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28

Genetic Diversity within Species

ABSTRACT

Based on our review of literature and survey of geneticists working on California taxa, we find genetic information lacking for most species in the Sierra Nevada. This situation is likely to remain in the future, with specific groups of taxa or occasional rare or high-interest species receiving specific study. Where we do have empirical information, we find few generalities emerging, except occasionally within closely related or ecologically similar taxa. Despite these difficulties in assessing genetic diversity, we direct attention to situations estimated to be most deserving of attention from a genetic standpoint.

Severe wildfire: With the significantly increased risk of severe fires currently facing the Sierra Nevada, large, stand-replacing fires present significant risks to gene pools of most middle- and low-elevation Sierran forests, with direct and indirect consequences to the genetic diversity of plants and animals that live in them.

Habitat alteration: For most taxonomic groups evaluated in the Sierra Nevada, the major threat to genetic diversity is habitat destruction, degradation, or fragmentation. Estimated effects involve not only direct losses of population-level genetic structural diversity but also changes in genetic processes (gene flow, selection), effective population sizes, and genetically based fitness traits. High-priority areas would be the foothill zone on the west slope, several of the trans-Sierran corridors (especially in the central Sierra Nevada), and scattered locations of concentrated development elsewhere.

Silviculture: Management actions that are extensive across the landscape yet intensive in manipulating individuals and populations have the greatest theoretical potential (but limited if no empirical evidence) for direct and significant genetic effects. As such, silvicultural activities, including tree improvement programs, operational forest regeneration (artificial and natural), and timber harvest, potentially affect gene pools of target species. Fortunately, tree improvement programs in the Sierra Nevada (both public and private cooperatives) have long used sophisticated and ecologically appropriate genetic diversity and genetic conservation guidelines. Similarly, in operational forest regeneration, federal, state, and local regulations regarding genetic diversity in planting mostly have high standards and are backed by a fair amount of research. Seed banks exist for public and private reforestation that maintain high standards of seed origin and genetic diversity, although exigencies presented by potentially large, severe wildfire may not be adequately met. The focus for seed banking is the commercial conifers, and only slowly has seed banking emphasized other species with storable seeds. These programs, which have histories of several decades in the Sierra Nevada, serve as models for other taxa where similar activities occur (e.g., fish stocking).

Research is inconclusive about the long-term genetic consequences of timber harvest on commercial tree species. Nevertheless, traditional silvicultural practices, which were designed primarily to maximize growth of the target species, tended to result in spatial patterns of harvest and live-tree retention that acted in concert with genetic conservation guidelines. By contrast, some new forestry practices, which combine fiber production with ecological stewardship for wildlife and nontimber species, may have potential for minor dysgenic effects on native timber species. For instance, leaving clumps of trees, especially suppressed individuals (e.g., for wildlife protection) may promote inbreeding or lowered fitness if the members of the clumps are related, as they appear to be.

Ecological restoration: Practitioners of ecological restoration have only recently become aware of genetic concerns in planting. Although many programs focus on restoring correct native species, an understanding of the appropriate genetic material within species, its origin, diversity, and collection, remains missing or rudimentary in many programs. Thus, genetic contamination problems may be more severe than if exotic species

Sierra Nevada Ecosystem Project: Final report to Congress, vol. II, Assessments and scientific basis for management options. Davis: University of California, Centers for Water and Wildland Resources, 1996.

Back to CD-ROM Table of Contents

had been planted. The significance of this genetic threat in the Sierra Nevada is lowest in projects of ecological community restoration and highest in postfire erosion control projects. Frequently these involve grass species and occasionally forb mixes. Although exotic grasses (especially rye grass) previously were used routinely, native grasses are increasingly becoming favored. There is often little understanding of the potential genetic consequences of planting seeds of native species but unknown (often commercial nursery) origins.

Fish management: Management of fish species and genetic diversity within species in the Sierra Nevada is done in a way that potentially disrupts many native gene pools. The introduction of hatchery, nonlocal, and genetically altered genetic stocks of native fish species has had the direct effect of creating conditions for intraspecific hybridization, gene contamination, and gene pool degradation. Indirectly, the introduction of exotic fishes has large effects on biodiversity through displacement of native fish species and impacts on aquatic invertebrates and amphibia, which affects gene pools through loss of populations.

Range improvement: Similar to fish management, although lesser in effect in the Sierra Nevada, is the direction and intent of range improvement projects. In past decades, range shrubs, particularly bitterbrush, were widely planted in Great Basin areas (on the border of the Sierra Nevada) to improve rangelands for cattle. Very little of the shrub germ plasm planted in the past derived from local seed zones or followed genetic diversity guidelines that maintain native genetic structure. More recently, shrubs have been planted for wildlife habitat enhancement. These are increasingly falling under seed transfer and genetic diversity guidelines, with the result that native local seeds are being collected and planted.

Exotic pathogens: Exotic pathogens create direct and indirect genetic threats in the Sierra Nevada. For example, white pine blister rust is fatal to sugar pines that carry the susceptible gene. The resistant gene exists naturally in very low frequencies in sugar pine. Although a well-funded and genetically sophisticated program exists for developing and outplanting sugar pine that is resistant to white pine blister rust, there has been limited recognition of the genetic consequences of the current federal harvest practices for the species. At present, known resistant old-growth sugar pines are not cut, but susceptible trees may be harvested, and in areas where resistance is unknown, harvest proceeds without genetic testing. The potential loss of genetic diversity, through harvest, of traits other than the resistance loci is significant. Indirect genetic effects occur when populations are so devastated as to drastically decline in size or become extirpated. An example is the exotic pathogen that moves from domestic to native bighorn sheep This pathogen causes a disease that is extremely serious and usually fatal to bighorn sheep, exterminating populations.

Taxon-specific issues: Many activities theoretically have significant genetic effects on specific taxa in the Sierra Nevada. Examples of these include the sport collecting of butterflies, the harvesting of special forest products (especially mushrooms and other fungi, ladybird beetles, lichens, etc.), the use of biocides with wide action against native insects, and forest-health practices whose goals are to reduce or eliminate populations of native insects and pathogens.

Land management: Most human-mediated (as well as natural) activities have some genetic consequences. The question is not whether we create genetic change, but which effects are significant enough to warrant altering our behavior. In general, there has been a pervasive lack of awareness of the potential genetic consequences of land management, from local practices to regional landscape plans. Genetic awareness, evaluation, prescription, mitigation, monitoring, and restoration have generally been very low in public and private management and have been concentrated in a few land-use programs (e.g., tree regeneration). Although it is broadly recognized that most management actions have effects on wildlife, there are few instances where environmental analyses—for instance in National Environmental Policy Act (NEPA) contexts—have considered genetic effects. Land-management agencies do not place geneticists broadly throughout the Sierra Nevada, and genetic knowledge usually resides centralized (e.g., with tree improvement headquarters) or within silviculture staffs, where it is focused mostly on the already established genetic management programs of commercial timber species.

What is needed is a general awareness that genetic consequences must be considered and evaluated for land-management activities in general, and a framework and strategy for doing so. It is not enough to lump these concerns under general biodiversity evaluation, since this often takes into account only immediate effects on the population or species viability of a few indicator species. This chapter proposes some management guidelines and standards for preserving and enhancing genetic diversity in the Sierra Nevada.

