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

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

5 Historical and contemporary dynamics of adaptive differentiation in European oaks

Antoine Kremer, Valérie Le Corre, Rémy J. Petit, and Alexis Ducousso

INTRODUCTION

There is growing interest in estimating rates of evolutionary change, motivated by the ongoing environmental change (Gingerich 2001; Stockwell et al. 2003; Carroll et al. 2007). Particular concerns have been raised about forest trees, which are thought to be less able to adapt to these rapid changes due to their long generation time (Reich & Oleksyn 2008). Other authors have suggested that large standing genetic variation in trees may enable rapid adaptive responses, at a pace matching that of ongoing climate change (Kremer 2007; Aitken et al. 2008). An elegant approach to get some insights on the evolutionary responses to global warming is to reconstruct past genetic changes and processes that occurred during the postglacial periods, when temperatures were steadily increasing (Petit et al. 2008). The timing and direction of spread of wind-pollinated trees following the last ice age can be reconstructed from their pollen remains in sediments (e.g., Cheddadi et al. 2005). Palynological data have now been compared to phylogeographic approaches based on range-wide surveys of genetic fingerprints of maternally inherited organelle genomes (Petit et al. 2002b for oaks, Magri et al. 2006 for beech, Cheddadi et al. 2006 for Scots pine). This combination has elucidated genetic and demographic processes associated with tree responses to environmental change. A second approach for predicting adaptive responses to environmental changes is based on theory and simulations (Bürger & Lynch 1995; Bürger & Krall 2004; Sato & Waxman 2008). These studies have been limited so far to single populations and have focused on the amount of environmental change that a population can tolerate, given its genetic and demographic properties.

We will use both approaches to elucidate evolutionary changes associated with environmental changes in trees. First, we will concentrate on adaptive differentiation (Q_{ST}) among populations as an indicator of evolutionary change. Adaptive divergence measures differences between extant populations, and inferences about evolutionary change drawn from divergence are not straightforward unless evolutionary trajectories to ancestor populations are known (Hendry & Kinnison 1999). Second, we will use temperate European white oaks [mainly sessile oak, *Quercus petraea* (Matt.) Liebl.] as models. The postglacial history of temperate oaks in Europe has been reconstructed in detail by combining genetic and historical approaches (Kremer 2002). Moreover, oaks share many genetic, demographic,

and ecological attributes with other tree species (long-lived and out-crossing species, large population size, and asymmetry of seed-to-pollen gene flow). Finally, there is a vast body of data concerning population differentiation at various levels in oaks (organelle genomes, nuclear genes, and adaptive traits). To study genetic variation, forest geneticists have traditionally relied on common garden experiments – called provenance tests – by growing populations from various geographic origins in field trials at a common site (see König 2005 for a review on European trees). In the case of European oaks, provenance tests were first established in 1877 (Kleinschmit 1993), and new tests continue to be established today (Jensen & Hansen 2008).

Combining historical and theoretical approaches can overcome in part the obvious limitations of experimental studies of evolutionary change in long-lived species. The historical perspective over the past 15,000 years may disclose long-term trends that can be combined with the findings of the theoretical approach. Both methods may ascertain time frames of past evolution and help identify key drivers of current adaptive responses of trees to climate.

HISTORICAL DYNAMICS OF ADAPTIVE DIFFERENTIATION

How much evolutionary change has accumulated since the Last Glacial Maximum (LGM), 18,000 years ago? Ideally, assessments of change would compare past source populations with extant populations. Evolutionary change can hardly be monitored at the deoxyribonucleic acid (DNA) level unless DNA could be extracted and analyzed from macrofossil remains of oaks. Such assessments are impossible for traits of adaptive significance. We will instead proceed indirectly, by subdividing differentiation of extant populations, assessed in provenance tests, into historical components (e.g., ancient and recent sources of population divergence). Inferring various historical sources is possible due to the detailed knowledge of colonization dynamics provided by the combined pollen and chloroplast DNA (cpDNA) analysis in the case of sessile oak.

Ancient differentiation

The distribution of temperate white oaks in Europe has shifted recurrently from Mediterranean to boreal regions during interglacial and glacial periods (Cheddadi et al. 2005). At the end of the LGM, oak forests were largely restricted to the Iberian Peninsula, Italy, and the Balkan Peninsula (Greece and the western coast of the Black Sea) (Fig. 5–1). A pan-European survey of the pollen fossil remains (Brewer et al. 2002) showed that all refugial sites were located in mountainous areas (e.g., Sierra Nevada in Spain, the Southern Apennine chain in Italy, and the Pindos Mountains in Greece). During the postglacial period, between 13,000 and 10,000 before present (BP), oaks increased in abundance in mountainous areas (Pyrénées, Southeastern Alps, and Carpathian). The cooling of temperatures during 11,000 BP to 10,000 BP stopped this expansion and resulted in reductions of existing populations. After 10,000 BP, oaks spread throughout Europe and reached their extant distribution at approximately 6,000 BP (Fig. 5–1). The expansion was more

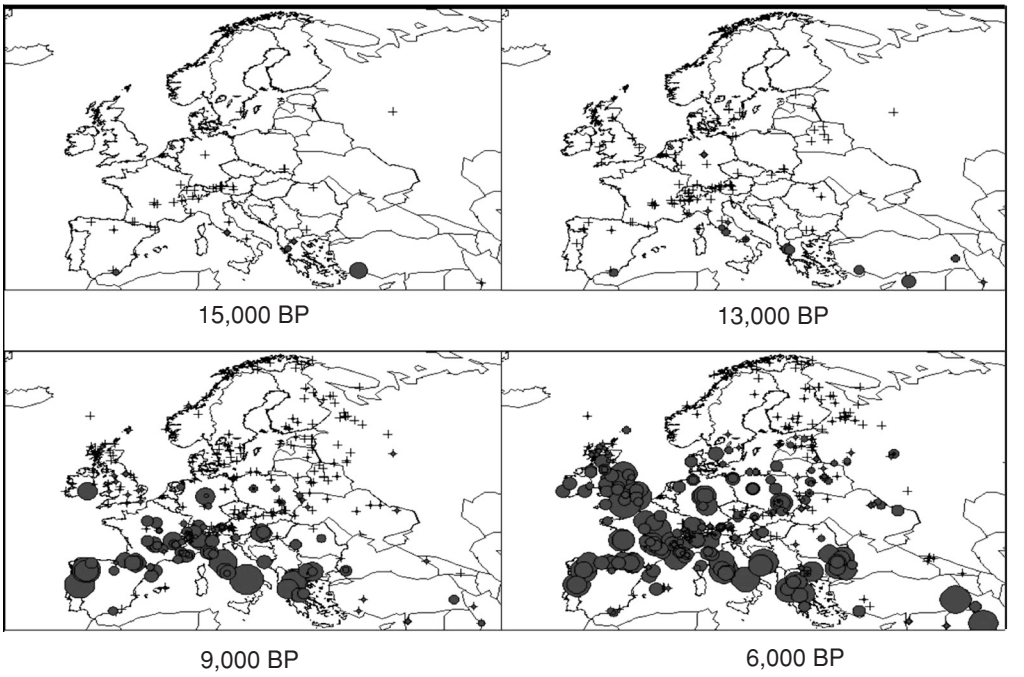


Figure 5–1: Variation of pollen percentages of deciduous oaks as extracted from the European Pollen Database (according to Brewer et al. 2002, Fig. 2). Crosses indicate locations of sites; sizes of the red circles indicate percentages varying from 1% to 50% (1%, 10%, 25%, and 50%). *See Color Plate V.*

rapid in the west and was reduced in the center and east due to the Alps and the Carpathian Mountains.

Major refugial populations were likely to be genetically differentiated at the end of the last glacial period. Refugial populations were genetically isolated. Pollen fossil and genetic data indicate that the western (Iberian Peninsula) and central (Italy) regions where oaks persisted were physically separated during the LGM. Indeed, despite the lowering of the Mediterranean Sea level by more than 100 meters during the LGM (Rabineau et al. 2006), the Iberian and Italian Peninsulas remained separated (Thiede 1978). Evidence for physical separation of the Italian and Balkan refugial population is not supported by geography or genetic data, however. The Adriatic Sea was partially filled in its northern part (Eckerle et al. 1996), favoring connections between the peninsulas. The duration of geographic separation between the refugial zones lasted for more than 100,000 years, during the last glacial period (Cheddadi et al. 2005). Shorter, milder periods did occur during the glacial period, but the migration north of the Pyrénées and connection of oak populations between Italy and Spain appear unlikely (Cheddadi et al. 2005). Finally, isolation and ancient differentiation are also suggested by genetic data (Fig. 5–2). Approximately forty-eight cpDNA haplotypes, identified in a broadscale survey of cpDNA diversity across Europe, cluster in six different maternal lineages (Petit et al. 2002b). The lineages spread as parallel longitudinal strips from the Atlantic coast to the Ural Mountains. Each lineage extends from a refugial zone to the extreme northern latitude of the current distribution,

