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Genetic consequences of forest population dynamics influenced by historic climatic variability in the western USA

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Abstract

We review recent advances in climate science that show cyclic climatic variation over multiple time scales and give examples of the impacts of this variation on plant populations in the western USA. The paleohistorical reconstructions we review and others indicate that plant species track these cycles in individualistically complex ways. These dynamic histories suggest that genetic structures are in a non-equilibrium state, with populations constantly lagging their environmental optima. Such dynamism may serve to maintain genetic variation in populations, which may be a hedge against rapid environmental change. We also discuss how population history affects the way we analyze and interpret genetic data and, conversely, the way genetic theory affects historical reconstructions.
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"... For the uncertain future has yet to come, with every possible variety of fortune ..."
Plutarch's "Solon"

1. Introduction

Traditional models in population genetics often assume equilibrium conditions (Wright, 1969; Crow and Kimura, 1970) or consider changes in parameters over many generations. Moreover, simulations in population genetic studies are often carried out for hundreds of generations (Gilpin, 1991; Nichols and Hewitt, 1994; Epperson, 1995; Austerlitz and Garnier-Géré, 2003), often assuming constant background conditions.

Climate science has made considerable advances over the past 20 years, indicating substantial climatic variability at multiple time scales. Detailed analyses of the fossil record have shown that plant species track these variations individualistically in multiple ways, resulting in shifting vegetational assemblages and indicating that populations are in nonequlibrium states. We review some of these climatic cycles, giving examples of vegetation response. We then review the potential consequences of these cycles on the pattern and extent of genetic variation. Finally, we discuss the contextual impact of cyclic climates on the interpretation and analysis of genetic data. We also discuss how genetics can affect our interpretations of past climates.

2. Climate cycles and vegetation response

Cyclic climatic patterns in the Quaternary have been identified with periods ranging from interannual

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to multimillennial. In general, the longer the period of these cycles, the greater the amplitude of climatic change. We briefly summarize some dominant cycles, from low frequency to high, and their impact on vegetation. These cycles and their impact on vegetation assemblages in the western USA have been reviewed by Millar (2004) and Millar and Woolfenden (1999b).

2.1. Multimillennial cycles

The now familiar Milankovich cycles (Milankovich, 1941) have periods ranging between 20,000 and 100,000 years and are coupled with cyclic changes in the Earth's orbit and position, driving glacial–interglacial cycles. Periods between interglacials are long and those between glacials are short. Regionally, there have been abrupt temperature changes as much as 21 °C between alternate phases and up to 15 °C within 50-year periods (White et al., 2001). The impact of the Milankovich cycles on vegetation is illustrated by the history of Californian oak (*Quercus*) species. The palynological record from lake and offshore cores indicates that oak is rare, presumably in small, isolated populations, during glacial periods and common during the interglacials (Adam, 1988; Heusser, 1995). As the Milankovich cycles are composed of three orbital characteristics of differing periodicities, these result in sub-Milankovich cycles apparent during the last glacial as interstadial/glacial shifts. These are reflected in Monterey pine (*Pinus radiata*) population dynamics in the late Quaternary (Millar, 1999). In contrast to the oaks, the coastal closed cone pines were common during the transitions between the glacial/interglacial shifts and during interstadials (Heusser and Sirocko, 1997).

2.2. Century to millennial cycles

Climatic periods identified in the late Pleistocene, such as the Younger Dryas, Heinrich events (Heinrich, 1988), and Dansgaard/Oeschger interstadials (Dansgaard et al., 1993), had been thought to be unique extreme climatic events. The Younger Dryas resulted in a retreat in the early Holocene northward advance of *Quercus* species in western Europe (Brewer et al., 2002). In the Late Glacial, Heinrich events, extreme cold episodes, resulted in opposing cycles of *Pinus* and *Quercus* in Florida, USA (Grimm et al., 1993), whereby the former species was common during the cooler, wetter events and the latter common in dry. These events have recently been identified as part of pervasive, regular modes, called Bond cycles (Bond et al., 1997) with periods ranging 1350–1550 years and are now thought to be driven by solar variability (Bond et al., 2001). Temperature changes have been greater than 8 °C, occurring over a decade. Although these changes were originally thought greatest during glacial periods, this interpretation has been recently questioned (Bond et al., 2002).

The effects on vegetation of these century to millennial climatic oscillations are illustrated by late Pleistocene and Holocene vegetation dynamics in the Great Basin (GB) of the USA (R. Tausch, adapted from: Wigand et al., 1995; Tausch et al., 2004), partitioned into nine periods: (1) Late Pleistocene (>11,500 years before present (yBP)). Semi-arid woodlands of limber (*P. flexilis*), bristlecone (*P. longaeva*), and whitebark pines (*P. albicaulis*) were 1000 m lower than present in elevation and piñon pine (*P. monophylla*) was near Las Vegas, NV, and to the south. Western (*Juniperus occidentalis*) and Utah (*J. osteosperma*) junipers were in scattered locations. (2) Early Holocene (11,500–8000 yBP). In southern Nevada, piñon-juniper woodlands replaced limber pine at intermediate elevations; this was the beginning of the northern migration of piñon and expansion of juniper. (3) Mid-Holocene Warm Period (8000–5500 yBP). This was the warmest part of the Holocene. Piñon-juniper woodlands were 300–500 m higher than today and some species were pushed off the tops of lower mountains (e.g., *Abies lasiocarpa* was extirpated from the GB). (4) Transition period (5500–4500 yBP). There was a gradual increase in precipitation. Piñon-juniper moved downward in elevation and northward into the GB; western juniper arrives in NE California and eastern Oregon. (5) Neoglacial (Neopluvial) (4500–2500 yBP). The climate was much cooler and wetter than that of the mid-Holocene. There was a lowering of upper tree lines, an increase of woodlands at mid to lower elevations; and a reduction of desert shrub vegetation. Western juniper continues its expansion into the northern GB. (6) Post-Neoglacial drought (2500–1300 yBP). There was a significant drop in precipitation, a decrease in woodlands, and increasing dominance of desert shrubs. (7)

Medieval Warm Anomaly (1300–900 yBP). Precipitation increased and shifted to the greater proportion coming in late spring and early summer, resulting in an increase in the grasses, a re-expansion of the woodlands, and a northward migration of *P. monophylla*. (8) Transitional dry period (900–550 yBP). Winters were dry, with lowered temperatures. Grass and tree dominance decreased and shrubs increased. This period and the late Medieval Warm were also one of two century-scale droughts in California (Stine, 1994). (9) Little Ice Age (LIA) (550–150 yBP). The climate was much cooler and wetter; fire frequencies were much higher than today. There were the lowest tree lines since the early Holocene and there was a re-expansion of the piñon-juniper woodlands, which were more open than today.