INTRODUCTION

Genetic diversity is not a front-page, public issue. Whereas species extinctions, loss of old-growth forests, and degradation of air and water quality are readily grasped and easily comprehended, to many people gene pool integrity remains arcane, invisible, and dismissable as academic. Yet genes are the fundamental unit of biodiversity, the raw material for evolution, and the source of the enormous variety of plants, animals, communities, and ecosystems that we seek to protect and use. Genetic variation shapes and defines individuals, populations, subspecies, species, and ultimately the kingdoms of life on earth. The gene pool of widespread species is spread throughout many populations; for a rare species it may consist of a single population. From one species to the next, the composition and structure of individual gene pools vary. Each has a unique relationship to the viability and long-term survival of the population and species.

Human actions on the landscape almost always have some genetic effect. While many changes in genetic diversity occur naturally (genetic change is the basis of evolution), human activities in the Sierra Nevada, as elsewhere, may accelerate or change the direction of evolution in undesired ways. Genetic erosion, genetic engineering, genetic contamination, and extinctions of populations and species are potential effects or sources of genetic change mediated by humans. What are the responsibilities of SNEP and of decision makers in the Sierra Nevada for addressing genetic concerns in policy development and land management? As is the case with other biodiversity issues, the main questions regarding genetic diversity are

- What important compositional, structural, and functional genetic diversity exists in Sierra Nevada taxa?
- How much, what kind, and what distribution of genetic diversity is desired or enough?
- How do human activities affect, both directly and indirectly, genetic diversity detrimentally, and what actions can be taken to prevent or mitigate undesired consequences?

Although these questions are reasonable theoretically, our ability to answer them is extremely limited by lack of information. If we consider that the genes of all organisms from all species (known and unknown) of the Sierra Nevada collectively make up the gene pool of the range, we begin to see why even a basic inventory of genetic diversity is impossible to obtain practically. Genetic diversity is difficult to measure; cannot be observed, counted, or monitored directly in the field; and requires the use of either elaborate laboratory methods or long-term field trials for detection. Genetic interpretation depends on information from proxies and markers that don’t necessarily reflect traits of interest to managers. Ultimately, it is unknowable today what genes will be important as raw material for the evolution of adaptations to meet unknown environmental challenges of the future.

With one significant exception, genetic conservation concerns in land management have for the most part been lumped into the category of biodiversity management and not directly tackled in regional land-management policy or practice. Forest genetic programs have long made use of sophisticated genetic conservation and management policies and practices, both in operational forest regeneration and in tree improvement programs. Beyond the scope of commercial forest trees, however, the ecological consequences of genetic changes brought about by land management have only begun to be addressed programmatically. The U.S. Forest Service (USFS), for example, has expanded its forest genetics programs to provide guidance to all taxa (Hessel 1992). In 1992, a scientific roundtable convened in Wisconsin to develop regional management recommendations for ecosystem management of the Chequamegon and Nicolet National Forests. This is one of the few bioregional efforts where genetic diversity concerns pertaining to many aspects of land management were addressed (Crow et al. 1994).

Objectives

The inherent nature of genetic diversity and its recalcitrance to measurement and interpretation make the task of assessing genetic diversity in the Sierra Nevada quite different from assessments of other biodiversity attributes. Notwithstanding practical barriers, genetic theory is very well developed and has been tested and confirmed in extremely successful genetic manipulations in medicine, agriculture, and animal husbandry. This theory, along with the direct genetic studies that have been done for some taxa in the Sierra Nevada, provide the basis for both our genetic assessments and our suggestions for genetic management. Since geneticists tend to focus on specific taxonomic groups rather than working across taxa, there has been little sense of how much information is actually available in total, what the genetic patterns are for various taxa (whether the patterns are concordant or conflicting), or what the implications of this information for management might be. Information on genetic diversity of the Sierra Nevada is scattered in the literature and has not previously been compiled under a common theme. The objectives for this chapter, therefore, also differ somewhat from other SNEP assessments:

- Inform the public and land managers about pertinent questions and priorities regarding genetic diversity and its role in ecosystem health and sustainability; bring them to a broader awareness and understanding of the concerns and opportunities of genetic diversity.
- Compile information collectively about genetic diversity for major taxonomic groups in the Sierra Nevada, summarizing patterns of within- and among-population genetic composition and structure relevant to the long-term health, sustainability, and management of populations.
- Assess genetic diversity in the few cases where information is available, recognizing that general trends cannot be developed from these specific cases.
- Assess genetic diversity indirectly, using inferential tools as available. In many cases, the best that can be done is to develop conceptual frameworks to guide future individual, local, and case-specific assessments.
- Suggest approaches for integrating genetic diversity concerns and opportunities into land-management planning and practice.

This report documents efforts to address the SNEP assessment and management questions as they pertain to genetic variation within species of the Sierra Nevada:

- What are the current conditions? We develop here a summary overview of what is known about the gene pools of major taxonomic groups within the Sierra Nevada—the amount and pattern of genetic variation, which species are best genetically studied, and which are least well understood. We further attempt to identify, at a broad level, genetic significance in terms of rich, rare, or representative portions of the gene pools and any evidence of the factors underlying the genetic patterns observed.

- What were historical conditions, trends, and variabilities? Very little historical information exists on genetic variation, and even less exists that is specific to the Sierra Nevada. Many of the tools currently in use for measuring and monitoring genetic variation are relatively recent (e.g., allozymes and DNA techniques). The few species that have been the subject of temporal genetic studies (e.g., a few insect and fish species) have brief life cycles, and the studies investigated less than a decade in the lifetime of the species. The extinction of species and the expansion and contraction of their ranges is frequently a subject for study through the pollen record (e.g., Anderson 1990), and the impact on levels of genetic variation is inferred (e.g., Critchfield 1986). However, the changes in genetic variation over the lifetime of extant species are rarely assessed directly.

  Researchers frequently analyze historical relationships among taxonomic groups by studying current levels of genetic variation and inferring the time since divergence of these species based on the amount of genetic dissimilarity or distance. However, assumptions, rather than direct evidence, form the basis for this type of study, and these assumptions are built on tenuous theoretical or empirical foundations. Further, they are more often directed at relationships among species rather than relationships among subspecies or populations within a species. This type of study has not been included in this chapter.

  Thus, the genetic answer to the question regarding historical conditions relies mainly on theoretical, rather than empirical, evidence. Any evidence of historical trends, including any apparent relationships with climatic or geographic factors, has been reported in the section "Inferences of Genetic Significance."

- What are the trends and risks under current policies and management? Threats to the genetic integrity of Sierra Nevada species can be either direct (e.g., genetic contamination of native gene pools of fish by hybridization with introduced exotics or non-native populations) or indirect (e.g., increased inbreeding leading to inbreeding depression of certain species due to fragmentation of their habitats via land-conversion practices). We address these threats with empirical evidence or specific examples where available, and with implications of theoretical consequences in the absence of such data. Particularly vulnerable areas or species are identified. We identify specific policies and practices that historically, currently, or potentially affect genetic composition and/or structure, as well as the nature of the effects on gene pools (e.g., increases or decreases in genetic diversity). The difference between a positive outcome and a negative one is one of context: the species targeted and the specific quality of the populations affected, the temporal and spatial context, and the manner and scale in which the policy or practice is applied dramatically affect whether an action is a genetic threat or not.