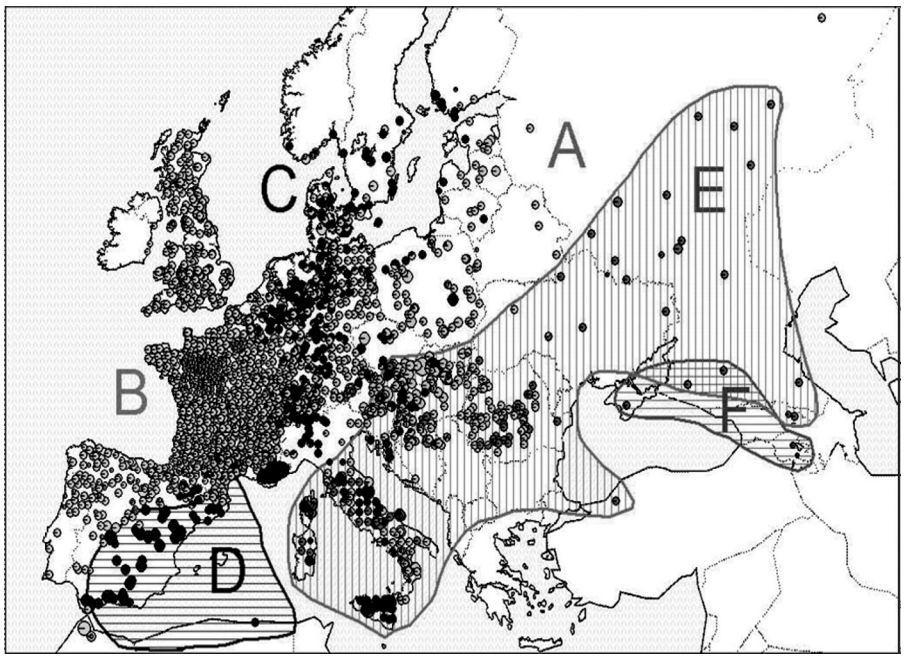


Figure 5–2: Map of cpDNA lineages in deciduous oaks (according to Petit et al. 2002b, Fig. 3). Forty-eight different haplotypes were identified that cluster in six major lineages indicated by colors and letters. *See Color Plate VI*.

with one exception. Lineage D (Fig. 5–2) was indeed restricted to Spain and did not extend across the Pyrénées. CpDNA lineages are not shared between Spain and Italy (Fig. 5–2). Italy and the Balkans, however, share three lineages, suggesting that refugial populations inhabiting these regions were not isolated. The lineages most likely date back to the Pleistocene if not to the Tertiary epoch. The spread of the lineages from extreme southern to northern latitudes allows retrospective identification of the maternal origin of modern populations (Petit et al. 2002a). Given the large sizes of oak populations, the extant distribution of cpDNA variation must reflect the original genetic structure established during colonization. Therefore, cpDNA divergence between refugial populations of Spain, Italy, and the Balkans was likely present at the end of the glacial period. There can be no such retrospective reasoning for nuclear genomes, as pollen flow may have blurred the ancient differentiation. Not only were refugia isolated from each other, they were also undergoing divergent selection pressures due to the different ecological conditions prevailing within the refugia. These speculations suggest that differentiation was widespread not only for cpDNA but also for nuclear DNA and for phenotypic traits.

Assuming that the Spanish and Italian–Balkan refugial populations were genetically separated for more than 100,000 years, we can estimate the minimum genetic differentiation accumulated by neutral factors (drift and mutation) during this period. The expected between-population genetic variance would have amounted to $2tV_m$ (Lynch 1990), where t is the number of generations separating the eastern and western refugial populations from their common ancestor, and V_m is the mutational variance. We assumed that the same traits in the two

populations had the same heritability and that the mutational variance represents 10^{-3} of the environmental variance (Houle et al. 1996). Under these assumptions, genetic differentiation of traits (Q_{ST}) between the refugial populations would range from 0.75 to 0.92 for a trait whose heritability varies from 0.2 to 0.5. For adaptive traits, diversifying selection (or convergent selection) due to different (or similar) ecological conditions prevailing in the refugial areas may have further increased (or reduced) Q_{ST}. These figures provide a rough estimate of the minimal genetic differentiation created during the last glacial period due to genetic separation of the refugial areas.

Transient differentiation during colonization

The velocity of oak migration during the postglacial recolonization period (between 15,000 and 6,000 BP) averaged 500 meters/year (Huntley and Birks 1983; Brewer et al. 2002), reaching in some cases up to 1,000 meters/year (Brewer et al. 2005). These figures are much larger than predicted by diffusion models of the advancing wave of the species. If rare long-distance dispersal (LDD) (Nathan 2006) events are included in the diffusion models, however, then the overall expansion results from the combined effects of the advancing wave (diffusion) and the aggregation of the many populations that were founded by the LDD events. Rates of LDD as low as 10^{-4} (in probability) may be sufficient to account for the rapidity of the expansion as deduced from fossil pollen (Le Corre et al. 1997b; Bialozyt et al. 2006). Considering the high fecundity of oaks, LDD may have occurred repeatedly even if their frequency was low. It is interesting that the occurrence of LDD did not only increase the velocity of the colonization, it also contributed to the maintaining of the overall diversity of the species (Bialozyt et al. 2006). The immediate consequence of LDD is the creation of new populations by a limited number of colonizers generating strong founder effects. Footprints of founder effects are easily recognizable in the patchy geographic structure of cpDNA haplotypes (Petit et al. 1997). Ancient differentiation was most likely increased by founder events due to LDD. According to theory, recently founded populations at the leading edge of the distribution should increase the overall differentiation among populations (Le Corre & Kremer 1998) while colonization is proceeding. Given that colonization lasted more than 7,000 years, transient differentiation was maintained and affected organelle and nuclear genes and traits. As the range of a species expands, transient differentiation should decrease (Le Corre & Kremer 1998). After the full size of the range had been reached (6,000 BP), gene flow resulted in the decay of differentiation.

Erasing ancient differentiation

As migration proceeded northward from the different source populations, the colonization routes merged in central Europe and admixture of the different populations resulted in genetic homogenization. Ancient differentiation was almost totally erased after full admixture of the migration fronts and extensive pollen flow among populations originating from different refugia. Large-scale analysis of nuclear gene diversity across Europe has consistently found low levels of genetic differentiation among modern populations regardless of the markers used

Table 5–1. Genetic differentiation between *Quercus petraea* populations assessed with cytoplasmic and nuclear genetic markers

Marker	Number of loci	Number of pops	Geographic distribution	F_{ST}	Reference
cpDNA	1 (cpDNA molecule)	650	Range-wide	0.835	Petit et al. 2002b
Isozymes	13	7	Range-wide	0.032	Zanetto et al. 1994
Isozymes	13	81	Range-wide	0.025	Zanetto & Kremer 1995
RAPDs	31	21	Western part of natural range	0.024	Le Corre et al. 1997a
AFLPs	107	7	Range-wide	0.044	Mariette et al. 2002
Microsatellites	6	7	Range-wide	0.023	Mariette et al. 2002

(Zanetto & Kremer 1995; Le Corre et al. 1997a; Mariette et al. 2002), which we attribute to gene flow (Fig. 5–3 and Table 5–1). Extensive pollen flow has been demonstrated by parentage analyses conducted in *Q. petraea* or *Q. robur* stands (Streiff et al. 1999; Valbuena-Carabana et al. 2005). More than half of the pollen contributing to the next generation came from outside the study stands,

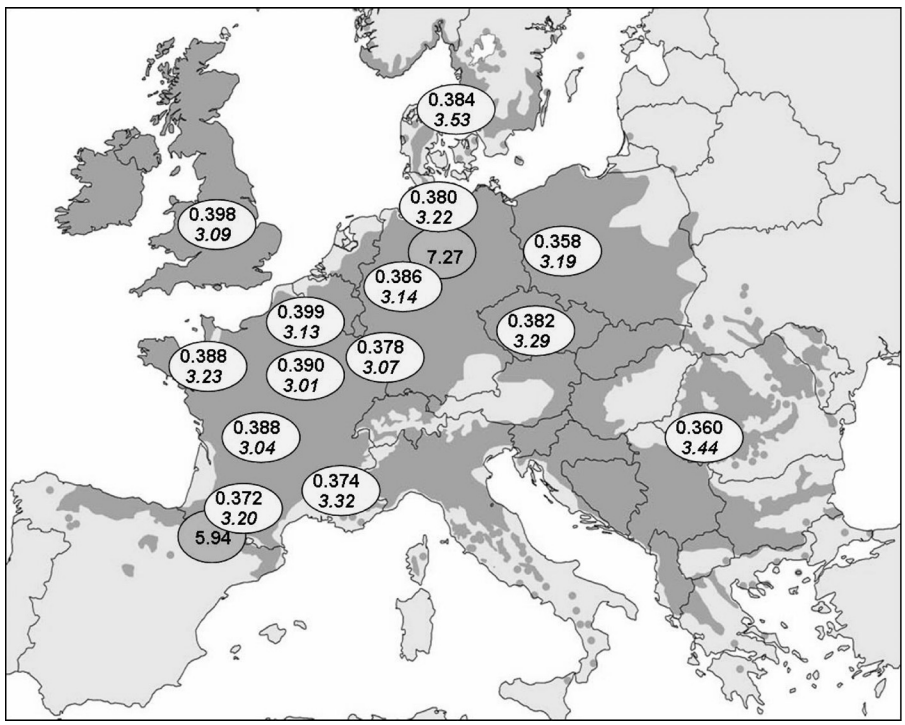


Figure 5–3: Geographic range of *Quercus petraea* and distribution of genetic diversity based on nuclear data (according to Zanetto & Kremer 1995, figs. 2 and 3, and unpublished data). Data in yellow circles correspond to thirteen isoenzymatic loci and represent observed heterozygosity (in bold characters) and allelic richness (in italic). Each circle is the mean value obtained from two to eleven populations. Data in pink circles correspond to nucleotide diversity (π values) obtained from nine candidate genes of bud burst, from fifty sequences in North Germany, and fifty sequences in the Pyrénées. Distribution map was obtained from Euforgen (http://www.bioversityinternational.org/networks/euforgen/Euf_Distribution_Maps.asp). *See Color Plate II.*