These vegetation dynamics reflect the steep environmental gradients and the diversity of landforms in the Great Basin. Similar patterns of significant and abrupt vegetation dynamics have been shown in the USA in the central west slope of the Sierra Nevada, CA (Anderson and Smith, 1994) and the Pacific Northwest (Barnosky et al., 1987), the eastern North America (Bennett, 1993; Graumlich and Davis, 1993), and Europe (Huntley, 1990; Tzedakis and Bennett, 1995; Carrion et al., 2001), although the actual expression of climate may differ among the regions. In total, this evidence demonstrates that populations experienced significant changes as a result of these higher frequency climatic fluctuations.

2.3. Interannual to decadal cycles

A well-known interannual cycle is the El Niño/Southern Oscillation, which has periods of extreme events every 3–6 years. In North America, positive phases of this cycle, El Niño, are characterized by warm, wet winters in the southwest and cool and dry in the northwest; negative phases, La Niña are the converse. A recently described interdecadal cycle, the Pacific Decadal Oscillation (PDO), is a northern Pacific Ocean circulation pattern with a period of 40–60 years (Mantua et al., 1997). Positive phases of this cycle enhance El Niño events and negative phases enhance La Niña events. Although the PDO is thought to primarily affect the northern Pacific Coast, cycles of PDO periodicity have been detected in tree-ring time series in Southern and Baja California (Biondi et al., 2001) and in the Rocky Mountains to the north and east (Gray et al., 2003).

We illustrate climatic influences at the interannual to decadal scale with a study of whitebark (*P. albicaulis*) and lodgepole pine (*P. contorta*) invasions into formerly persistent snowfields and invasions by subalpine *P. contorta* into upper montane meadows in the eastern Sierra Nevada (Millar et al., 2004). Trees were sampled on line transects into the center of each snowfield or meadow, and tree ages determined by ring counts and by internode counts. In the snowfield invasions, tree ages gradually decreased from the forest edge to the center of the snowfield, suggesting a relatively continuous expansion into sectors that melt earlier into the growing season (Millar et al., 2004). Ages at the forest border ranged between 30 and over 300 years, whereas ages near the center of the snowfield were often less than 25 years. The rate of snowfield invasion was not constant, however, but corresponded to multidecadal trends in minimum temperature. In contrast to the snowfields, meadow invasion occurrence was in a single dominant pulse from 1945 to 1976 at all sites, regardless of local environmental conditions or land-use history. Tree age also decreased rapidly from the forest border and remained relatively constant to the center of the meadow. PDO was a dominant factor in statistical modeling of climate against tree invasion and significant interactions of PDO with minimum temperature and yearly precipitation described episodic invasions. Thus the tempo of plant growth and population recruitment at these scales are modulated by these higher frequency events.

"This is déjà vu all over again..."

(Yogi Berra)

While climatic events are often described as cyclic, their periodicities range in length. Moreover, combined cycles at different time scales result in a complex composite time series so that warm or cold phases in each cycle are not analogous to the previous events, as indicated by the examples above. Species dynamically track these climatic cycles in multiple ways (Tausch et al., 1993; Davis and Shaw, 2001). The rapid northward range expansion of species following deglaciation in the Northern Hemisphere is well known and supported by the paleohistorical record in the eastern USA (but see Clark, this volume) and in Europe (Hewitt, 1999), and is also illustrated by the

northward expansion of *P. monophylla* and *P. edulis*, the single leaf and Colorado piñons, and *P. ponderosa* var. *scopulorum* (ponderosa pine) in the West. However, accumulated data have shown that species in the western USA have shifted little in latitude. So in contrast to the Rocky Mountain race, the Pacific race of ponderosa pine has merely shifted in elevation (Anderson, 1989). Some species, like limber pine, have contracted in extent in the GB since the beginning of the Holocene, retreating into subalpine refugia, whereas others, like Utah juniper, have undergone range expansion and continues to expand (Miller and Tausch, 2001; Lyford et al., 2004). A similar picture is given for the Sierra Nevada by Millar and Woolfenden (1999a), who showed that species diversity has remained relatively unchanged over the Quaternary, excepting the extirpation of *Picea engelmannii*.

A theoretical model behind the individualistic responses to climatic changes that we describe above has been proposed in Jackson and Overpeck (2000) (JO). The potential niche space of a species at any particular point of time, illustrated in Thompson et al. (1999), is defined in JO as the intersection of the realized climate space and the fundamental niche space in the overall environmental hyperspace, thus determining whether a species is widespread or rare at any given point in time. These fundamental niches are indicated in the paleohistorical records for species. However, because of geographic heterogeneity and non-analogous climates, current niche spaces can neither fully explain those of past populations nor predict those of future ones (Jackson and Overpeck, 2000).

2.4. Genetic consequences of climatic variability

The evolutionary impact of Milankovich cycles has been reviewed in Bennett (1990) and Hewitt (1996). Bennett (1990) argues that these relatively frequent climatic reversals prevent macroevolutionary change, except for parapatric speciation, and that adaptations developed over stable climatic periods will be lost under changed environments. Jansson and Dynesius (2002) extend these issues further, concluding that high, orbitally forced range dynamics (ORD) result in low macroevolutionary divergence, low genetic divergence within species and subspecies, coarse geographic subdivision and large ranges, and individuals with high vagility (dispersal) and low specialization. Critchfield (1984b) lists examples from North American conifers on the impacts of Milakovich cycles on range-wide variation, focusing primarily on effects since the last glacial termination. In some cases, variation has decreased, in others transitory races or subspecies have emerged, or variation has increased through the formation of hybrid zones. In one case, a species went extinct: a large-coned relative of white spruce in the eastern USA. In contrast, an apparent relative of ponderosa pine, Washoe pine (*P. washoensis*) may have been widespread in the last glacial, but is now limited to a few high elevation sites and may be on its way to extinction, as most of these populations are demographically restricted to old-age classes with little recruitment (Critchfield, 1984a; but see Rehfeldt, 1999). Quaternary population dynamics of the coastal California closed-cone pines (Millar, 1999), noted above, suggest a non-equilibrium or intermediate metapopulation structure (Harrison and Hastings, 1996) over the larger temporal scale, supported by high interpopulation genetic differences (Millar et al., 1988).