- What are the genetic management options for the future? We summarize some specific ongoing programs in the Sierra Nevada, suggest generic guidelines that could be more broadly applied in land management and policy situations, and offer general strategies for integrating genetic diversity considerations into land management.

Assumptions

We made the following assumptions in the preparation of this chapter:

- We assume that the goal of land management is to maintain and promote ecosystem health and sustainability. This also becomes the goal of genetic conservation, as explicitly assumed in this chapter, and the standard by which we evaluate the status and trends of genetic diversity in the Sierra Nevada.

- Genetic diversity is fundamental to, and thus critically important for, the short- and long-term viability of Sierra Nevada taxa and to the integrity of the ecosystems they compose. Most traits of interest in managing taxa, populations, and ecosystems have genetic bases, although environmental variation plays an important role in determining phenotypic plasticity and response.

- Changes in gene pools occur naturally and continuously, in response to natural selection and stochastic effects (e.g., gene flow, mutation, genetic drift).

- Human actions affect genetic diversity. Some kinds of genetic change mimic natural change or are negligible, acceptable, or desirable; others are undesired and warrant preventative actions or mitigation.

- Direct genetic data are extremely limited, and interpretations regarding the ecological and evolutionary significance of genetic changes are limited.

- In the absence of direct data, genetic and genecological theory is strong enough to support cautious inferences regarding assessments of genetic diversity, to evaluate management effects, and to suggest practical management and monitoring guidelines.

- Case-by-case assessments, evaluations, and management prescriptions are essential and are not developed here other than to provide examples. Few generalizations are robust across taxa and situations. When offered, they are tentative.

BACKGROUND AND METHODS

Genetic variation is not readily measured in organisms from native habitats because of the confounding effect of genetic and environmental influences on phenotypic variation. To measure genetic variation nearly always requires removing individuals from their native habitats and either growing them in experimentally controlled environments or using laboratory analyses to assess traits whose expression is not greatly influenced by the environment. Because these analyses are neither field based nor particularly intuitive, we give background information on these methods here to aid the reader in understanding and interpreting their results.

Genetic Hierarchies

Because genes are basic building blocks of biological organisms (e.g., populations and species) and biological assemblages (e.g., communities and ecosystems), their diversity is expressed at hierarchical levels. Different processes are more important at the various levels, and thus assessments and management considerations must take these scalar issues into account, remaining cognizant of the relevant context. Genetic diversity is manifested as differences within and among gametes or embryos (haploid/diploid), individuals within populations, interbreeding populations (also called demes), ecotypes, local races or strains, geographic races and subspecies, and species.

Factors that influence and determine the structure of genetic diversity play different roles at the various levels (table 28.1). Mutation occurs within individuals and is expressed among individuals within populations; gene flow (geographic migration and exchange of genes) occurs among individuals within populations, among populations, and occasionally among ecotypes or races or at higher levels (e.g., interspecific hybridization). Natural selection exists on all levels but gains in ecological and evolutionary significance at the level of individuals within populations and among populations. Genetic drift (stochastic changes in genetic diversity due to sampling phenomena of small population size) occurs within and among populations. Inbreeding is another genetic process that is significant within small populations of some species.

The genetic effects of natural and human actions also vary in significance at the different levels. At the level of individual organisms, change in phenotype (including death) is the most obvious effect of mutation. At the population level, effects are observed as changes in allele, genotype, and phenotype frequencies and, correspondingly, in population expansions and population extinctions. At the species level, genetic effects result in the creation of new species (speciation) or extinction. Although genetic diversity is relevant from the molecular to the ecosystem level, the focus of this chapter is on aspects of genetic biodiversity within species.

TABLE 28.1

Structural, compositional, and functional levels of genetic diversity (only functions that are most significant for the level are given).

Structure	Composition	Function
Gametes, embryos	Sperm, pollen, spores, seeds	Mutation, fertilization
Individuals	Individual plants, animals, etc.	Mutation, mate selection
Populations, demes	Interbreeding individuals	Gene flow, natural selection, drift, inbreeding
Ecotypes, local races	Genetically distinct demes	Natural selection, drift, gene flow
Geographic races and subspecies	Genetically distinct groups of ecotypes and local races	Natural selection, drift
Species	Genetically distinct groups not regularly interbreeding	Natural selection, drift

Although genetic variation can be considered at various spatial scales, it is difficult to standardize across species, since the relevant domain varies according to the size, mobility, and genetic structure of the species. For example, more-local scales might be appropriate for discussing genetic variation in small, relatively immobile (e.g., nonmigratory, having a restricted gene flow), and/or locally adapted species, while broader scales would be more appropriate for larger, highly vagile (e.g., migratory, having pollen flow or seed dispersal across long distances), and/or broadly adapted species. The scale at which genetic information is available for any given species is also a function of the sampling design of available studies. Thus, genetic variation is discussed at the level most appropriate and for which there is information available across species groups.

To summarize, we recognize the following aspects to genetic diversity in regard to ecosystem health and sustainability:

- Genetic diversity, both structure and process, is both input to ecological systems (i.e., it influences and determines fitness, viability, and evolution) and output (i.e., ecological and environmental effects determine genetic structure and process) at many ecosystem levels (individual to population to species to community).
- Genetic diversity is but one factor that contributes to the status and health of ecological systems. The significance of

genetic diversity relative to other factors (e.g., demography, reproduction, and stochastic events such as disturbance) varies by taxon, location, season, and so on.

- Because each species has unique life histories and unique ecological relationships, the resulting genetic architectures and the importance of genes to viability and sustainability are unique.
- Human actions in ecosystems are analogous in their potential impacts to natural forces and are potent in their ability to alter genetic structures and processes, with diverse effects on viability and sustainability. Human actions can take place in concert with natural processes or can run counter to them.

The standards against which we implicitly measure status and trends of genetic diversity in the Sierra Nevada in this chapter are those that exist in those native Sierran ecosystems that have been minimally disturbed by human activities relative to their historical condition. For example, many wilderness and noncommercial forestlands in public ownership would be regarded as reference conditions, despite the effects of fire suppression, grazing, air pollution, and so on. From a genetic standpoint, even many manipulated lands (e.g., those used for timber) may not be far from an original condition, depending on the silvicultural treatments used. We recognize that these conditions are not "natural" or "pristine" in being uninfluenced by humans, either prehistorically or historically, directly or indirectly. We assume that effects on genetic diversity of prehistoric human use and of many recent human activities, however, are relatively minor at the broad scale in the Sierra Nevada, although local effects may have been intense.

Accepting such conditions as a reference standard does not imply that they are optimally adapted, inherently ideal, or naturally in balance. We accept this reference for evaluating genetic diversity for several reasons:

- Near-natural systems are the closest analogs to sustainable systems that we can describe—the dynamism and change in such systems are of a level that we accept in management.
- In many cases we cannot actually measure either the quantitative status of genetic diversity or absolute values of the contribution of genetic diversity to individual, population, and species viability. We can, however, make an assessment of whether particular actions have caused or might cause deviation from the present state, we can predict what the genetic consequences might be, and we can project what the impacts of such actions on health and sustainability might be. Thus, because our ability to evaluate impacts is limited to relative change, we take the present, minimally disturbed state as the standard for comparison.
- By accepting minimally disturbed conditions as reference, we do not risk the arrogance of assuming that humans can predict, understand, or create optimal conditions better than natural structures and processes can; instead we simply compare results between the reference and the manipulated lands.