and pollen-dispersion curves are characterized by long tails. As in the case of acorns for the colonization of new territories, LDD of pollen may have played an important role in gene flow. Most investigations based on parentage analysis are limited at this point to Local Neighborhood Diffusion (LND) (Hengeveld 1989), whereas LDD has received less attention. LDD may be caused by uplifting air movements into the upper layer of the atmosphere, where the pollen can be transported long distances but is also exposed to high ultraviolet (UV) radiation. A recent study based on an atmospheric model of air movements and taking into account loss of pollen viability due to UV radiation showed that oak pollen can be transported and maintain viability over 100 kilometers (Schueler et al. 2005; Schueler & Schlünzen 2006).

The persistence of ancient differentiation among the modern populations was tested by comparing populations belonging to different cpDNA lineages, as each lineage witnesses the glacial origin of the population. A meta-analysis was conducted across all provenance tests that were established throughout Europe (Kremer et al. 2002) and for all phenotypic traits that were assessed so far. The analysis compiled data from sixty-two trait–test combinations from sixteen provenance tests in France, Germany, and England. Each test comprised between twenty and ninety-four provenances. Phenotypic traits that were assessed were related to growth, phenology, dendrometry, and morphology, most of which would affect trees' fitness. Each provenance was fingerprinted for its cpDNA and was assigned to one of the maternal lineages. The test for persistence of ancient differentiation was made in two different ways: 1) by comparing lineage and population components of variance in a hierarchical analysis of variance; and 2) by comparing genetic distances between the haplotypes assigned to populations and their phenotypic divergence using multiple Mantel tests. Among the sixty-two trait–test comparisons, only two exhibited significant associations with maternal lineage. These results strongly suggest that the ancient differentiation, if it existed, did not persist and was entirely erased by gene flow that followed colonization, by new selection pressures that occurred since colonization, or by their joint actions.

Recent differentiation

The meta-analysis revealed that despite the lack of variation of phenotypic traits among maternal lineages, there is much variation among modern populations for all traits assessed, accounting for "recent" differentiation that has built up since population establishment. It is interesting that the geographic patterns of variation observed were consistent across the different maternal lineages. This consistency is best illustrated by the bud-flushing variation in *Q. petraea* (Fig. 5–4) that can be observed in today's provenance test. Populations show a clear latitudinal trend of variation, southern populations flushing earlier than northern populations. The clinal pattern is consistent among the three major maternal lineages (A, B, and C), with minor differences in the regression slopes between bud-burst scores and latitude. Again, if ancient differentiation would have persisted, one would have expected different patterns of variation of bud burst in the different lineages. Depending on the part of the natural range that was prospected for

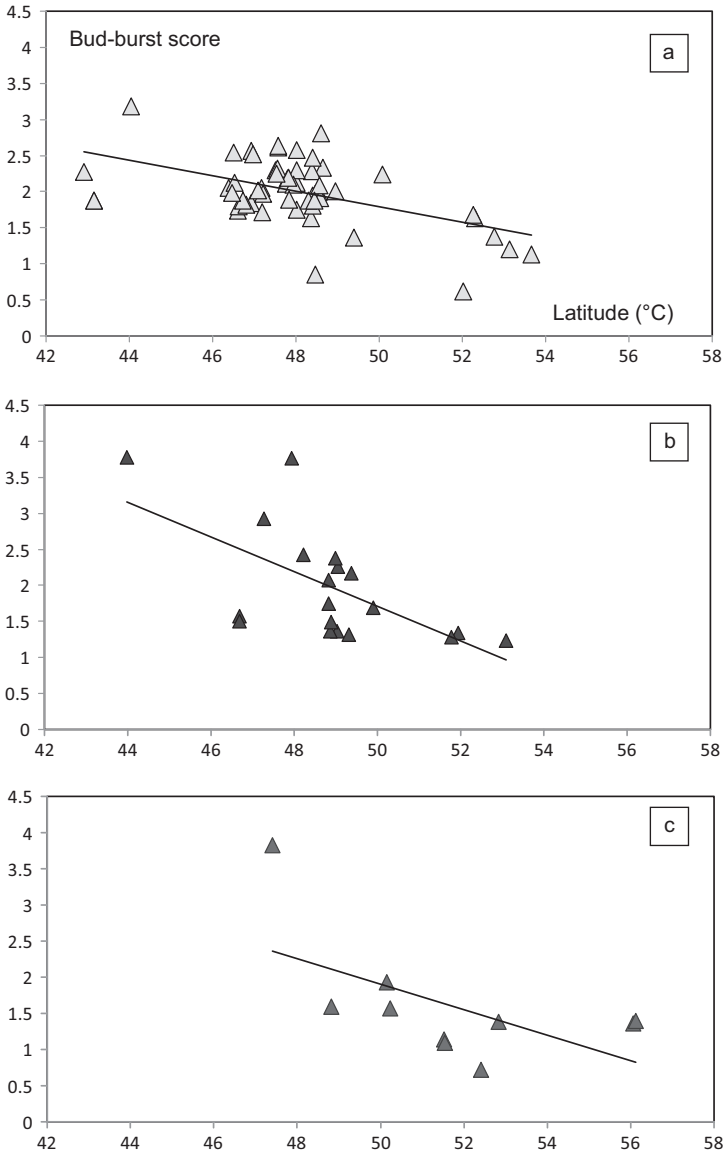


Figure 5–4: Variation of apical bud phenology of different populations of *Quercus petraea* in provenance tests. The analysis was done separately for each different maternal lineage to which modern populations belong. (a) yellow (B lineage) according to Fig. 5–2; (b) blue (A lineage) according to Fig. 5–2; (c) red (C lineage) according to Fig. 5–2. Bud development was recorded according to bud-burst scores varying from 0 (dormant) to 5 (elongating leaves). *See Color Plate VII.*

collecting populations to be installed in provenance tests, Q_{ST} values vary from 0.15 to 0.7 (Table 5–2). Many earlier studies emphasize the strong population variation observed in the provenance tests of sessile oak but did not provide data of Q_{ST} as this parameter has been used only in the past decade (Kleinschmit 1993; Liepe 1993; Ducousso et al. 1996; Jensen 2000). As extensive pollen mediated gene flow has homogenized populations across Europe, the differentiation now observed in provenance tests for adaptive traits was most likely created by

Table 5–2. Genetic differentiation between *Quercus petraea* populations assessed for phenotypic traits

Trait	Number of populations	Geographic distribution	Q_{ST}	Reference
Bud-burst score	21	Western part of natural range	0.503	Kremer et al. 1997
Bud-burst score	107	Range-wide	0.55	Ducousso et al. 2005
Bud-burst score	23[a]	Northern part of natural range	0.15 to 0.27	Jensen & Hansen 2008
Leaf coloration in the fall	23[a]	Northern part of natural range	0.15 to 0.18	Jensen & Hansen 2008
Leaf maintenance in the winter	107	Range-wide	0.54	Ducousso et al. 2005
Height at age 6	21	Western part of natural range	0.32	Kremer et al. 1997
Height at age 10	107	Range-wide	0.70	Ducousso et al. 2005
Length of growing season	23[a]	Northern part of natural range	0.41	Jensen & Hansen 2008
Number of branches	107	Range-wide	0.36	Ducousso et al. 2005
Number of forks	107	Range-wide	0.10	Ducousso et al. 2005
Stem form	107	Range-wide	0.68	Ducousso et al. 2005
Crown form	107	Range wide	0.71	Ducousso et al. 2005

[a] This study comprises mostly *Q. robur* populations.

diversifying selection. Temperate oaks are widely distributed in Europe and occupy diverse ecological sites, thus stimulating diversifying selection.

Summing up the conclusions of the historical and genetic survey, the pace of population differentiation during the past 15,000 years can be sketched in four phases:

(1) The glacial period ended with deciduous oaks distributed in three major refugia that were probably genetically differentiated at chloroplast markers, nuclear genes, and adaptive traits.
(2) As the climate warmed, oaks migrated northward as an advancing wave disrupted by LDD events, resulting in local founder events. Transient differentiation was generated by these founder events both for cpDNA and (probably to a lesser extent) for phenotypic traits.
(3) As oaks progressively occupied the central and northern part of Europe, pollen flow established communication between stands originating from eastern, central, and western refugia. Pollen migration increased as stands from different origins merged and reduced the ancient and transient differentiation for traits.
(4) Finally, local selection pressures acting on the recently established populations resulted again in differentiation, which constantly increased over time. New patterns of differentiation appeared, distinct from those existing at colonization.