The genetic consequences of century-to-millennial cycles (Bond and sub-Milankovich) have received far less attention. Bennett and others, focusing on the consequences of ORD, have asserted that specific adaptations are lost and one multi-purpose genotype evolves. However, Davis and Shaw (2001) and Pease et al. (1989) (PLB) argue that responses to higher frequency climatic variation do require adaptation. PLB used a habitat-based model to assess the contributions of adaptation and dispersal for a population to respond to a changing environment. Model results show that the greater the genetic variance in a population, the more the population is able to adapt to environmental change. But also, greater genetic variation will increase the lag between the current position in an environmental gradient and its optimal position, because the greater genetic variation results in a higher proportion of individuals that are adapted to the changed environment. The model also shows that higher dispersal rates allow the population to find suitable habitats. In their own review of the paleoclimatic records, they note that a frequently changing climate results in constantly shifting mosaics. So, as with the Red Queen, populations in regions of climatic change will be constantly catching-up, a notion that Namkoong (1979, p. 312) has long recognized, and

lends support to the concept of the non-optimality of local populations (Namkoong, 1969).

PLB assume a constant rate of change in space and time. But as we have shown, climatic change is not constant and environments are spatially heterogeneous. Extending the PLB model to include the interaction between quantitative genetic variation and population density, García-Ramos and Rodríguez (2002) (GR) examined the speed of invasion of a population in response to climatic change. Model analyses showed that spatial variation among ecological niches slowed invasion rates. Moreover, adaptation lagged population establishment by a few generations as a consequence of spatial heterogeneity and random dispersal. The interaction of this landscape heterogeneity, long-distance dispersal, and climatic variation is illustrated by the post-glacial spread of Utah juniper in Wyoming, reconstructed from a high-density network of woodrat (*Neotoma* spp.) midden records (Lyford et al., 2004). These data show dispersal events of 10–100 km, even though the species is dispersed by rodents. Such long-distance dispersal was also shown in *Pinus edulis* (Betancourt et al., 1991). The rate and extent of population coalescence from these dispersals were modulated by interannual to millennial climatic variability. Moreover, a spatially explicit habitat model indicates existing suitable habitats for Utah juniper that are not yet occupied, indicating further expansion potential. This pattern of expansion roughly fits a model of interacting particle systems (percolation) rather than the popular models of traveling waves (Durrett and Levin, 1994; Hastings, 1996). For plants, long-distance seed dispersal allows populations to find suitable habitats (although extended seed senescence is another way for plant species to cope with unfavorable environments). However, random dispersal diminishes adaptation to local environments and thus moves populations away from their adaptive optimum along an environmental gradient (PLB).

The above results point to a contextual paradox in forest genetics. Both direct and indirect estimators indicate that pollen-mediated gene flow is high (Muona, 1990; Smith et al., 1990; Adams, 1992; Ellstrand, 1992). This being the case, how can there be strong adaptation, even in traits with high heritability and under strong selection (Ellstrand, 1992; García-Ramos and Kirkpatrick, 1997)? However, most direct estimates are based on **census** numbers of males—results from recent models of mating systems analysis (Ritland, 1989) and gene flow (Smouse et al., 2001) indicate much smaller numbers of **effective** males (Muona et al., 1991; Sork et al., 2002). So these results and those from the Adams' model (Burczyk et al., 1995) suggest that the mating neighborhood is small and limited, although a small proportion of pollen can come from distant individuals (reviewed in Smouse and Sork, this volume). Still, the debate on this issue continues (Koenig and Ashley, 2003).

The observed cyclic population contractions, expansions, and migrations, coupled with theoretical models, then indicate that seed-mediated gene flow (i.e., migration) is important in responding to climatic changes. So the absence of isolation by distance shown in many studies may be more the consequence of cyclic, climatically driven, seed dispersal and much less by pollen dispersal. Consequently, populations may be of recent origin (Slatkin, 1993) or relationships among populations might be highly reticulate. However, hypotheses such as these are highly resistant to confirmation (Sober, 1993; Weir, 1996, p. 183). Simulations, though, if properly done (Cockerham and Weir, 1993, p. 863), can indicate whether factors such as long-distance dispersal will result in hypothesized genetic structuring. With respect to the effect of seed dispersal on genetic structures, Austerlitz and Garnier-Géré (2003) examined the effects of short- and long-distance seed dispersal and pollination on genetic diversity and differentiation. Their results, simulated over 10,000 years, indicated that long-distance dispersal will increase among population differences, in contrast to our expectation. However, their results do not fit most observed data: the lowest final value for the high dispersal model, $Fst = 0.21$, was significantly different ($p < 10^{-9}$) from the average for angiosperms, $\hat{G}st = 0.10$, from Hamrick et al. (1992); the value for low seed dispersal/high pollen dispersal model, $Fst = 0.065$, was significantly lower ($P < 0.01$) than that of the mean value for gymnosperms, $\hat{G}st = 0.073$. There are additional limitations: (1) the simulation was done on a one-dimensional landscape, whereas Austerlitz et al. (2000) show that the rate of increase in Fst will be attenuated in a two-dimensional model. (2) A uniform environment is assumed—an environmental gradient and environmental heterogeneity will also slow the rate

of colonization (García-Ramos and Rodríguez, 2002). (3) Decadal- to millennial-scale climatic cycles will affect the pace of recruitment and population expansion, as we note in examples above. So expanded conditions in such simulations are needed.

Repeated extirpations and expansions or migrations would result in variegated genetic structures, depending on local persistence of populations (PLB). For example, in a comparison between krummholz (prostrate) and upright forms of whitebark pine, $\hat{F}_{st}$, estimated by θ (Weir, 1996), between growth forms ranged between 0.052 and 0.062 over three sites in the eastern Sierra Nevada, CA (Rogers et al., 1999), differences that are very high, considering that the populations were only about 100 m apart. Krummholz patches in this species are highly persistent because their ability to propagate by layering, with some living for over 1500 years (King and Graumlich, 1998), whereas ages of the nearby upright clusters were less than 80 years. The demographic structures of the two growth forms indicate that the krummholz patches persisted during the Little Ice Age, whereas the upright forms did not and are recent migrants. Thus the two growth forms have likely originated from different source populations.

The models reviewed above also suggest that climatic variability contributes to the maintenance of quantitative genetic variability in populations. Environmental variation has been considered a potential contributor (Barton and Turelli, 1989; Gillespie, 1991), although the temporal extent considered was small. Recent analyses assessed the effects of cyclic environments on genetic variation and show that climatic influences are not simple (Bürger and Gimelfarb, 2002): in the absence of mutation, both random and periodic fluctuations in climates degrade both genetic variance and average fitness as the period of the environmental fluctuation increases. However, this analysis excludes genotype-by-environment interaction (G × E), which will maintain genetic variation in the absence of mutation (Gillespie and Turelli, 1989). Although the contribution of G × E to the maintenance of genetic variation is difficult to show experimentally (Barton and Turelli, 1989), as we illustrate below, well-constructed common garden studies show G × E is often substantial over diverse environments.