Where systems are highly altered and the current conditions obviously do not serve as adequate reference standards, standards must derive either from adjacent or analogous minimally disturbed locations or from an analysis of historic ranges of variability.

Measurement of Genetic Variation

Several kinds of data are used to measure levels and patterns of genetic variation. The longest-standing method is to describe readily observable attributes of individuals, such as various metric traits, color, time required to reach certain developmental stages, and so on. (The collective attributes of an individual, the result of both genetic and environmental influences, is a phenotype.) This is typically called morphological data, or morphometric if quantitative. However, to detect heritable variation in these traits, the environment in which the individuals are raised or grown must be uniform and subject to experimental controls (i.e., replication and randomization); otherwise, observed differences could simply be environmental effects rather than genetic differences. For obvious reasons, plants are more amenable to this type of genetic assessment. This type of data has historically been used for genetic studies and does not necessarily require any sophisticated equipment. Whereas common-garden studies identify genetic differences within the same generation, the complementary type of analysis more common for animals—pedigree analysis—requires several generations.

A second type of commonly collected genetic data is biochemical traits, including enzymes, terpenes, flavonoids, blood groups, and other physiological markers. The most commonly studied of these traits are differences in isoenzymes—called allozymes. Such enzymes can readily be extracted from tissue samples, such as leaves or blood. In general, these enzymes have been shown to be under strict genetic control, and differences in the forms of each enzyme can be interpreted as genetic differences between the individuals sampled. This technique has been in common use for a broad range of organisms since the 1970s. Because the enzymes are typically not modified by the environment of the organism, samples can be taken from individuals in diverse geographic areas and reliably given a genetic interpretation.

The third type of genetic data, and the most recent to become available, is derived from a collection of techniques that assess molecular traits, such as DNA (from the nucleus, mitochondria, and/or chloroplast) and RNA. For example, DNA can be extracted from tissue samples from individuals, and variation between individuals can then be assessed either by comparing random segments of the DNA or by sequencing the DNA directly. Like the allozyme data, most DNA data are free from environmental influences and can be directly interpreted as genetic differences. This type of data has been gaining in popularity since the late 1980s.

The relationships among these kinds of genetic data (morphometric, allozyme, and DNA) are not well understood: sometimes they present concordant patterns, sometimes not. The genetic basis and freedom from environmental influence of biochemical and molecular traits makes them attractive for genetic studies. However, the adaptive and ecological importance of the genetic variation they reflect is uncertain. To some extent, observed differences among the results from the three data types may reflect study parameters and assumptions. For example, morphometric data for animal taxa are often confounded by environmental influences. Plant species are more amenable to being grown in common gardens; the morphometric traits measured in such situations therefore reflect genetic differences, the environmental component having been controlled. When morphometric data are obtained in common-garden studies in native habitats, or when correlations are found with environments, they are often considered to reflect some aspect of adaptively significant genetic variation.

Allozyme data, often considered to reflect neutral genetic variation (i.e., variation that is not under selective pressure and therefore represents time-dependent divergence based on reduction or lack of gene flow rather than adaptively significant genetic variation), sometimes show levels and patterns of genetic variation that are concordant with the morphometric data, especially when they are analyzed by multivariate methods. Often, however, they overemphasize certain patterns (e.g., within-population versus among-population genetic variation) relative to morphometric data. In some instances, certain genetic markers have been shown to be under the influence of strong selection, challenging the assumption that they are basically neutral. The significance of allozyme data thus seems to depend on a variety of factors, including the number and type of allozymes studied, the taxon under consideration, and the type of data treatment.

DNA studies sometimes agree with the results from one or both of the other two data types and sometimes present a different perspective. Current and common understandings of DNA studies suggest that, since plastid (chloroplast or mitochondrial) DNA evolves more quickly than the nuclear DNA (which is the basis of morphometric and allozyme data, as well as some molecular—e.g., PCR—data), studies of plastid DNA reflect more recent influences on genetic variation. Under this model, for example, a recently colonized species might show little genetic variation based on allozyme data but more variation in plastid DNA within and/or among populations, suggestive of recent and local processes, including adaptation.

Clearly, we are still learning about the relationships among the questions we are asking, the types of genetic data we collect, and the adaptive, evolutionary, management, and conservation implications of these data. In general, we recognize the effects of study design (including amount of data, scale at which data were collected, etc.) in determining this relationship. Life history characteristics are also likely to figure greatly into this relationship. There may also be some general trends according to taxonomic group, again largely a function of life history characteristics. Thus, our presentation of genetic information includes reference to the type of data and how the results agree or disagree among data types. The genetic significance is then discussed relative to the type of data, type of studies, level of representation of the available studies, and taxonomic group. If there are generalizations that can be made within a taxonomic group, these are also presented.

Conventional measures of genetic variation often refer to the hierarchical organization described earlier. Within-population genetic variation, when measured with allozymes, is often expressed as heterozygosity, an estimate of the percentage of individuals in a population who have two alternate forms of a gene, averaged over all the genes considered in the study. A statistic represented as F_{ST} reflects the amount of genetic differentiation within a species or the relative amount of variation among populations. The various forms of each (studied) gene present, and their frequencies, are often compared among populations, subspecies, or even closely related species, using indices that reflect the amount of genetic similarity or, conversely, genetic difference. The latter is more commonly known as genetic distance. Standards for measuring genetic diversity and population differences have changed over the twenty years that allozyme data have been collected, from similarity measures to the various genetic distances (Nei's and Rogers' are most commonly cited) to measures of population differentiation—F_{ST} (Wright 1978).

Information Acquisition

The information contained in this chapter was assembled in a three-stage process. First, the SNEP Genetics Workshop was convened in Placerville, California, on September 22 and 23, 1994. On that occasion, the attending individuals offered their research findings, general understandings, and educated opinions regarding genetic variation in various taxa within the Sierra Nevada. Approximately twenty-five scientists participated (appendix 28.2). The information gained from this workshop was captured in a preliminary report. Second, literature searches were conducted to fill in information gaps from the preliminary report and to include available references and context for the information offered during the workshop. Finally, the expanded report was circulated to all workshop participants, and also to approximately fifteen others, for review and comment. This chapter incorporates all review comments.

CURRENT CONDITIONS

Genetic Variation of Major Taxonomic Groups in the Sierra Nevada

Our general objective is to summarize the available information on genetic variation in species of the Sierra Nevada ecosystems. This is not an exhaustive inventory but rather a summary of the types of information available, highlighting the taxa that are best and least studied in each major taxonomic grouping (table 28.2). Life forms have been included and categorized according to the availability of data. Thus, we present information organized within seven taxonomic divisions: plants, mammals, birds, amphibians and reptiles, fish, insects, and fungi.

Information is included from many available sources, not only the published literature, and may refer to data from morphological, allozyme, and DNA studies. In general, the summary is limited to intraspecific genetic variation rather than the taxonomic or systematic studies at the species level, although this is noted when only the latter types of information are available. Patterns in genetic architecture, when known, are noted. Associations between geographic and genetic patterns are described, either as generalizations or by specific examples if data do not support generalizations. Further, any relationships between life history characteristics and patterns of genetic variation for that taxonomic group are presented. Finally, major research needs or concerns, as expressed by workshop participants, are noted.