CONTEMPORARY DYNAMICS OF DIFFERENTIATION

This historical overview indicates that the differentiation of extant populations is large and has been established recently, but it does not provide any time frame for

its dynamics. Was evolutionary change generated continuously over the warming period or did it take place faster? How much change can be generated during short periods (i.e., fewer than thirty generations)? The historical overview also showed that despite extensive gene flow, differentiation of traits could accumulate, finally exceeding by far differentiation at neutral markers (Tables 5–1 and 5–2). To learn about the dynamics during shorter time frames and to investigate the apparent contradiction between differentiation and gene flow, we first subdivided complex traits into their elementary components (e.g., genes) to compare differentiation at the same level for markers and traits. In a second step, the dynamics of the components of Q_{ST} were monitored under different evolutionary scenarios mimicking the oak situation.

Components of adaptive differentiation (Q_{ST})

Using standard quantitative genetics reasoning (e.g., a trait controlled by a set of loci with additive actions of their alleles) and further assuming that each locus was biallelic (i.e., each allele having the same effect but of the opposing sign), we obtained the following relationship between population differentiation measured at the level of genes (F_{ST}, mean value of all genes contributing to the trait) and of the trait (Q_{ST}) (Le Corre & Kremer 2003).

$$Q_{ST} = (1 + \theta_B)F_{ST}/[(\theta_B - \theta_W)F_{ST} + 1 + \theta_W] \quad (1)$$

As expected, there is a positive relationship between both measures. The relationship is affected, however, by two other parameters (θ_B and θ_W), which represent the relative importance of covariances of additive effects of alleles present at the different loci at the between- (θ_B) and within- (θ_W) population level. If there are n genes contributing to the trait, then the genetic variance (V_W) of the trait within a population can be decomposed into the variance due to allelic effects at each locus i (σ^2_{wi}) and into covariances among allelic effects between loci Cov_{wij}:

$$V_W = \sum_i \sigma^2_{wi} + \sum_i \sum_{j=i} Cov_{wij}, \quad (2)$$

and θ_W is the relative contribution of covariance terms to the variance terms:

$$\theta_W = \sum_i \sum_{j \neq i} Cov_{wij} / \sum_{\mathrm{i}} \sigma^2_{wi}. \quad (3)$$

Similar reasoning can be followed for the between-population genetic variance to obtain θ_B. Equation (1) provides a formal framework to understand the relationships between differentiation of a trait and its elementary components; it extends earlier approaches by decomposing the between- and within-population trait variances into covariances and variances of allelic effects (Latta, 1998, 2003; McKay and Latta, 2002).

The relationship between F_{ST} and Q_{ST} derived in the simplified two-allele model holds in a large range of multiallelic cases, as was empirically tested by Le Corre and Kremer (2003). The relationship also holds at any point in time, regardless of equilibrium or non-equilibrium conditions among selection, migration,

and drift. The two θ parameters represent the amount of covariances among alleles contributing to the additive value of a trait weighted by the genic variances. Covariances themselves depend on the disequilibria among alleles and the products of allelic effects, meaning that the θ values are generated by nonrandom associations of alleles at the between- and within-population level. Positive θ_B values indicate that populations tend to assemble alleles with effects of the same sign regardless of individuals that bear those alleles. Conversely, negative θ_B values indicate that alleles with opposite signs are associated in the same populations, whereas a θ_B value close to 0 would mean that alleles are randomly associated among populations. Similarly, negative θ_W values indicate that alleles of opposite signs are associated within individuals.

From Equation (1), it can be shown that when θ_B is greater than θ_W, then Q_{ST} will always be greater than F_{ST}. Conversely, when θ_B is less than θ_W, then Q_{ST} is less than F_{ST}. Hence, the comparison of Q_{ST} and F_{ST} depends on the comparison between θ_B and θ_W. These analytical predictions were confirmed by simulations of a wide range of evolutionary scenarios with various levels of gene flow and strength of selection (Le Corre & Kremer 2003). We summarize here the main conclusions regarding the equilibrium values of the components of Q_{ST} (e.g., θ_B, θ_W, and F_{ST}) in the case of an outcrossing species with large population sizes, as is usually the case in tree species.

θ_W is negligible in most scenarios tested, except when the strength of intrapopulation selection is strong, in which case slightly negative values can be reached ($\theta_W < 0.3$). Limited θ_W is expected for large outcrossing populations, where recombination will decrease disequilibria at a constant rate over generations.

θ_B is positive when gene flow is large [Nm (= number of migrant genes per population) > 1] and when diversifying selection occurs (e.g., populations are driven by selection to different optimal values for the trait investigated), due to ecological heterogeneity across the landscape, which is the case for forest trees. It is interesting that θ_B increases as gene flow increases and as diversifying selection is more pronounced. Strength of within-population selection will, however, decrease θ_B, becoming negative in extreme cases. Overall, θ_B exceeds 1 when migration is high ($Nm > 10$), diversifying selection is important, and the strength of within-population selection is weak (Le Corre & Kremer 2003).

F_{ST} increases as diversifying selection increases, the strength of within-population selection gets stronger, and gene flow decreases. Under weak selection intensity, the F_{ST} value of genes contributing to the trait undergoing selection will remain at the level of that of neutral markers.

These opposing trends for θ_B and F_{ST} in outcrossing species comprising large populations and with extensive gene flow among populations are further inflated when the number of loci increases, to the extent that allelic frequencies of genes may reach the level observed at neutral markers (data not shown).

To sum up, in oaks, θ_B is the main driver of Q_{ST}, especially for traits controlled by a large number of loci. These results suggest that adaptive divergence is mainly caused by covariances among allelic effects and not by variances of allelic frequencies (Latta 2003). They also provide an interpretation of the persistence of large, adaptive divergence in the context of high rates of gene flow (see Chapter 8 by Hamrick et al). Intuitively speaking, large gene flow causes constant import

of genes, offering new opportunities for associations with resident genes and, hence, increasing θ_B values.

These conclusions, based on theoretical developments and simulations, were recently supported by first results where differentiation was assessed at neutral markers, candidate genes putatively controlling an adaptive trait, and the trait itself, on the same set of populations. In Norway spruce (Heuertz et al. 2006) and in European aspen (Hall et al. 2007), large adaptive divergence was observed for phenological and growth traits, whereas differentiation for candidate genes amounted to levels similar to those found at neutral markers.

Dynamics of adaptive differentiation

How fast does adaptive differentiation (Q_{ST}) build up? How do the components contribute to this trend? To answer these questions, we monitored Q_{ST} in silico using the Metapop simulator (Le Corre et al. 1997b; Le Corre & Kremer 2003), available at request of the author. The simulations were designed to mimic the evolution of a set of oak populations after their installation following colonization. Simulations consisted in creating from a large source population a set of twenty-five populations exchanging pollen and seed according to the island model and undergoing different selection scenarios. We considered a trait controlled by ten genes located on different chromosomes. We considered large population sizes ($N = 500$), high gene flow ($Nm = 10$), and uniform mutation rates (10^{-5} for all loci). These input parameters were chosen to mimic realistic situations for oak forests (large population sizes, extensive gene flow, and moderate-to-low heritability) and were kept constant across all simulations. Contrasting values of parameters, mimicking the effects of natural selection, were selected to test the impact of selection on θ_B and θ_W, Q_{ST}, and F_{ST}. Selection is modeled in two different ways: 1) Stabilizing selection is considered to occur within populations, and the strength of selection is driven by ω^2 (Turelli 1984) (with ω^2 varying between 5 [strong selection] to 50 [weak selection]), and 2) diversifying selection is driven by *VarZopt*, the variance of optimal values of the trait that were assigned to each population (*VarZopt* = 1, weak selection to *VarZopt* = 5, strong diversifying selection). Populations were distributed in a two-dimensional array, and optimal values were assigned to populations along a one-dimensional gradient to reproduce clinal patterns of variation. In these scenarios, the twenty-five populations are at equilibrium at generation 0 (θ_B and $\theta_W = 0$, Q_{ST} and $F_{ST} = 0$). Population differentiation was then monitored over generations for a phenotypic trait submitted to selection, for its underlying genes, and for neutral markers.