As the model of PLB predicts, adaptation in populations will lag climatic change. In common-garden provenance tests, trait maxima are often found in populations lower in latitude or elevation than that of the test locations (reviewed in Wright, 1973, 1976; Matyas, 1996), suggesting such a lag in source population response to 20th century warming. However, most of these studies tested populations in few sites over environmental gradients. A notable exception is Rehfeldt (1999) (R99), who present 20-year trait responses of 120 British Columbian lodgepole pine populations, planted over 60 sites. Results presented are a demonstration of Pease et al. (1989, p. 1660), although this may not be immediately apparent. Specifically, PLB represent the adaptive surface as the probability density of mean fitness of a given population along an environmental gradient. So if one moves a population along that gradient, fewer genotypes will give maximal response, resulting in the norms of reaction shown in Fig. 1, adapted from Rehfeldt et al. (2001, p. 362), and in Rehfeldt et al. (1999, p. 387); the area under each curve in Fig. 1 represents the niche breadth under the PLB model for each population along the environmental gradient. Fig. 1 also illustrates the lag in population optima along a temperature gradient. The solid-lined arrow indicates the height maximum of a population from a location with low annual temperature. At that location, however, a population from a warmer location (and presumably lower in latitude) is maximal, indicated by

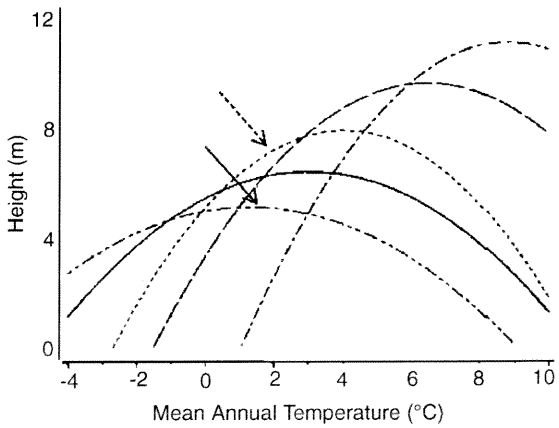

Fig. 1. Predicted norms of reactions in height for five *Pinus contorta* populations over a temperature gradient. The solid arrow indicates the maximal response of one population; the dotted arrow indicates the population with the maximal response at that location along the temperature gradient. Adapted from Rehfeldt et al. (2001).

the dashed line arrow. This difference between the maxima of the local and maximal population diminishes to zero as one moves along the gradient to warmer temperatures. A further notable feature of these norms of reactions is that they illustrate the inseparability of genotype and environment (Gregorius and Namkoong, 1986, 1987), also a consequence of the PLB and García-Ramos and Kirkpatrick (1997) models.

The approaches taken by R99 and R01 are innovative. However, a number of alternative and, for us, informative approaches can be taken. First, rather than the single-variate, second-order equations used in R99, two- or three-variate trend surface models may show different optima (maxima/minima) (Box et al., 1978, pp. 510–513) and would be more representative of the Hutchinsonian hyperspace that R99 reference frequently. Secondly as R99 note, alternative models, such as the logistic equation, $y = a/[1 + e^{b-cx}]$ (Baker, 1988, pp. 500–502), may show differing maxima or minima than in R99. Finally, rather than independent estimates of demographic consequences of climate change made in R01, these can be jointly estimated, using a combination of adaptations of the PLB and later models and density-dependent modifications of stage-based projection matrices over time (Caswell, 1989) or by individual-based modeling. An important issue to raise in these models is that the younger age classes may be more responsive to selection than older ones (Namkoong et al., 1972; Namkoong and Conkle, 1976). This is supported by Lloyd (1997), who found that adult mortality in foxtail pine (*P. balfouriana*) was unaffected by climate, although extreme climatic events can affect adult mortality (Lloyd and Graumlich, 1997), whereas recruitment and density did respond to climate. So the models used in R99 and R01 and resulting projections are dependent on their validity and on the assumptions made. Nonetheless, the data presented in R99 and R01 are significant in that they form the basis of the role of genetic variation in modeling the response of populations to climatic change and they raise important issues.

3. Discussion and conclusions

Quaternary vegetation history indicates that populations are under non-equilibrium states with cyclic climatic variability under differing scales. With continual climatic change, populations of tree species, like the Red Queen (or Court Jester, Barnosky, 2001), are constantly chasing their adaptive optima in environments. Moreover, repeated range contractions, expansions, and migration indicate that seed dispersal is an important, sometimes dominant, component of gene flow.

The contextual frameworks we place ourselves in will affect the analytical methods we use (Kuhn, 1970; Ruse, 1999). So how we view the extent of climatic variability and its effect on populations will affect both our choice of genetic statistics and their interpretation. If, for example, we assume stable, though randomly variable environments over many generations, one can make a strong case for equilibrium relationships among a finite set of populations. Under such assumptions *Gst* (Nei, 1973), which is dependant on the number of sample populations and is a fixed-effect estimator (Cockerham and Weir, 1993), can be used. However, with cyclic climatic variability and consequent range expansions, contractions, and migration, populations can be considered random effects in time—and space—so Weir's θ would be more appropriate (Weir, 1996, pp. 161–162). Such considerations also affect the choice of genetic distances, although the choice is less clear. The highly popular Nei's (1972) distance, which assumes equilibrium conditions in drift and mutation and assumes constant rates of evolution, is appropriate in conditions of long-term evolution. But it is not appropriate in situations of scant mutation or nearly pure drift (Weir, 1996, p. 197), where geometric distances like Cavalli-Sforza and Edwards (1967) or others like, co-ancestry, or θ (Reynolds et al., 1983; Weir, 1996), are well behaved. The general rule is to use distances like co-ancestry where populations have diverged by four generations or less (Weir, 1996). The Mahalanobis distance might be desirable as a general purpose measure, as it is superficially assumption-free.

Our views of population histories also affect population sampling designs and our choice of analytical methods. As Le Corre et al. (1998) argue, dense, range-wide sampling, as in Petit et al. (1997), are needed to make meaningful historical inferences from data. Similarly, a representative network of test environments is needed for useful projections of climatic changes on quantitative traits, as Namkoong (2001) also notes. With regard to analytical methods,

bifurcating trees have been the most favored and have recently been applied to infer post-glacial histories (e.g., see the detailed work in Petit et al., 2002a,b). But do two-dimensional bifurcating trees fully describe population histories? The combination of coalescence theory with network models (Posada and Crandall, 2001) provides opportunities for making reticulate reconstructions of population histories, giving trees in three or more dimensions that can be tested against fossil records (Cruzan and Templeton, 2000). We wonder, though, how deep in time such reticula can accurately represent. Higher-dimensional methods may be more informative, with such geostatistical methods as kriging and variograms (Le Corre et al., 1998). Similarly, Wartenberg (1985) makes a case for applying canonical trend surface and redundancy analyses to the interpretation of complex population histories. Such issues should be revisited.

