetic evidence of, 44
 HYVs for, 41–42
 molecular markers for, 47
 morphology of, 42
 origin of, 41
 population spread of, 44–45
 wild, 42
- western larch, pedigree reconstruction for,
 285–286
- wild rice, 42
- wildlife reintroduction, 296–314
 development of, 296
 early limitations in, 297
 for forest species, 307–309
 American chestnut tree, 63, 307–309
 disease resistance and, 308–309
 founding event phase of, 303–305
 age structures in, 305
 capture techniques during, 303–304
 population size in, 304
 sex composition during, 304–305
 genetic consequences of, 299–303
 to gene flow, 301
 genetic drift as, 299
 from interdependent sampling events,
 301–302
 lack of genetic diversity as, 299–301
 from sampling period, 303–313
 population establishment phase of,
 305–310
 environmental factors in, 306–309
 mating tactic as factor during,
 309–310
 social structure as factor during, 310
 population growth phase of, 310–313
 behavioral constraints in, 312
 biological constraints in, 311
 during bottleneck event, 312–313
 environmental constraints in, 311
 spatial constraints in, 312
 temporal components in, 313
 population theory and, 297–298, 299
 variation predictions for, 298