The dynamics of θ_B and θ_W show contrasting patterns among generations (Figs. 5–5 and 5–6). These figures depict the evolution of Q_{ST}, F_{ST}, θ_B, and θ_W during the first 100 generations, whereas simulations where conducted up to 3,000 generations to obtain equilibrium values. As expected, θ_W is always extremely low. Disequilibria between alleles at different genes are disrupted at each generation by random mating in large populations. They build up only under strong within-population stabilizing selection, where θ_W values become slightly negative during the first generations when stabilizing selection is strong (Fig. 5–5, a and c). As

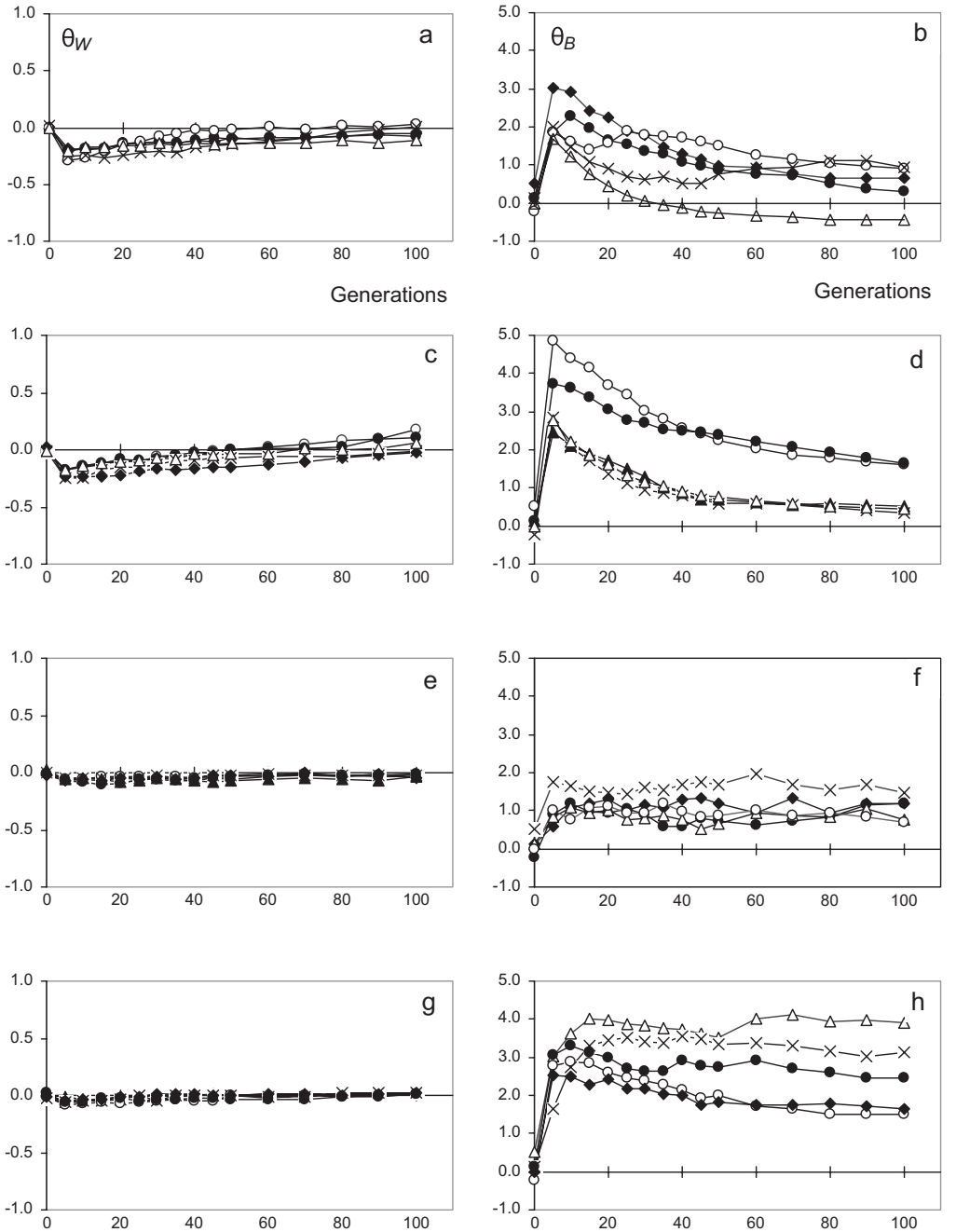


Figure 5–5: Dynamics of θ_W and θ_B along generations in different evolutionary scenarios. a, c, e, and g correspond to the variation of θ_W; b, d, f, and h correspond to the variation of θ_B. a and b: strong stabilizing selection ($\omega^2 = 5$) and weak diversifying selection (*VarZopt* = 1); c and d: strong stabilizing selection ($\omega^2 = 5$) and strong diversifying selection (*VarZopt* = 5); e and f: weak stabilizing selection ($\omega^2 = 50$) and weak diversifying selection (*VarZopt* = 1); g and h: weak stabilizing selection ($\omega^2 = 50$) and strong diversifying selection (*VarZopt* = 5). The five curves correspond to five independent repetitions of the evolutionary scenarios with the same genetic input parameters.

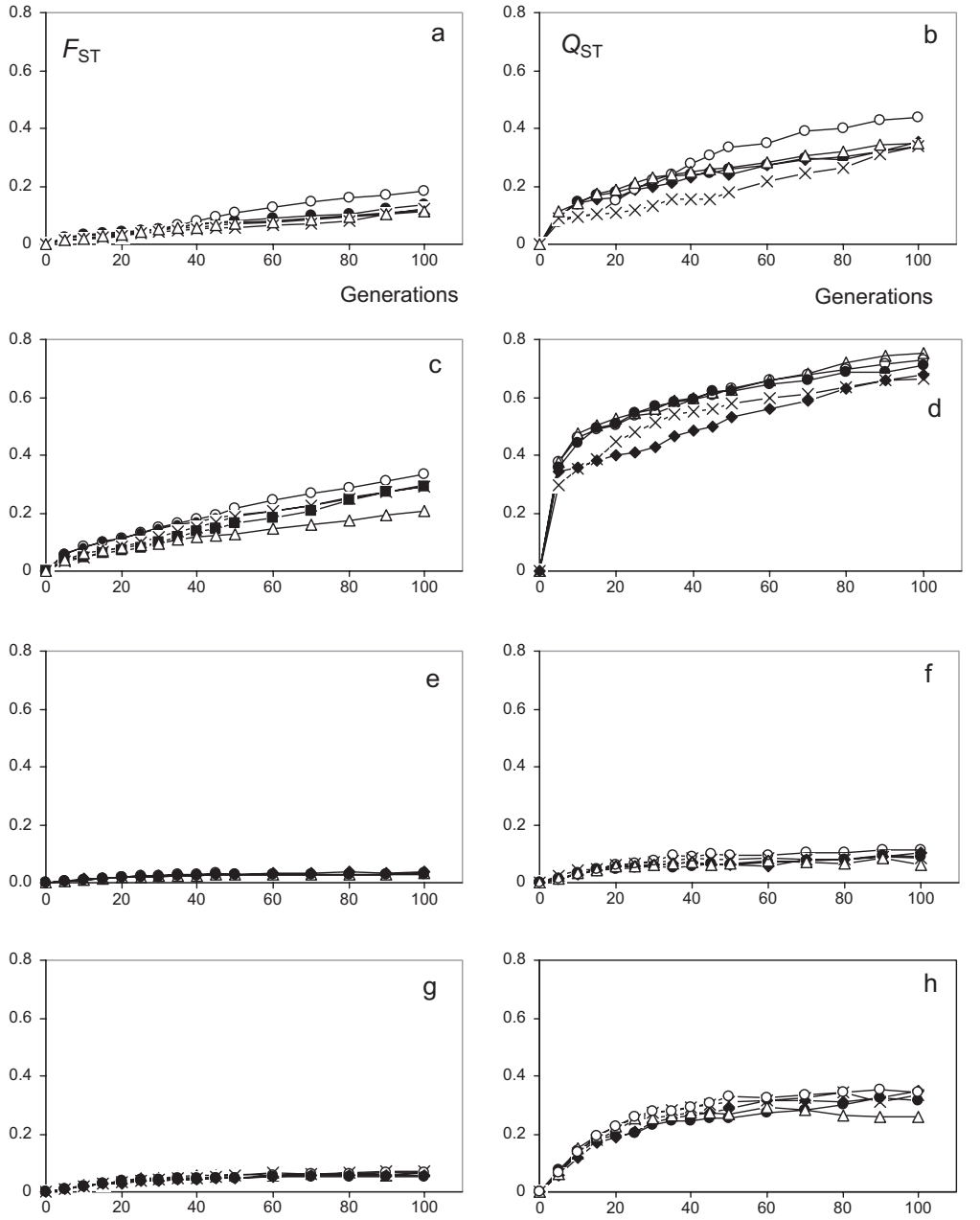


Figure 5–6: Dynamics of F_{ST} and Q_{ST} along generations in different evolutionary scenarios. a, c, e, and g correspond to the variation of F_{ST}; b, d, f, and h correspond to the variation of Q_{ST}; a and b: strong stabilizing selection ($\omega^2 = 5$) and weak diversifying selection (*VarZopt* = 1); c and d: strong stabilizing selection ($\omega^2 = 5$) and strong diversifying selection (*VarZopt* = 5); d and f: weak stabilizing selection ($\omega^2 = 50$) and weak diversifying selection (*VarZopt* = 1); g and h: weak stabilizing selection ($\omega^2 = 50$) and strong diversifying selection (*VarZopt* = 5). The five curves correspond to five independent repetitions of the evolutionary scenarios with the same genetic input parameters.