Genetic theory can also inform our interpretations of past climates (Pease et al., 1989, p. 1662). For example, tree-ring time series, referred to as chronologies, have commonly been used to reconstruct past climates (Hughes and Brown, 1992; Hughes and Graumlich, 1996; Briffa, 2000). The common understanding amongst dendrochronologists is that growth in the upper-forest tree line responds to temperature, which is limiting in this environment, while growth in the lower responds to precipitation, which is limiting there (Hughes and Graumlich, 1996; Briffa, 2000). They further assume that populations are genetically identical and differences in response are attributed to phenotypic plasticity. What has not been considered is the potential that selection contributes to these differences. Climatic reconstructions from these time series entail a detailed screening process of monthly, sometimes daily, weather records from nearby weather stations to develop a model combining precipitation and temperature that is maximally correlated with the tree ring-width data (e.g., Graumlich, 1993). As the contemporary weather station records rarely extend further back than 1900 CE, nearly all the trees representing the late part of the composite chronology are living. In contrast, the further one goes back in time in the chronology, the greater is the proportion of dead trees that constitutes the chronology; if the chronology is long enough, its earliest portion is entirely computed from dead wood series. Moreover, in many cases, there are no living trees currently in the vicinity of the dead wood; often this dead wood is at elevations o aspects different than that of the contemporary liv stands. So, as geneticists, we question whether gen frequencies in trees of stands represented by dea wood, when living, were the same as those in curren live stands. Thus we wonder whether reconstruction based on current live trees fully represent growt responses in trees that are now dead. Our doubt are reinforced by our current work (unpublished) o among- and within-site synchrony among sites in th eastern Sierra Nevada and Great Basin. At these sites we sampled cores or cross-sections of 10 to over 10 trees, and from tree-ring measurements, have developed master (composite) chronologies. First, we find decrease in synchrony by geographic distance, a measured by the correlation of tree-ring width between sites, among the master chronologies. Moreover, looking at the correlation of tree-ring series o individual trees at one site against a master chronolog at another site, we see that some trees are highl synchronous against the master, whereas other tree are wholly uncorrelated. In other cases, portions of time series for a tree will be correlated with the maste of another site and uncorrelated in other portions. Moreover, even at sites where most trees are highl synchronous with their own master chronology, there are some live trees that are wholly not cross-datable against their peers. Often all these observations are attributed to microsite differences. Instead, these differences may also reflect genetic diversity. So even though extreme events are shown in region-wide tree-ring records, as in the late 16th century mega drought in the western USA (Gray et al., 2003), genetic changes over time in tree populations forming the record may affect interannual responses in a time series to climate and thus dampen low-frequency variation in the tree-ring record.

"...some rise, some fall, some climb..."
(From "Terrapin Station" by J. Garcia and R. Hunter)

The developing paleoclimatic record suggests that climatic changes, even at sub-multimillennial frequencies, have been considerable. Such variation should affect the way we view population histories, as well as the way we view genetic and phenotypic data. As most species have survived past rapid climatic changes (Alley et al., 2003), there must be sufficient plasticity in individuals to tolerate these change and

enough genetic variation in populations to respond to such changes (Jackson and Overpeck, 2000). But because there have been substantial anthropogenic changes of landscapes, the prospect of future climatic changes raises important issues in biological conservation (Davis and Shaw, 2001).

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References

Adam, D.P., 1988. Palynology of two upper Quaternary cores from Clear Lake, Lake County, California. USGS. Professional Paper 1363.

Adams, W.T., 1992. Gene dispersal within forest tree populations. New Forests 6, 217–240.

Alley, R.B., Marotzke, J., Nordhaus, W.D., Overpeck, J.T., Peteet, D.M., Pielke Jr., R.A., Pierrehumbert, R.T., Rhines, P.B., Stocker, T.F., Talley, L.D., Wallace, J.M., 2003. Abrupt climate change. Science 299, 2005–2010.

Anderson, R.S., 1989. Development of the Southwestern ponderosa pine forests: What do we really know? In: Multiresource Management of Ponderosa Pine Forests, Flagstaff, AZ, November 14–16, 1989. USDA Forest Service, Gen. Tech. Report RM-185, pp. 15–22.

Anderson, R.S., Smith, S.J., 1994. Paleoclimatic interpretations of meadow sediment and pollen stratigraphies from California. Geology 22, 723–726.

Austerlitz, F., Mariette, S., Machon, N., Gouyon, P.H., Godelle, B., 2000. Effects of colonization processes on genetic diversity: differences between annual plants and tree species. Genetics 154, 1309–1321.

Austerlitz, F., Garnier-Géré, P.H., 2003. Modelling the impact of colonisation on genetic diversity and differentiation of forest trees: interaction of life cycle. Heredity 90, 282–290.

Baker, R.J., 1988. Differential response to environmental stress. In: Weir, B.S., Eisen, E.J., Goodman, M.M., Namkoong, G. (Eds.), Proceedings of the Second International Conference Quant. Genetics. Sinauer Assoc., Inc., Sunderland, MA, pp. 492–504.

Barnosky, A.D., 2001. Distinguishing the effects of the Red Queen and Court Jester on Meiocene mammal evolution in the northern Rocky Mountains. J. Vertebr. Paleontol. 21, 172–185.

Barnosky, C.W., Anderson, P.M., Bartlein, P.J., 1987. The northwestern US during deglaciation; vegetational history and paleoclimatic implications. In: Ruddiman, W.F., Wright, H.E. (Eds.), North America and Adjacent Oceans During the Last Deglaciation. Geological Society of America, Boulder, CO, pp. 289–321.

Barton, N.H., Turelli, M., 1989. Evolutionary quantitative genetics: how little do we know? Annu. Rev. Genet. 23, 337–370.

Bennett, K.D., 1993. Holocene forest dynamics with respect to southern Ontario. Rev. Palaeobot. Palynol. 79, 69–81.

Bennett, W.D., 1990. Milankovich cycles and their effects on species in ecological and evolutionary time. Paleobiology 16, 11–21.

Betancourt, J.L., Schuster, W.S., Mitton, J.B., Anderson, R.S., 1991. Fossil and genetic history of a pinyon pine (*Pinus edulis*) isolate. Ecology 72, 1685–1697.

Biondi, F., Gershunov, A., Cayan, D.R., 2001. North Pacific decadal climate variability since. J. Clim. 14, 5–10.

Bond, G., Showers, W., Cheseby, M., Lotti, R., Almasi, P., de Menocal, P., Priore, P., Cullen, H., Hajdas, I., Bonani, G., 1997. A pervasive millennial-scale cycle in North Atlantic Holocene and glacial climates. Science 278, 1257–1266.