Plants

There are approximately 3,500 species of vascular plants in the Sierra Nevada, representing approximately 50% of the taxa in California (Shevock 1996). Of those, approximately 45 are tree species (Griffin and Critchfield 1972). Among Sierran plant species, most genetic studies have been on tree species, and most of these have focused on the widespread and commercially important conifer species (table 28.3). Best studied are several pine species, most notably ponderosa pine (Pinus ponderosa) (e.g., Conkle and Critchfield 1988) and sugar pine (P. lambertiana) (e.g., Harry et al. 1983), followed closely by Douglas fir (Pseudotsuga menziesii) and white fir (Abies concolor) (e.g., Hamrick 1976). For these species, there are comprehensive accounts of genetic variation among and within populations in the Sierra, based on both morphological and allozyme data. Most other pine species of the Sierra, as well as other conifers such as giant sequoia (Sequoiadendron giganteum) (Fins and Libby 1982) and incense cedar (Calocedrus decurrens) (Harry 1984) have been studied at the morphological and/or allozyme levels. Some genetic information is also available for Jeffrey pine (Pinus jeffreyi), Washoe pine (P. washoensis), whitebark pine (P. albicaulis), foxtail pine (P. balfouriana), grey or foothill pine (P. sabiniana), knobcone pine (P. attenuata), lodgepole pine (P. contorta), red fir (Abies magnifica), and cypress species (Cupressus spp.) (see appendix 28.1). Recently, interest stemming from conservation concerns has prompted genetic studies of several oak (Quercus) species, resulting in data on allozyme variation within and among populations (Millar et al. 1990a). There is some population-level genetic information for a few other angiosperm species, but much of it is inferred from studies outside of the Sierra Nevada (as is the case with Populus trichocarpa) (Dunlap et al. 1994).

The substantial amount of information on the genetic architecture of many Sierran tree species is based largely on morphological and/or allozyme data. Because common-garden studies were the early standard for genetic studies of forest tree species (begun over fifty years ago in the Sierra Nevada), the "morphological" variation referred to here is

TABLE 28.2

Characterization of information on genetic variation for the biota of the Sierra Nevada.

Taxon Division	Research Emphasis	Least Studied
Plants	Gymnosperms: commercially significant tree species, pines in particular Angiosperms: Exotic annuals, low-elevation species, herbaceous dicots, oaks, woody shrubs, widespread species	Most angiosperm species, especially geographically restricted and/or endemic species
Mammals	Pre-1940s distributions of species and subspecies Population studies for a few species of ground squirrels, gophers, rats and mice	Current distributions of species and subspecies Populations of most species Bats
Birds	Population studies for approximately 15 species in Sierra Nevada	Raptors
Reptiles and amphibians	In general, commercial species and rare or endemic species Turtles (one species); some information on lizards Salamanders; some toads and frogs	Widespread, common species All snake species
Fish	Salmonids, commercial species	Non-game-fish species Salmonids in central/western Sierra Nevada
Insects	Human-interest species, including insect pests to crops and trees, disease-vector species, and butterfly species (aesthetics)	Most species, including such major taxonomic groups as aquatic species and (specialist) species with rare host plants
Fungi	Fungal pathogens of commercially significant plants (e.g., *Heterobasidium, Verticicladiella, Peridermium* spp.)	Most fungal species, especially those in the Zygomycota and Chytridiomycota

TABLE 28.3

Genetic variation (heterozygosity) within populations of Sierra Nevada plants.

Species	Number of Loci	Heterozygosity[a]	F_{ST}	Sampling Range	Reference
Gymnosperms					
Abies concolor		0.24		Central Sierra Nevada	Conkle 1992
Calocedrus decurrens	20	0.21	0.042	California	Harry 1984
Pinus attenuata		0.14	0.12	California	Millar et al. 1988
Pinus jeffreyi	20	0.185	0.068	Central Sierra Nevada	Furnier and Adams 1986
	20	0.255	0.092	Southern Sierra Nevada	Furnier and Adams 1986
	25	0.137	0.004	Mono County	Millar et al. 1993
Pinus lambertiana		0.25		Oregon and California	Conkle 1992
Pinus ponderosa		0.21		Sierra Nevada	Conkle 1992
Pinus sabiniana		0.14		California	Conkle 1992
Pinus washoensis	26	0.15		Oregon and California	Niebling and Conkle (1990)
Pseudotsuga menziesii		0.28		?	Conkle 1992
Sequoiadendron giganteum	8	0.143		Sierra Nevada	Fins and Libby 1982
Taxus brevifolia	11	0.170	0.107	Continental U.S. and Alaska	Doede et al. in press
Angiosperms					
Antennaria corymbosa	19	0.078	0.173	Rocky Mountains	Bayer 1988
Antennaria media	19	0.058	0.07	Sierra Nevada	Bayer 1989b
Antennaria rosea	19	0.114	0.378	Western U.S.	Bayer 1989a
Avena spp.					Allard et al. 1968
Bromus tectorum	25	0.012	0.478	U.S.	Novak el al. 1991
Calochortis minimus	16	0.168		Sierra Nevada	Ness et al. 1990
Calochortis nudus	16	0.095		Sierra Nevada	Ness et al. 1990
Clarkia speciosa	17	0.183	0.043	Kern County	Soltis and Bloom 1986
Elymus glaucus	20	0.086	0.549	Washington, Oregon, California	Knapp and Rice in press
Ipomopsis aggregata	23	0.099		Sierra Nevada	Wolf et al. 1991
Lewisia spp.	22		0.541	Sierra Nevada	Carroll et al. n.d.
Lewisia cantelovii	22	0.208		Yuba and Sacramento Rivers	Carroll et al. n.d.
Lewisia congdonii	22	0.234		Yosemite and Kings Canyon National Parks	Carroll et al. n.d.
Lewisia serrata	22	0.148		American River	Carroll et al. n.d.
Salix exigua	15	0.122	0.258	Southwestern U.S.	Brunsfeld et al. 1991
Salix melanopsis	15	0.147	0.180	Northwestern U.S.	Brunsfeld et al. 1991
Scutellaria bolanderi	18	0.023	0.720	Sierra Nevada	Olmstead 1990
Scutellaria californica	18	0.129	0.288	California	Olmstead 1990
Scutellaria nana	18	0.117	0.327	Northern California and Nevada	Olmstead 1990
Scutellaria siphocampyloides	18	0.042	0.628	California	Olmstead 1990
Wyethia					Ayers (SNEP Genetics Workshop)
Ferns					
Cheilanthes gracillima			0.286	Eldorado County	Soltis et al. 1989

[a] Heterozygosity is the proportion of heterozygous genotypes per locus per individual.

genetically based, without the problems of plasticity that typify studies where field observations of morphology are made without controlled tests. Some common-garden studies, taking advantage of vegetative propagation techniques, have examined genetic architecture from the population to the clonal level of variation (e.g., Fins and Libby 1982). The general trend seen in most genetic architecture studies is one of substantial genetic variation residing within populations, although the amount of such variation ranges widely among traits and can change with age (Namkoong and Conkle 1976).