expected from earlier investigations in single populations, negative correlations between additive values at different genes built up at the early phase of selection (corresponding to the so-called Bulmer effect [Bulmer 1980]). θ_B values vary quite differently: They are in most cases positive and larger than θ_W. When diversifying selection is important (Fig. 5–5, d and h), the covariances among allelic effects are up to 5 times larger than the variances of allelic effects. The most striking feature, however, is the rapid increase of Q_{ST} during the early stages. Indeed, Q_{ST} approaches asymptotic values in fewer than thirty generations, when stabilizing selection is weak (Fig. 5–6, f and h). The increase is more progressive when stabilizing selection is stronger (Fig. 5–6, b and d), although 40–60% of the asymptotic values of Q_{ST} are reached after thirty generations. The rapid increase of differentiation during the first generations is due to the variation of θ_B. Peak values *of* θ_B are reached in fewer than fifteen generations regardless of the selection model chosen (Fig. 5–5, b, d, f, and h). After reaching their maximum, θ_B values slightly decrease along generations when stabilizing selection is strong (Fig. 5–5, b and d) but remain close to their maximum when stabilizing selection is weak (Figure 5-5, f and h). In contrast, F_{ST} steadily increases over generations. The rate of increase is low when stabilizing selection is weak (Fig. 5–6, e and g); in this case, asymptotic values of F_{ST} of genes are close to those of F_{ST} of neutral markers. The rate is higher and continuous when stabilizing selection is strong (Fig. 5–6, a and c). This finding suggests that diversifying selection generates strong associations between alleles at different loci at the between-population level. To sum up, the dynamics of adaptive differentiation can be decomposed in two stages: 1) the early stage (first thirty generations) when Q_{ST} is increasing very rapidly (this pattern is generated by the rapid increase of θ_B, regardless of the selection scenario); and 2) the subsequent stage when Q_{ST} continues to increase but at lower rates. In the case of strong stabilizing selection, F_{ST} will be the main driver of the increase of Q_{ST}. Under weak stabilizing selection, the increase of Q_{ST} is lower and is brought about equally by F_{ST} and θ_B.

Coexistence of strong adaptive differentiation and high gene flow

The following conclusions regarding the tempo of differentiation can be drawn from the comparative analysis of the dynamics of Q_{ST}, F_{ST}, and their components (θ_B and θ_W) along different evolutionary scenarios:

(1) In European oaks, extant genetic differentiation at phenotypic traits is large, in contrast with differentiation at molecular markers, and involves most traits. This differentiation is neither a result of ancient differentiation existing prior to the warming period nor the consequence of founder events at the time of colonization because pollen flow and population admixture have been extensive. It has instead accumulated recently by diversifying selection caused by the ecological heterogeneity across the European continent.
(2) Differentiation (Q_{ST}) of adaptive traits does not solely depend on differences in allelic frequencies (F_{ST}) of loci contributing to the traits. Due to their multilocus structure, covariances among alleles at different loci

(θ_B and θ_W) are additional components, whose contribution to Q_{ST} exceeds by far the contributions of individual loci (F_{ST}).

(3) This trend (e.g., the predominant contribution of θ_B to Q_{ST}, as opposed to a contribution of individual loci to F_{ST}) increases as the number of loci contributing to the trait increases. Hence, fitness-related traits that are usually more composite than others will exhibit extremely contrasted F_{ST} and Q_{ST}.

(4) The important contribution of θ_B to Q_{ST} solves the apparent contradiction of coexistence of large differentiation in the context of extensive gene flow in trees. θ_B is increasing as gene flow imports new genes in populations, offering new opportunities to increase covariances between alleles.

(5) When selection (stabilizing or diversifying) starts to operate, the main and immediate driver of Q_{ST} is θ_B. For multilocus traits, diversifying selection is capturing first beneficial allelic associations (θ_B) distributed among the loci contributing to the trait, prior to modifying allele frequencies. During the early phases of selection and even later under certain evolutionary scenarios, allelic frequencies may even be insensitive to selection and behave as neutral markers.

(6) Trees are prone to respond rapidly to selection induced by environmental change, as they possess attributes that inflate θ_B, such as high gene flow and high genetic diversity. Furthermore, the low F_{ST} values for loci controlling traits suggest that θ_B can build instantaneously as adaptive alleles are evenly distributed in natural populations.

CONCLUSION

In this review, the historical and contemporary dynamics of differentiation has focused mainly on European oaks, where fossil and genetic data have been assembled across their entire continental distribution. The conclusions can, however, be extended to many other widespread tree species as they share similar biological features such as high genetic diversity and gene flow (Petit & Hampe 2006; Savolainen et al. 2007). Another example of population differentiation in the case of extensive gene flow is illustrated by the acorn barnacle (Box 5 by S. Palumbi 2010). Assembling lessons from phylogeography, paleobotany, and simulations, we conclude that long-lived tree species have responded quite rapidly to environmental change, despite their low evolutionary rate at the gene level (Smith & Donoghue 2008). Indeed, and as suggested by theoretical investigations, the tempo of differentiation is driven by the standing level of genetic diversity and gene flow. In comparison to earlier studies that highlighted these features of trees (Hamrick 2004), our review shows the mechanisms by which the interaction between gene flow and local selection pressures accelerates the rate of differentiation, by building up favorable allelic associations among genes contributing to fitness-related traits. Intergenic allelic associations are the cause of the rapid differentiation, and they explain the coexistence of strong phenotypic differentiation in trees (as assessed in provenance tests) and extensive gene flow.

It is likely that these mechanisms were actually favored during the repeated interglacial–glacial periods allowing widespread tree species to colonize and adapt

BOX 5: ADAPTIVE SHIFTS IN NATURAL POPULATIONS OF HIGH DISPERSING SPECIES

Stephen R. Palumbi

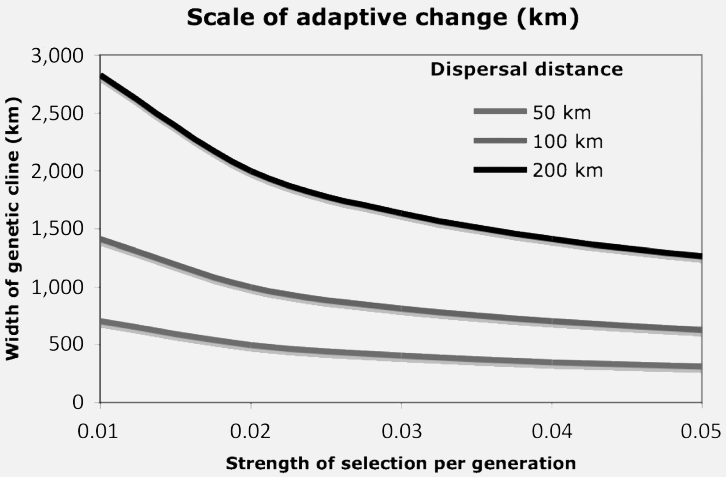
Problem

Geographic differences in the phenotypes of individuals of a widely distributed species can signal the impact of selection (Kremer et al., this volume). How isolated from one another do populations have to be to accumulate gene-frequency differences due to natural selection? Simple theory of populations connected by immigration suggests that when the selection coefficient s is much greater than the per capita rate of migration among populations m, then local adaptation can result in significant gene-frequency shifts (Wright 1969). As a result, species with potentially high gene flow, such as many marine species, are thought to provide fewer examples of local adaptation, and these are likely to be limited to examples where selection on single loci is particularly strong (Place & Powers 1979; Schmidt & Rand 1999). How often do open populations of marine species with high potential gene flow show adaptive genetic differentiation?

Case Study

The acorn barnacle (*Balanus glandula*) is a sessile marine species in the high intertidal zone of the west coast of North America. It releases swimming larvae that spend three to four weeks in the plankton, drifting with prevailing currents until settlement occurs on intertidal rocks. The species lives from Baja, California, to Alaska across a strong thermal gradient. How likely is it that adaptation to local conditions can occur? The width of an ideal, stable genetic cline is proportional to $(V/s)^{1/2}$, where V is the variance of migration distances from parent to offspring, and s is the selection differential (Sotka & Palumbi 2006, see also Slatkin 1973). For dispersal distances of 50, 100, and 200 km, this relationship suggests that selection differentials of only 1–2% can generate a stable cline in gene frequencies across 500 to 2,700 km (Box Fig. 5–1). Because the thermal gradient across which *B. glandula* lives occurs over this spatial scale, it is possible that relatively weak selection can generate stable clines and produce local genetic adaptation.