Bond, G., Kromer, B., Beer, J., Muscheler, R., Evans, M.N., Showers, W., Hoffmann, S., LottiBond, R., Hajdas, I., Bonani, G., 2001. Persistent solar influence on North Atlantic climate during the Holocene. Science 294, 2130–2136.

Bond, G.C., Dwyer, G.S., Bausch, H.A., 2002. The Big Chills. Eos Trans. AGU 83(47), Fall Meet. Suppl., Abstract PP71C-13.

Box, G.E.P., Hunter, W.G., Hunter, J.S., 1978. Statistics for Experimenters. An Introduction to Design, Data Analysis, and Model Building. J. Wiley & Sons, New York.

Brewer, S., Cheddadi, R., de Beaulieu, J.L., Reille, M., 2002. The spread of deciduous *Quercus* throughout Europe since the last glacial period. For. Ecol. Manage. 156, 27–48.

Briffa, K.R., 2000. Annual climate variability in the Holocene: interpreting the message of ancient trees. Quarter. Sci. Rev. 19, 87–105.

Burczyk, J., Adams, W.T., Shimizu, J.Y., 1995. Mating patterns and pollen dispersal in a natural knobcome pine (*Pinus attenuata* Lemmon.) stand. Heredity 77, 251–260.

Bürger, R., Gimelfarb, A., 2002. Fluctuating environments and the role of mutation in maintaining quantitative genetic variation. Genet. Res. 80, 31–46.

Carrion, J.S., Andrade, A., Bennett, K.D., Navarro, C., Munuera, M., 2001. Crossing forest thresholds: inertia and collapse in a Holocene sequence from south-central Spain. Holocene 11, 635–653.

Caswell, H., 1989. Matrix Population Models: Construction, Analysis, and Interpretation. Sinauer, Sunderland, MA.

Cavalli-Sforza, L.L., Edwards, A.W.F., 1967. Phylogenetic analysis: models and estimation procedures. Evolution 21, 550–570.

Cockerham, C.C., Weir, B.S., 1993. Estimation of gene flow from *F*-statistics. Evolution 47, 855–863.

Critchfield, W.B., 1984a. Crossability and relationships of Washoe pine. Madroño 31, 144–170.

Critchfield, W.B., 1984b. Impact of the Pleistocene on the genetic structure of North American conifers. In: Lanner, R.M. (Ed),

Proceedings of the Eighth North American Forest Biology Workshop, Logan, UT. Utah State University, Logan, UT, pp. 70–118.

Crow, J.F., Kimura, M., 1970. An Introduction to Population Genetics Theory. Alpha Editions, Edina, MN.

Cruzan, M.B., Templeton, A.R., 2000. Paleoecology and coalescence: phylogeographic analysis of hypotheses from the fossil record. Trends Ecol. Evol. 15, 491–496.

Dansgaard, W., Johnsen, S.J., Clausen, H.B., Dahljensen, D., Gundestrup, N., Hammer, C., Hvidberg, C., Steffensen, J., Sveinbjornsdottir, A., Jouzel, J., Bond, G., 1993. Evidence for general instability of climate from a 250-kyr ice-core record. Nature 364, 218–220.

Davis, M.B., Shaw, R.G., 2001. Range shifts and adaptive responses to Quaternary climate change. Science 292, 673–679.

Durrett, R., Levin, S.A., 1994. Stochastic spatial models—a user's guide to ecological applications. Philos. Trans. R. Soc. London Ser. B: Biol. Sci. 343, 329–350.

Ellstrand, N.C., 1992. Gene flow among seed plant populations. New Forests 6, 241–256.

Epperson, B.K., 1995. Spatial structure of two-locus genotypes under isolation by distance. Genetics 140, 365–375.

García-Ramos, G., Kirkpatrick, M., 1997. Genetic models of adaptation and gene flow in peripheral populations. Evolution 51, 21–28.

García-Ramos, G., Rodríguez, D., 2002. Evolutionary speed of species invasions. Evolution 56, 661–668.

Gillespie, J.H., Turelli, M., 1989. Genotype–environment interactions and the maintenance of polygenic variation. Genetics 121, 129–138.

Gillespie, J.H., 1991. The Causes of Molecular Evolution. Oxford University Press, Oxford.

Gilpin, M., 1991. The genetic effective size of a metapopulation. Biol. J. Linnean Soc. 42, 165–175.

Graumlich, L.J., 1993. A 1000-year record of temperature and precipitation in the Sierra-Nevada. Quarter. Res. 39, 249–255.

Graumlich, L.J., Davis, M.B., 1993. Holocene variation in spatial scales of vegetation pattern in the upper Great Lakes. Ecology 74, 826–839.

Gray, S.T., Betancourt, J.L., Fastie, C.L., Jackson, S.T., 2003. Patterns and sources of multidecadal oscillations in drought-sensitive tree-ring records from the central and southern Rocky Mountains. Geophys. Res. Lett. 30, 1316–1319.

Gregorius, H.-R., Namkoong, G., 1986. Joint analysis of genotypic and environmental effects. Theoret. Appl. Genet. 72, 413–422.

Gregorius, H.-R., Namkoong, G., 1987. Resolving the dilemmas of interaction, separability, and additivity. Math. Biosci. 85, 51–69.

Grimm, E.C., Jacobson, G.L., Watts, W.A., Hansen, B.C.S., Maasch, K.A., 1993. A 50,000 year record of climate oscillations from Florida and its temporal correlation with the Heinrich events. Science 261, 198–200.

Hamrick, J.L., Godt, M.J.W., Sherman-Broyles, S.L., 1992. Factors influencing levels of genetic diversity in woody plant species. New Forests 6, 95–124.

Harrison, S., Hastings, A., 1996. Genetic and evolutionary consequences of metapopulation structure. Trends Ecol. Evol. 11, 180–183.

Hastings, A., 1996. Models of spatial spread—is the theor complete? Ecology 77, 1675–1679.

Heinrich, H., 1988. Origin and consequences of cyclic ice rafting i the northeast Atlantic Ocean during the past 130,000 years Quarter. Res. 29, 142–152.

Heusser, L., 1995. Pollen stratigraphy and paleoecologic inter pretation of the 160 k.y. record from Santa Barbara Basin, Hol 893A. In: Lyle, M. (Ed.), Proceedings of the Ocean Drillin Program, Scientific Results, vol. 146, Pt. 2, College Station TX. Ocean Drilling Program, pp. 265–277.