Genetic diversity within populations (as measured by allozymes) tends to be relatively high in Sierran conifer populations (table 28.3) in comparison with that found in gymnosperm species in general (e.g., mean heterozygosity is 0.151 [Hamrick et al. 1992]). Differences among populations tend to be fairly low ($F_{ST} < 0.10$) (table 28.3), consistent with gymnosperms in general and with woody plant species that are wind dispersed and wind pollinated (Hamrick et al. 1992). As is the case with metric traits, differentiation can be greater along elevational gradients in the Sierra than along latitudinal ones. For example, the F_{ST} among four elevational transects in sugar pine, which ranged from the Eldorado National Forest in the north to the Sequoia National Forest in the south, was 0.015, whereas differences from low to high elevation along each transect averaged 0.038 (Westfall 1995). Among congeneric species, the distribution of genetic variation fluctuates. Among the pines, there tend to be large genetic differences among species, as is the case among the closed-cone pines (Millar et al. 1988). In the cypresses, the differences are much more modest (Millar and Delany n.d.). This pattern is not uniform among all genetic markers. For example, differences among the closed-cone pine species are much lower in mitochondrial DNA (Strauss et al. 1993) than in allozymes.

As these patterns are based largely on studies of the widespread conifer tree species—outcrossing, wind-pollinated gymnosperms—it is not known whether they will hold true for species with different life forms, specific habitats (e.g., riparian), or different mating systems, dispersal systems, or modes of reproduction (e.g., clonal species). Also, some replicated common-garden experiments point to the existence of genotype x environment interactions in some species. However, these data are neither abundant nor consistent enough to permit generalizations about the significance of these interactions.

The taxa best represented in the genetic knowledge of nontree plants in the Sierra Nevada are characterized as exotic annuals, especially low-elevation species. For example, Novak and colleagues (1991) found substantial rangewide differentiation in Bromus tectorum. Beyond the exotics, native taxa have been studied in a nonordered fashion, with scattered representation from both herbaceous dicots and shrubs (table 28.3), and much of this work has focused on taxonomic issues rather than intraspecific genetic structure. Comprehensive information on the genetic architecture of species is scarce. The studies of widespread species have focused on among-population variation, while the little information available for more restricted species is usually reflective of within-population variation.

Levels of genetic diversity within populations of many of the Sierran angiosperms are nearly as high as those of the gymnosperms (table 28.3). In some species, especially those limited in range or habitat, such as Bolanders skullcap (Scutellaria bolanderi), diversity is low (Olmstead 1990). Genetic differentiation among populations of many of the angiosperm species studied is quite high compared to that of gymnosperms, suggesting genetic isolation among populations. For example, differences among Sierran willow (genus Salix) populations isolated by river drainages tend to be high (Brunsfeld et al. 1991). In recent studies of the native grasses Nassella and Danthonia, Knapp (1994) and Knapp and Rice (1994b), respectively, have noted that allozyme variation is correlated with geographic distance. However, this is not the case for blue wild rye (Elymus glaucus) (Knapp and Rice 1995). Genetic drift (in small populations) and interruption of gene flow have been suggested as the genetic processes responsible for this lack of relationship (Slatkin 1993). Few direct studies of gene flow between species have been conducted. Nason and colleagues (1992) found evidence for first-generation gene flow between two Sierran species of manzanita (genus Arctostaphylos), one occupying dry sites and the other moist ones.

Few studies are available that have investigated clonal diversity in asexually reproducing plants in the Sierra Nevada. In a study of Antennaria rosea over much of its range in western North America, it was observed that populations tend to be composed of one or a few rather localized clones (Bayer 1990). Samples from the Sierra Nevada had some of the highest numbers of clones per population (i.e., eleven clones). The proportion of polyclonal populations detected (73%) is similar to the average reported for a wide range of clonal plant species (77%) (Ellstrand and Roose 1987).

Differentiation in other biochemical traits has also been studied in Sierran species, both gymnosperms and angiosperms. Desrochers and Bohm (1993) found greater complexity in flavonoid compound (responsible, in part, for color) profiles in southern Lasthenia californica populations than in northern ones. In the monoterpene profiles (monoterpenes being components of pine pitch), Zavarin and colleagues (1993) found differentiation between the Sierran and the Great Basin and Rocky Mountain populations.

A major constraint in assessing the genetic variation in plants of the Sierra Nevada other than trees is the lack of basic biological information, such as fine-scaled species-distribution maps and approximate population sizes. As it is not feasible to conduct common-garden studies for all plant species, plasticity poses a problem for genetic studies based on variation in morphological characters observed in the field. One approach to widespread genetic assessments is to attempt to link certain life history characteristics, such as mating system, with patterns of genetic variation (e.g., Hamrick et al. 1992). However, there might be many exceptions to such generalizations, and even basic life-history characteristics (e.g., mating system) are not known for many species and cannot necessarily be inferred from morphology. Allozyme studies, as we mentioned earlier, are convenient, but the relationship between this level of genetic variation and adaptive or evolutionarily significant variation is unclear. The best hope for gaining comprehensive information on genetic variation in many species lies in defining some morphological markers under known genetic control. Patterns in such simply inherited characters have been similar to those in allozymes. For example, in stem-surface phenotypes in Sierran pondersosa pine, one of which confers resistance to the gouty pitch midge (Cecidomyia piniinopsis), Ferrell et al. (1989) show a complex geographic pattern in the Sierra Nevada very similar to that in allozymes (Westfall and Conkle 1992; Westfall et al. n.d.). In trees, a suite of independently varying characters, such as growth, bud break, and cold hardiness, has been used in forming seed-transfer guidelines (Campbell 1986; Rehfeldt 1990). It is possible that such approaches will be necessary in other plant groups.

Mammals

About 110 species of mammals are found in the Sierra Nevada (Zeiner et al. 1990b). Most of the available information consists of distributions of species and subspecies. However, much of this was collected before 1940 and hence may not reflect the current situation. Modern studies cover a small and scattered sample (about 25% to 30%) of all taxa, and most have focused on non-Sierran and arid-land populations.

The genetic information available on Sierran mammals is mostly based on allozyme data (i.e., genetically based variants of certain enzymes) and nuclear and mitochondrial DNA (mtDNA); there is some information on chromosomal data and a small amount on morphological characters that distinguish species and subspecies. Early studies focused on taxonomic issues; more recently they have tackled population structures.

Few genetic studies have been conducted on populations within the Sierra Nevada. Exceptions include the well-studied pocket gopher (Thomomys bottae), some kangaroo rats (genus Dipodomys), some mouse species (genus Peromyscus), and the kit fox (Vulpes macrotis). Within-population genetic diversities in allozymes (i.e., observed heterozygosity) for the few Sierran mammals surveyed tend to be low, generally less than 0.05 (table 28.4). Heterozygosities in allozymes for some of the mouse (Peromyscus) species, at 0.07–0.09, are among the highest for mammals (Avise et al. 1979). In contrast, allozyme variation within species of the kangaroo rat (Dipodomys spp.) is very low and approaches zero for one population of Panamint kangaroo rat (D. panamintinus) sampled within the Sierra Nevada (Johnson and Selander 1971).