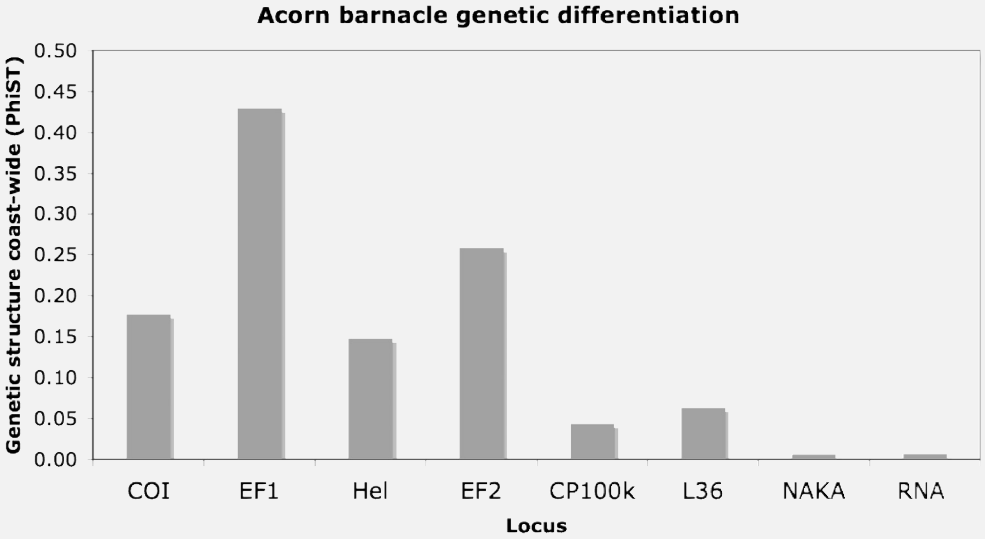
Estimates of gene-frequency shifts at nuclear and mitochondrial loci show evidence of such a cline along the California coast (Sotka et al. 2004; Sotka & Palumbi 2006), with cline widths of approximately 500 km. Furthermore, an analysis of six more nuclear loci show significant genetic structure at four of the six loci and significant clines at three loci (Jacobs-Palmer & Palumbi, unpublished data, Box Fig. 5–2). Differentiation at many loci could be due to selection acting individually locus by locus (see Endler 1977 for a discussion of cline evolution and maintenance). Alternatively, southern and northern populations may have diverged in allopatry, producing locally adapted gene pools that are coming together in the present day through migration. The spatially variable alleles diverged long ago (Wares & Cunningham 2005), suggesting that the current cline may be ancient



Box Figure 5–1: Width of a stable genetic cline resulting from the balance of dispersal distance and natural selection. Dispersal distances between 50 and 200 km, probably a reasonable range for planktonically dispersing barnacles (Kinlan & Gaines 2003; Sotka et al. 2004) and selection of 1–2% per generation can produce genetic clines 500–2,700 km in width (see the values within the red box). The observed genetic cline in the barnacle *Balanus glandula* is approximately 500 km wide (Sotka et al. 2004).

in origin. In either case, selection is implicated in the origin or maintenance of the cline.

Evidence of selection on gene frequencies in *B. glandula* over time is weak. There are only subtle shifts in gene frequency from larvae to settled juvenile



Box Figure 5–2: Genetic differentiation along the central California coast in eight protein-coding loci from the barnacle *Balanus glandula*. Six of eight loci show highly significant shifts along the coast, and five of these have strong clinal signatures with cline widths of approximately 450–550 km. Loci are protein-coding regions from cytochrome oxidase I, elongation factor 1, ribonucleic acid (RNA) helicase, elongation factor 2, a cement gland protein, the ribosomal protein L36, a sodium potassium ATPase, and RNA polymerasse II (Jacobs-Palmer, Galindo, & Palumbi, in preparation).

to adult, and no clear change in northern versus southern alleles in adults that have settled in low versus high intertidal locations (Wares & Cunningham 2005). Yet the theory just outlined suggests that clines of the width we observe in this species can be sustained by mild selection that alters fitness by only 1–2%. Such low rates of selection are unlikely to be visible to any but the most stringent ecological analysis, yet can generate strong genetic patterns in the face of active dispersal.

Evidence that a continuously distributed, high-dispersal marine species has evolved distinct genetic clines across a thermal gradient has implications for the likely impact of coastal climate change. West Coast species distributions are already shifting in response to warming seawater temperatures (Sagarin et al. 1999), and southern species of intertidal barnacles are immigrating into central California locations such as Monterey Bay (Barry et al. 1995). It may be that southern alleles of species also are moving north if selection coefficients are changing. In such cases, biogeographic shifts of species, a commonly tallied index of global change effects in ecosystems (Root et al. 2005; Parmesan 2006), may only capture some of the biological changes associated with global warming.

REFERENCES

Barry JP, Baxter CH, Sagarin RD, Gilman SE (1995) Climate-related, long-term faunal changes in a California rocky intertidal community. *Science*, **267**, 672–675.

Endler JA (1977) *Geographic Variation, Speciation, and Clines*. Princeton University Press, Princeton, NJ.

Kinlan B, Gaines S (2003) Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology*, **84**, 2007–2020.

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics*, **37**, 637–669.

Place AR, Powers DA (1979) Genetic-variation and relative catalytic efficiencies – lactate dehydrogenase-B allozymes of Fundulus heteroclitus. *Proceedings of the National Academy of Sciences USA*, **76**, 2354–2358.

Root TL, MacMynowski DP, Mastrandrea MD, Schneider SH (2005) Human-modified temperatures induce species changes: joint attribution. *Proceedings of the National Academy of Sciences USA*, **102**, 7465–7469.

Sagarin RD, Barry JP, Gilman SE, Baxter CH (1999) Climate-related change in an intertidal community over short and long time scales. *Ecological Monographs*, **69**, 465–490.

Schmidt PS, Rand DM (1999) Intertidal microhabitat and selection at MPI: interlocus contrasts in the northern acorn barnacle, *Semibalanus balanoides*. *Evolution*, **53**, 135–146.

Slatkin M (1973) Gene flow and selection in a cline. *Genetics*, **75**, 733–756.

Sotka EE, Palumbi SR (2006) The use of genetic clines to estimate dispersal distances of marine larvae. *Ecology*, **87**, 1094–1103.

Sotka EE, Wares JP, Barth JB, Grosberg RK, Palumbi SR (2004) Strong genetic clines and geographic variation in gene flow in the rocky intertidal barnacle *Balanus glandula*. *Molecular Ecology*, **13**, 2143–2156.

Wares JP, Cunningham CW (2005) Isolation before glaciation in *Balanus glandula*. *Biological Bulletin*, **208**, 60–68.

Wright S (1969) *Evolution and the Genetics of Populations* (*Vol. 2*): *The Theory of Gene Frequencies*. University of Chicago, Chicago.

to new suited environments. How these mechanisms are acting during ongoing climatic change remains to be investigated in detail, but these processes are critical to predicting how species will adapt to changing environments. Because of the changes in levels of gene flow, we anticipate strong differences between species having continuous distribution and species with scattered distribution. The rate of adaptive differentiation may also be quite different between the leading edge and the rear end of distribution. As suggested by predictive models of bioclimatic envelopes (Thuiller et al. 2005), populations at the northern and eastern limit will be at the leading edge of range shifts and may benefit from immigrating genes via pollen flow from southern latitudes. In contrast, fitness of populations at the southern limit (rear end) may suffer from immigrating genes with lower fitness. The dynamics of differentiation need to be considered under different spatial settings of populations, and genetic associations with different allelic effects should be integrated into conservation and management strategies.

REFERENCES

Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S (2008) Adaptation, migration, or extirpation: climate change outcomes for tree populations. *Evolutionary Applications*, **1**, 95–111.

Bialozyt R, Ziegenhagen B, Petit RJ (2006) Contrasting effects of long-distance seed dispersal on genetic diversity during range expansion. *Journal of Evolutionary Biology*, **19**, 12–20.

Brewer S, Cheddadi R, De Beaulieu JL, Reille M (2002) The spread of deciduous *Quercus* throughout Europe since the last glacial period. *Forest Ecology and Management*, **156**, 27–48.

Brewer S, Hely-Alleaume C, Cheddadi R et al. (2005) Postglacial history of Atlantic oakwoods: context, dynamics and controlling factors. *Botanical Journal of Scotland*, **57**, 41–57.

Bulmer MG (1980) *The Mathematical Theory of Quantitative Genetics*. Oxford University Press, Oxford.

Bürger R, Krall C (2004) Quantitative genetic models and changing environments. In: *Evolutionary Conservation Biology* (eds. Ferrière R, Dieckmann U, Couvet D), pp. 171–187. Cambridge University Press, Cambridge, UK.

Bürger R, Lynch M (1995) Evolution and extinction in a changing environment: a quantitative genetic analysis. *Evolution*, **49**, 151–163.

Carroll SP, Hendry AP, Reznick DN, Fox CW (2007) Evolution on ecological time scales. *Functional Ecology*, **21**, 387–393.

Cheddadi R, De Beaulieu JL, Jouzel J et al. (2005) Similarity of vegetation dynamics during interglacial periods. *Proceedings of the National Academy of Sciences USA*, **39**, 13939–13943.

Cheddadi R, Vendramin GG, Litt T et al. (2006) Imprints of glacial refugia in the modern diversity of *Pinus Sylvestris*. *Global Ecology and Biogeography*, **15**, 271–282.

Ducousso A, Guyon JP, Kremer A (1996) Latitudinal and altitudinal variation of bud burst in western populations of sessile oak (*Quercus petraea* (Matt.) Liebl.). *Annales des Sciences Forestières*, **53**, 775–782.

Ducousso A, Louvet JM, Jarret P, Kremer A (2005) Geographic variations of sessile oaks in French provenance tests. In: *Proceedings of the Joint Meeting of IUFRO Working Groups Genetic of Oaks and Improvement and Silviculture of Oaks* (eds. Rogers R, Ducousso A, Kanazashi A), pp. 128–138. Tsukuba, Japan. FFPRI (Forestry and Forest Products Research Institute) Scientific Meeting Report 3.