Heusser, L.E., Sirocko, F., 1997. Millennial pulsing of environ mental change in southern California from the past 24 k.y.: record of the Indo-Pacific ENSO events? Geology 25, 243–246

Hewitt, G.M., 1996. Some genetic consequences of ice ages and their role in divergence and speciation. Biol. J. Linn. 58 247–276.

Hewitt, G.M., 1999. Post-glacial re-colonization of European biota Biol. J. Linnean Soc. 68, 87–112.

Hughes, M.H., Brown, P.M., 1992. Drought frequency in centra California since 101 B.C. recorded in giant sequoia tree rings Clim. Dyn. 6, 161–167.

Hughes, M.K., Graumlich, L.J., 1996. Multilmillennial dendrocli matic studies from the western United States. In: Jones, P.D. Bradley, R.S. (Eds.), Climatic Variations and Forcing Mechanisms of the Last 2000 Years. Springer-Verlag, Berlin, pp. 109–124.

Huntley, B., 1990. European post-glacial forests: compositiona changes in response to climate change. J. Veg. Sci. 1, 507–518

Jackson, S.T., Overpeck, J.T., 2000. Responses of plant populations and communities to environmental changes of the late Quaternary. Paleobiology 25, 194–220.

Jansson, R., Dynesius, M., 2002. The fate of clades in a world of recurrent climatic change: Milankovitch oscillations and evolution. Annu. Rev. Ecol. Syst. 33, 741–777.

King, J.C., Graumlich, L.J. 1998. Stem-layering and gene longevity in whitebark pine (*Pinus albicaulis*). Laboratory of Tree Ring Research, University of Arizona, Tucson, AZ.

Koenig, W.D., Ashley, M.V., 2003. Is pollen limited? The answer is blowin' in the wind. Trends Ecol. Evol. 18, 157–159.

Kuhn, T.S., 1970. The Structure of Scientific Revolutions, 2nd ed., vol. 2. University of Chicago Press, Chicago, IL.

Le Corre, V., Roussel, G., Zanetto, A., Kremer, A., 1998. Geographical structure of gene diversity in *Quercus* petraea (Matt.) Liebl. III. Patterns of variation identified by geostatistical analyses. Heredity 80, 464–473.

Lloyd, A.H., 1997. Response of tree-line populations of foxtail pine (*Pinus balfouriana*) to climate variation over the last 1000 years. Can. J. Forest Res. 27, 936–942.

Lloyd, A.H., Graumlich, L.J., 1997. Holocene dynamics of treeline forests in the Sierra Nevada. Ecology 78, 1199–1210.

Lyford, M.E., Jackson, S.T., Betancourt, J.L., Gray, S.T., 2004. Influence of landscape structure and climate variability on a late Holocene plant migration. Ecol. Monogr. 73, 567–583.

Mantua, N.J., Hare, N.J., Zhang, Y., Wallace, J.M., Francis, R.C., 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bull. Am. Meteorol. Soc. 78, 1069–1079.

Matyas, C., 1996. Climatic adaptation of trees—rediscovering provenance tests. Euphytica 92, 45–54.

Milankovich, M., 1941. Canon of insolation and the ice-age problem. Royal Serbian Academy Special Publ. No. 132.

Millar, C.I., Strauss, S.H., Conkle, M.T., Westfall, R.D., 1988. Allozyme differentiation and biosystematics in the California closed-cone pines (Subsection Oocarpae Little & Critchfield, Genus *Pinus*). Syst. Bot. 13, 351–370.

Millar, C.I., 1999. Evolution and biogeography of *Pinus radiata*, with a proposed revision of its Quaternary history. NZ J. For. Sci. 29, 335–365.

Millar, C.I., Woolfenden, W.B., 1999a. Sierra Nevada forests: where did they come from? Where are they going? In: McCabe, R.E., Loos, S.E. (Eds.), Natural Resources Management: Preceptions and Realities. Trans. 64th North American Wildlife and Natural Recources Conference, Wildlife Management Institute. Washington, DC, pp. 206–236.

Millar, C.I., Woolfenden, W.B., 1999b. The role of climate change in interpreting historical variability. Ecol. Appl. 9, 1207–1216.

Millar, C.I., Westfall, R.D., Delany, D.L., King, J.C., Graumlich, L.J., 2004. Response of subalpine conifers in the Sierra Nevada, California, USA, to twentieth century warming and decadal climate variability. Arctic, Antarctic, & Alpine Research 36, 181–200.

Millar, C.I., 2004. Climate change as an ecosystem architect: implications to rare plant ecology, conservation, and restoration. In: Brooks, Melissa (Ed.) Proceedings of the Conference on Rare Plants of Northern California. Feb. 6–9, 2002, Arcata, California. California Native Plant Society, Sacramento, CA. pp. 139–157.

Miller, R.F., Tausch, R.J., 2001. The role of fire in juniper and pinyon woodlands: a descriptive analysis. In: Galley, K.E.M., Wilson, T.P. (Eds.), Proceedings of the Invasive Species Workshop: The Role of Fire in the Control and Spread of Invasive Species. Miscellaneous Publication, Tall Timbers Research Station, Tallahasse, FL, pp. 15–30.

Muona, O., 1990. Population genetics in forest tree improvement. In: Brown, A.H.D., Clegg, M.T., Kahler, A.L., Weir, B.S. (Eds.), Plant Population Genetics, Breeding, and Genetic Resources. Sinauer Associates, Inc., Sunderland, MA, pp. 282–298.

Muona, O., Moran, G.F., Bell, J.C., 1991. Hierarchical patterns of correlated mating in *Acacia melanoxylon*. Genetics 127, 619–626.

Namkoong, G., 1969. Nonoptimality of local races. In: Tenth South. For. Tree Improv. Conf., Texas For. Serv., Texas A&M University Press, College Station, TX, pp. 149–153.

Namkoong, G., Usanis, R.A., Silen, R.R., 1972. Age-related variation in genetic control of height growth in Douglas-fir. Theoret. Appl. Genet. 42, 151–159.

Namkoong, G., Conkle, M.T., 1976. Time trends in genetic control of height growth in ponderosa pine. Forest Sci. 22, 2–12.

Namkoong, G., 1979. Introduction to Quantitative Genetics in Forestry. USDA Forest Service Tech. Bull. No. 1588.

Namkoong, G., 2001. Forest genetics: pattern and complexity. Can. J. Forest Res. 31, 623–632.

Nei, M., 1972. Genetic distance between populations. Am. Nat. 106, 283–292.

Nei, M., 1973. Analysis of gene diversity in subdivided populations. Proc. Nat. Acad. Sci. USA 70, 3321–3323.

Nichols, R.A., Hewitt, G.M., 1994. The genetic consequences of long distance dispersal during colonization. Heredity 72, 312–317.