In addition, differentiation among populations of many Sierran species is also low (table 28.5), suggesting high amounts of gene flow or recent history (Slatkin 1993). Genetic similarities among populations within species of kangaroo rats (genus Dipodomys) are very high, even in the wide-ranging species (Johnson and Selander 1971). Although no data exist for Sierran populations, low levels of differentiation are observed in such wide-ranging species as the mule deer (Odocoileus hemionus) among populations ranging across the western United States ($F_{ST} = 0.048$) (Cronin 1991). Differences were very low ($F_{ST} = 0.004$) between deer populations that were adjacent but separated by the Continental Divide (Cronin et al. 1991b). In the Brazilian free-tailed bat (Tadarida brasiliensis), southwestern populations that include those occupying distinct migrational groups show low F_{ST} values (0.05), even though band and recapture data suggest low exchange among migratory groups (Svobda et al. 1985). Intercolony differences in the bat species are even lower ($F_{ST} = 0.008$) (McCracken et al. 1994).

Patterns in some rodent species that occupy the Sierra contrast greatly with those just described. Although rangewide population differences are relatively low in the deer mouse, P. maniculatus ($F_{ST} = 0.16$), this value is relatively high in comparison to that for the coyote ($F_{ST} = 0.09$), which is equally wide-ranging. Californian populations of this deer mouse

TABLE 28.4

Genetic variation (heterozygosity) within populations of Sierra Nevada mammal species.

Taxonomic Name	Common Name	Number of Loci	Heterozygosity[a]	Sampling Range	Reference
Thomomys bottae	Pocket gopher	23	0.093	Southwestern U.S., including Sierra Nevada	Patton and Yang 1977
Dipodomys ordii	Ord's kangaroo rat	17	0.008	Western U.S.	Johnson and Selander 1971
Dipodomys microps	Chisel-toothed kangaroo rat	17	0.007	Western U.S.	Johnson and Selander 1971
Dipodomys agilis	Pacific kangaroo rat	17	0.040	Western U.S.	Johnson and Selander 1971
Dipodomys heermanni	Hermann's kangaroo rat	17	0.042	Western U.S.	Johnson and Selander 1971
		22	0.00	Butte County	Patton et al. 1976
Dipodomys panamintinus	Panamint kangaroo rat	17	0.000	Western U.S., including Sierra Nevada	Johnson and Selander 1971
		22	0.05	Kern County	Patton et al. 1976
Dipodomys deserti	Desert kangaroo rat	17	0.010	Western U.S.	Johnson and Selander 1971
Dipodomys merriami	Merriam's kangaroo rat	17	0.051	Western U.S.	Johnson and Selander 1971
Dipodomys nitratoides	San Joaquin kangaroo rat	17	0.040	Western U.S.	Johnson and Selander 1971
Peromyscus maniculatus	Deer mouse	22	0.091	U.S. and Canada, including Sierra Nevada	Avise et al. 1979
Peromyscus californicus	California mouse	31	0.027–0.124	Coastal California, Baja California and foothills of Sierra Nevada	Smith 1979
Microtus californicus	California vole	4[b]	0.24	California Coast Range	Bowen 1982
Canus latrans	Coyote	53	0.050	Zoo	Fisher et al. 1976
Canus latrans	Coyote	10[c]	0.50	Southern California	Roy et al. 1994
Vulpes macrotis	Kit fox	24	0.025–0.111	Western U.S., including Sierra Nevada	Dragoo et al. 1990
Ursus americana	Black bear	33	0.015	Yosemite National Park	Manlove et al. 1980
Martes americana	Marten	24	0.170	Wyoming	Mitton and Raphael 1990

[a] Heterozygosity is the proportion of heterozygous genotypes per locus per individual.
[b] Variable loci only.
[c] Microsatellite (repeated) DNA.

TABLE 28.5

Population differentiation (F_{ST}) among populations of Sierra Nevada mammal species.

Taxonomic Name	Common Name	Number of Loci	F_{ST}[a]	Sampling Range	Reference
Tadarida brasiliensis	Brazilian free-tailed bat	38	0.05	Southwestern U.S.	Svoboda et al. 1985
Marmota flaviventris	Yellow-bellied marmot	8[b]	0.07	East River Valley, Colorado	Schwartz and Armitage 1980
Peromyscus maniculatus	Deer mouse	22	0.16	U.S. and Canada, including Sierra Nevada	Avise et al. 1979
Microtus californicus	California vole	4[b]	0.04	California Coast Range	Bowen 1982
Odocoileus hemionus hemionus	Rocky Mountain mule deer	9[b]	0.048	Western U.S.	Cronin 1991
Odocoileus hemionus hemionus;*Odocoileus hemionus columbianus*	Mule and black-tailed deer	9[b]	0.38	Western Canada	Cronin 1991
Canus latrans	Coyote	10[c]	0.09	Southern California	Roy et al. 1994

[a] F_{ST} is the amount of genetic differentiation among populations of a species.
[b] Variable loci only.
[c] Microsatellite (repeated) DNA.

diverged significantly from the rest of the western populations (based on variation in mitochondrial DNA) and also showed substantial genetic diversity within the populations. Differentiation among populations was greater for the pinyon mouse (P. truei), which occupies more restricted habitats (Avise et al. 1979).

One of the most intensively studied species, the pocket gopher (Thomomys bottae), also has relatively high genetic diversities within populations (heterozygosity of 0.09) and geographic structuring that follows chromosomal patterns (Patton and Yang 1977; Smith and Patton 1980). This species shows more genetic variation among than within populations. In areas where populations are small and widely spaced, genetic drift has resulted in considerable genetic homogeneity within populations. In the Sierra Nevada, Patton and Smith (1990) list major geographic subdivisions in the pocket gopher as northern and southern Sierran foothills, the Yosemite Valley, the Kern River Plateau, the Inyo-White Mountains, and the Mount Whitney complex. Dispersal is limited and effective population sizes low, which results in substantial population structuring, but dispersal among more distant populations is sufficient to maintain genetic diversity (Daly and Patton 1990; Patton and Feder 1981). Similar dispersal patterns and geographic structures are suggested in the marmot, Marmota flaviventris (Schwartz and Armitage 1980), and in some non-Californian species of ground squirrel, Spermophilus (e.g., van Staaden et al. 1994).

Genetic differences among species are also low, even among morphologically distinct and geographically separated taxa. In an allozyme and morphological study of the kit fox (Vulpes macrotis, sampled in the northeastern Sierra) and the swift fox (V. velox), Dragoo et al. (1990) found little differentiation between the two species (Nei's distances ranged 0.000 to 0.013) and concluded that the two should be reclassified as subspecies. Johnson and Selander (1971) found similarly low levels of differentiation among species of the kangaroo rat (including some Sierran and near-Sierran populations), another wide-ranging arid-land taxonomic group in the West.

Variation in mitochondrial DNA (mtDNA) has also been studied in taxonomic relationships in Sierran and proximal-Sierran species. Based on this type of data, Cronin (1992) found little genetic variation in elk (Cervus elaphus), both within and between the two Californian subspecies. The same study found substantial genetic variation in the mule deer subspecies of O. hemionus (populations east of the Sierra Nevada), but none in the black-tailed deer (populations west of the Sierran and Cascade crests). Cronin and colleagues (1991a) also found substantial genetic diversity in mitochondrial DNA clones in black bear populations of the Pacific Northwest, suggesting maternally based structuring. Although Cronin (1991b) claimed to find gene flow between mule deer and black-tailed deer in a contact zone between the subspecies (in British Columbia), mtDNA and allozyme F_{ST} values (0.56 and 0.378) suggest very little gene flow (equivalent to 0.2 to 0.41 individuals per generation). In a study of interspecific and intraspecific mitochondrial DNA variation in grasshopper mice (genus Onychomys), Riddle and Honeycutt (1990) found regional subdivisions that conform to existing taxonomic subdivisions, with relatively little differentiation within regions (based on single-individual samples). The northern grasshopper mouse (O. leucogaster) was clearly differentiated from the southern (O. torridus); the data suggested that the Great Basin populations of O. leucogaster had become isolated from the populations to the east during the Pleistocene.