Eckerle M, Chakari A, Meyruis P, Zonneweld KAF (1996) Paleoclimatic reconstruction of the last deglaciation (18–8ka BP) in the Adriatic Sea region; a land–sea correlation based on palynological evidence. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **122**, 89–106.

Gingerich P (2001) Rates of evolution on the time scale of the evolutionary process. *Genetica*, **112–113**(1), 127–144.
Hall D, Luquez V, Garcia VM et al. (2007) Adaptive population differentiation in phenology across a latitudinal gradient in European Aspen (*Populus tremula*, L.): a comparison of neutral markers, candidate genes, and phenotypic traits. *Evolution*, **61**, 2849–2860.
Hamrick JL (2004) Response of forest trees to global environmental change. *Forest Ecology and Management*, **197**, 323–335.
Hendry AP, Kinnison MT (1999) Perspective: the pace of modern life, measuring rates of contemporary microevolution. *Evolution*, **53**, 1637–1651.
Hengeveld R (1989) *Dynamics of Biological Invasions*. Chapman & Hall, London.
Heuertz M, De Paoli E, Källmann T et al. (2006) Multilocus patterns of nucleotide diversity, linkage disequilibrium, and demographic history of Norway Spruce. *Genetics*, **174**, 2095–2105.
Houle D, Morikawa B, Lynch M (1996) Comparing mutational variabilities. *Genetics*, **145**, 1467–1483.
Huntley B, Birks HJB (1983) *An Atlas of Past and Present Pollen Maps for Europe: 0–13000 Years Ago*. Cambridge University Press, London.
Jensen JS (2000) Provenance variation in phenotypic traits in *Quercus robur* and *Quercus petraea* in Danish provenance trials. *Scandinavian Journal of Forest Research*, **15**, 297–308.
Jensen JS, Hansen JK (2008) Geographical variation in phenology of *Quercus petraea* (Matt.) Liebl. and *Quercus robur* L. oak grown in a greenhouse. *Scandinavian Journal of Forest Research*, **23**, 179–188.
Kleinschmit J (1993) Intraspecific variation of growth and adaptive traits in European oak species. *Annales des Sciences Forestières*, **50**, 166s–186s.
König AO (2005) Provenance research: evaluating the spatial pattern of genetic variation. In: *Conservation and Management of Forest Genetic Resources in Europe* (eds. Geburek Th, Turok J), pp. 275–238. Zvolen, Slovakia.
Kremer A, editor (2002) Range-wide distribution of chloroplast DNA diversity and pollen deposits in European white oaks: inferences about colonisation routes and management of oak genetic resources. *Forest Ecology and Management*, **156**, 1–223.
Kremer A (2007) How well can existing forests withstand climate change? In: *Climate Change and Forest Genetic Diversity: Implications for Sustainable Forest Management in Europe* (eds. Koskela J, Buck A, Teissier du Cros E), pp. 3–17. Bioversity International, Rome.
Kremer A, Kleinschmit J, Cottrell J et al. (2002) Is there a correlation between chloroplastic and nuclear divergence, or what are the roles of history and selection on genetic diversity in European oaks? *Forest Ecology and Management*, **156**, 75–87.
Kremer A, Zanetto A, Ducousso A (1997) Multilocus and multitrait measures of differentiation for gene markers and phenotypic traits. *Genetics*, **145**, 1229–1241.
Latta RG (1998) Differentiation of allelic frequencies at quantitative trait loci affecting locally adaptive traits. *The American Naturalist*, **151**, 283–292.
Latta RG (2003) Gene flow, adaptive population divergence and comparative population structure across loci. *New Phytologist*, **161**, 51–58.
Le Corre V, Dumolin-Lapègue S, Kremer A (1997a) Genetic variation at allozyme and RAPD loci in sessile oak *Quercus petraea* (Matt.) Liebl.: the role of history and geography. *Molecular Ecology*, **6**, 519–529.
Le Corre V, Machon N, Petit RJ, Kremer A (1997b) Colonization with long-distance seed dispersal and genetic structure of maternally inherited genes in forest trees: a simulation study. *Genetics Research*, **69**, 117–125.
Le Corre V, Kremer A (1998) Cumulative effects of founding events during colonisation on genetic diversity and differentiation in an island and stepping-stone model. *Journal of Evolutionary Biology*, **11**, 495–512.
Le Corre V, Kremer A (2003) Genetic variability at neutral markers, quantitative trait loci and trait in a subdivided population under selection. *Genetics*, **164**, 2005–2019.
Liepe K (1993) Growth chamber trial on frost hardiness and field trial on bud burst of sessile oak (*Quercus petraea* Liebl.) and *Q. robur* L. *Annales des Sciences Forestières*, **50**, 208–214.
Lynch M (1990) The rate of morphological evolution in mammals from the standpoint of the neutral expectation. *The American Naturalist*, **136**, 727–741.

Magri D, Vendramin GG, Comps B et al. (2006) A new scenario for the quaternary history of European beech populations: palaeobotanical evidence and genetic consequences. *New Phytologist*, **171**, 199–221.

Mariette S, Cottrell J, Csaikl UM et al. (2002) Comparison of levels of genetic diversity detected with AFLP and microsatellite markers within and among mixed *Q. petraea* (Matt.) Liebl. and *Q. robur* L. stands. *Silvae Genetica*, **51**, 72–79.

McKay JK, Latta RG (2002) Adaptive population divergence: markers, QTLs and traits. *Trends in Ecology and Evolution*, **17**, 285–291.

Nathan R (2006) Long-distance dispersal in plants. *Science*, **313**, 786–788.

Petit RJ, Brewer S, Bordacs S et al. (2002a) Identification of refugia and post-glacial colonisation routes of European white oaks based on chloroplast DNA and fossil pollen evidence. *Forest Ecology and Management*, **156**, 49–74.

Petit RJ, Csaikl UM, Bordacs S et al. (2002b) Chloroplast DNA variation in European white oaks: phylogeography and patterns of diversity based on data from over 2,600 populations. *Forest Ecology and Management*, **156**, 5–26.

Petit RJ, Hampe A (2006) Some evolutionary consequences of being a tree. *Annual Review of Ecology Evolution and Systematics*, **37**, 187–214.

Petit RJ, Hu FS, Dick CK (2008) Forests of the past: a window to future changes. *Science*, **320**, 1450–1452.

Petit RJ, Pineau E, Demesure B et al. (1997) Chloroplast DNA footprints of postglacial recolonization by oaks. *Proceedings of the National Academy of Sciences USA*, **94**, 9996–10001.

Rabineau M, Berne S, Olivet JL et al. (2006) Paleo sea levels reconsidered from direct observation of paleo shoreline position during Glacial Maxima (for the last 500,000 yr). *Earth and Planetary Science Letters*, **252**, 119–137.

Reich PB, Oleksyn J (2008) Climate warming will reduce growth and survival of Scots pine except in the far north. *Ecology Letters*, **11**, 588–597.

Sato M, Waxman D (2008) Adaptation to slow environmental change, with apparent anticipation to selection. *Journal of Theoretical Biology*, **252**, 166–172.

Savolainen O, Pyhajarvi T, Knurr T (2007) Gene flow and local adaptation of trees. *Annual Review of Ecology, Evolution and Systematics*, **38**, 595–619.

Schueler S, Schlünzen KH (2006) Modeling of oak pollen dispersal on the landscape level with a mesoscale atmospheric model. *Environmental Modeling and Assessment*, **11**, 179–194.

Schueler S, Schlünzen KH, Scholz F (2005) Viability and sensitivity of oak pollen and its implications for pollen-mediated gene flow. *Trends in Ecology and Evolution*, **19**, 154–161.

Smith SA, Donoghue MJ (2008) Rates of molecular evolution are linked to life history in flowering plants. *Science*, **322**, 86–89.

Stockwell CA, Hendry AP, Kinnison MT (2003) Contemporary evolution meets conservation biology. *Trends in Ecology and Evolution*, **18**, 94–101.

Streiff R, Ducousso A, Lexer C et al. (1999) Pollen dispersal inferred from paternity analysis in a mixed oak stand of *Quercus robur* L. and *Q. petraea* (Matt.) Liebl. *Molecular Ecology*, **8**, 831–841.

Thiede J (1978) A glacial Mediterranean. *Nature*, **276**, 680–683.

Thuiller W, Lavorel S, Araujo MB, Sykes MT, Prentice JC (2005) Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences USA*, **102**, 8245–8250.

Turelli M (1984) Heritable genetic variation via mutation–selection balance: Lerch's zeta meets the abdominal bristle. *Theoretical Population Biology*, **25**, 138–193.

Valbuena-Carabana M, Gonzalez-Martinez SC, Sork VL et al. (2005) Gene flow and hybridisation in a mixed oak forest (*Quercus pyrenaica* Willd. and *Quercus petraea* (Matts.) Liebl.) in central Spain. *Heredity*, **95**, 457–485.

Zanetto A, Kremer A (1995) Geographical structure of gene diversity in *Quercus petraea* (Matt.) Liebl. I. Monolocus patterns of variation. *Heredity*, **75**, 506–517.

Zanetto A, Roussel G, Kremer A (1994) Geographical variation of inter-specific differentiation between *Quercus robur* L. and *Quercus petraea* (Matt.) Liebl. *Forest Genetics*, **1**, 111–123.