Pease, C.M., Lande, R., Bull, J.J., 1989. A model of population growth, dispersal and evolution in a changing environment. Ecology 70, 1657–1664.

Petit, R.J., Pineau, E., Demesure, B., Bacilieri, R., Ducousso, A., Kremer, A., 1997. Chloroplast DNA footprints of postglacial recolonization by oaks. Proc. Natl. Acad. Sci. USA 94, 9996–10001.

Petit, R.J., Brewer, S., Bordács, S., Burg, K., Cheddadi, R., Coart, E., Cottrell, J., Csaikl, U.M., van Dam, B., Deans, J.D., Espinel, S., Fineschi, S., Finkeldey, R., Glaz, I., Goicoechea, P.G., Jensen, J.S., König, A.O., Lowe, A.J., Madsen, S.F., Mátyás, G., Munro, R.C., Popescu, F., Slade, D., Tabbener, H., de Vries, S.G.M., Ziegenhagen, B., de Beaulieu, J.L., Kremer, A., 2002a. Identification of refugia and post-glacial colonisation routes of European white oaks based on chloroplast DNA and fossil pollen evidence. For. Ecol. Manage. 156, 49–74.

Petit, R.J., Csaikl, U.M., Bordács, S., Burg, K., Coart, E., Cottrell, J., van Dam, B., Deans, J.D., Dumolin-Lapegue, S., Fineschi, S., Finkeldey, R., Gillies, A., Glaz, I., Goicoechea, P.G., Jensen, J.S., König, A.O., Lowe, A.J., Madsen, S.F., Mátyás, G., Munro, R.C., Olalde, M., Pemonge, M.H., Popescu, F., Slade, D., Tabbener, H., Taurchini, D., de Vries, S.G.M., Ziegenhagen, B., Kremer, A., 2002b. Chloroplast DNA variation in European white oaks—phylogeography and patterns of diversity based on data from over 2600 populations. For. Ecol. Manage. 156, 5–26.

Posada, D., Crandall, K.A., 2001. Intraspecific gene geneologies: trees grafting into networks. Trends Ecol. Evol. 16, 37–45.

Rehfeldt, G.E., 1999. Systematics and genetic structure of Washoe pine: applications in conservation genetics. Silvae Genetica 48, 167–173.

Rehfeldt, G.E., Wykoff, W.R., Ying, C.C., 2001. Physiologic plasticity, evolution, and impacts of a changing climate on *Pinus contorta*. Climatic Change 50, 355–376.

Rehfeldt, G.E., Ying, C.C., Spittlehouse, D.L., Hamilton, D.A., 1999. Genetic responses to climate in *Pinus contorta*: niche breadth, climate change, and reforestation. Ecol. Monogr. 69, 375–407.

Reynolds, J., Weir, B.S., Cockerham, C.C., 1983. Estimation of the co-ancestry coefficient: Basis for a short-term genetic distance. Evolution 105, 767–779.

Ritland, K., 1989. Correlated matings in the partial selfer *Mimulus guttatus*. Evolution 43, 848–859.

Rogers, D.L., Millar, C.I., Westfall, R.D., 1999. Fine-scale genetic structure of whitebark pine (*Pinus albicaulis*): associations with watershed and growth form. Evolution 53, 74–90.

Ruse, M., 1999. Mystery of Mysteries: Is Evolution a Social Construction? Harvard University Press, Cambridge, MA.

Slatkin, M., 1993. Isolation by distance in equilibrium and non-equilibrium populations. Evolution 47, 264–279.

Smith, C.C., Hamrick, J.L., Kramer, C.L., 1990. The advantage of mast years for wind pollination. Am. Nat. 136, 154–166.

Smouse, P.E., Dyer, R.J., Westfall, R.D., Sork, V.L., 2001. Two-generation analysis of pollen flow across a landscape. I. Male gamete heterogeneity among females. Evolution 55, 260–271.

Sober, E., 1993. Philosophy of Biology. Westview Press, Boulder, CO.

Sork, V.L., Davis, F.W., Dyer, R.J., Smouse, P.E., 2002. Mating patterns in a savanna population of valley oak (*Quercus lobata*). In: Standiford, R.B., McCreary, D., Purcell, K.L. (Eds.), Proceedings of the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, USDA Forest Service Gen. Tech. Rep. PSW-GTR-184. UC Berkeley Press, Berkeley CA, pp. 427–439.

Stine, S., 1994. Extreme and persistent drought in California and Patagonia during Mediaeval time. Nature 369, 546–549.

Tausch, R.J., Nowak, C.L., Mensing, S., 2004. Climate change and associated vegetation dynamics during the Holocene: the Paleological record. In: Chambers, J.C., Miller, J.R. (Eds.), Great Basin Riparian Ecosystems: Ecology, Management and Restoration. Island Press, Covelo, CA, pp. 24–48.

Tausch, R.J., Wigand, P.E., Burkhardt, J.W., 1993. Viewpoint: plant community threshold, multiple steady states, and multiple successional pathways: legacy of the Quaternary? J. Range Manage. 46, 439–447.

Thompson, R.S., Anderson, K.H., Bartlein, P.J., 1999. Atlas of relations between climatic parameters and distributions of important trees and shrubs in North America. US Geological Survey Professional Paper 1650 A & B. http://pubs.usgs.gov/pp/1999/p1650-a/.

Tzedakis, P.C., Bennett, K.D., 1995. Interglacial vegetation succession—a view from southern Europe. Quarter. Sci. Rev 14, 967–982.

Wartenberg, D., 1985. Canonical trend surface analysis: a method for describing geographic patterns. Syst. Zool. 34, 259–279.

Weir, B.S., 1996. Genetic Data Analysis II. Sinauer Associates, Inc., Sunderland, MA.

White, J.W., Popp, T., Johnson, S.J., Masson, V., Jouzel, J., 2001. Clocking the speed of climate change: the end of the Younger Dryas as recorded by four Greenland ice cores. Abstract. In: Fall Meeting of the American Geophysical Union, San Francisco, CA, December 10–14, 2001, p. F22.

Wigand, P.E., Hemphill, M.L., Sharpe, S.S., Patra, S., 1995. Great Basin semi-arid woodland dynamics during the late Quaternary. In: Climate Change in the Four Corners and Adjacent Regions: Implications for Environmental Restoration and Land-use Planning. US Dept. Energy, Grand Junction, CO, pp. 51–70.

Wright, J.W., 1973. Genotype–environment interaction North Central United States. Forest Sci. 19, 113–123.

Wright, J.W., 1976. Introduction to Forest Genetics. Academic Press, New York.

Wright, S., 1969. Evolution and the Genetics of Populations, Vol. 2. The Theory of Gene Frequencies. University of Chicago Press, Chicago, IL.