In summary, many of the Sierran mammalian species sampled show fairly low levels of within-population genetic variation as well as high levels of gene flow among populations. However, there are notable exceptions, such as the pocket gopher, with its well-differentiated groups in the Sierra Nevada, and the California vole, with its relatively high level of heterozygosity. Most of the mammalian species native to the Sierra Nevada have not been genetically studied, and fewer still have been studied in Sierra Nevadan populations. Thus, it is unknown how well these trends represent the complete group of Sierran populations.

A widely communicated need at the SNEP Genetics Workshop is for population-level studies on most mammalian species. Also expressed was the need to study the temporal context for normal ranges of variation in populations, as demographic and genetic structures may vary over time (as in Patton and Feder 1981).

Birds

There are approximately two hundred bird species with winter and/or summer ranges in the Sierra Nevada bioregion (Zeiner et al. 1990a). Little genetic information is available for most species at the among-population or within-population level. Approximately fifteen species of birds in the Sierra Nevada have been the subject of population genetics studies (mostly allozyme-level studies, some of DNA data). Subspecies designations, based on morphometric characteristics, within bird species are common. Sierra Nevada examples of subspecies structuring include the fox sparrow (Passerella iliaca), northern flicker (Colaptes auratus), Hutton's vireo (Vireo huttoni), and spotted owl (Strix occidentalis). Recent mitochondrial DNA studies have even suggested species designations for some subspecies (e.g., the fox sparrow and Hutton's vireo). Thus, some subspecies or even populations within the Sierra Nevada may actually be distinct species rather than intraspecific genetic variants.

Bird species have several life history characteristics that are likely to be relevant to the amount and structure of genetic variation they exhibit. First is the mating system: most, but not all, bird species are monogamous (Lack 1968), allowing for more genetic variation than if the offspring were largely the result of a few males who mated with many females. Second is their pattern of distribution. Two distribution models are common: colonial and continuously dispersed. Colonial species tend to have greater population differentiation than do evenly distributed species (Barrowclough 1980). Third is the tendency to be either migratory or sedentary. One would expect sedentary populations to be less panmictic (i.e., less likely to exhibit random mating and hence less likely to have gene pools that are thoroughly mixed) than migratory populations, since there is less opportunity for mating among populations (e.g., Johnson and Marten 1992).

Another factor that has been demonstrated to influence genetic structure in avian species is directional bias in gene flow (i.e., immigration and hybridization between two populations may occur more frequently in one direction than in the other). Peterson (1991) studied gene flow between two groups of scrub jays (Aphelocoma coerulescens) that are strongly differentiated morphologically and are physically separated by geographic barriers, chiefly deserts. Using morphological criteria, he estimated that gene flow east to west across the Mojave Desert, from the woodhouseii populations to the californica populations, was two to seven times stronger than west-to-east movement. The two forms approach one another closely (within about 20 km [12 mi]) in the Owens Valley. Here, 16% of the individuals studied showed eastern influence and 4% were apparently first-generation immigrants. Peterson hypothesized that the bias in the direction of gene flow in this case was due to habitat differences in the two subspecies, and that a stronger psychological barrier to entering desert habitats exists for the californica jays. Their normal habitat is oak woodlands, which are structurally distinct from the desert, whereas the woodhouseii subspecies occupies a more diverse pinyon-juniper-woodland habitat that seems to grade directly into desert habitats.

Morphological differentiation in birds, the usual basis of subspecies designations, usually reflects both environmental and genetic influences, captive-rearing studies in birds (i.e., those where birds are raised in common environments so that genetic effects can be distinguished from environmental effects) being difficult to administer and rarely occurring in the literature. One exception is an egg transplant study in the red-winged blackbird (Agelaius phoeniceus), a widespread species that also inhabits the Sierra Nevada. Northern to southern and reciprocal transplants of eggs revealed that a large component of morphometric variation was indeed environmental (James 1983). This result may help explain why morphometric studies in bird species may show different patterns of variation than those revealed by allozyme or DNA studies.

Population differentiation (F_{ST}) in birds of the Sierra Nevada, mainly based on estimates from allozyme studies, is generally low (table 28.6). This is consistent with previous findings that North American avian species generally consist of populations of moderate to large effective size with moderate to high levels of gene flow (i.e., successful mating) among them (Barrowclough 1980; Barrowclough and Johnson 1988). Only four of the F_{ST} values for the Sierra Nevadan bird species listed are over 0.10 (this small value suggests little population differentiation, due to migration and mating among populations), and the larger values are for species with two or more subspecies in the study sample. For example, the California subspecies of Hutton's vireo (Vireo huttoni huttoni) and the interior subspecies in Arizona (V. h. stephensi) have a mean F_{ST} of 0.614, a value more characteristic of interspecific than intraspecific differentiation. This species is highly sedentary, and the two subspecies exist in different habitats. Indeed, these two taxa were probably isolated even prior to the Wisconsin glacial maximum (approximately 18,000 years BP) and are definitely approaching, or have already reached, species level (Cicero and Johnson 1992). The few studies showing F_{ST} values greater than 0.10 are also often based on very few polymorphic loci.

This pattern of little geographic structuring and moderate levels of gene flow among populations is reflected in Hammond's flycatcher (Empidonax hammondii), a species that nests in boreal forests and woodlands of western North America. Samples from breeding localities at the extremes of

TABLE 28.6

Genetic population structure (F_{ST}) for bird species of the Sierra Nevada.[a]

Taxonomic Name	Common Name	Number of Loci[b]	F_{ST}[c]	Sampling Range	Reference
Riparia riparia	Bank swallow	—	0.051	North America	Barrowclough 1980
Cistothorus palustris	Marsh wren	—	0.061	North America	Barrowclough 1980
Callipepla californica	California quail	37(16)	0.032	California and Baja California	Zink et al. 1987
Larus californicus	California gull	35(8)	0.004	California and Utah	Zink and Winkler 1983
Sphyrapicus ruber	Red-breasted sapsucker	39(7)	0.019	California and Oregon	Johnson and Zink 1983
Pipilo erythrophthalmus complex	Rufous-sided towhee	16(1)	0.229	Maine to California	Sibley and Corbin 1970
Passerella iliaca	Fox sparrow	38(14)	0.014	California, Oregon, Nevada	Zink 1986
Passerella iliaca	Fox sparrow	13(13)	0.013	California and Nevada	Burns and Zink 1990
Zonotrichia leucophrys	White-crowned sparrow	19(3)	0.047	California and Colorado	Baker 1975
Branta canadensis	Canada goose	35(24)	0.065	North America	Van Wagner and Baker 1986
Colaptes auratus	Northern flicker	3(3)	0.098	U.S.	Fletcher and Moore 1992
Amphispiza belli	Sage sparrow	41(17)	0.112	California and Nevada	Johnson and Marten 1992
Icterus galbula	Northern oriole	2(2)	0.027	North America	Corbin et al. 1979
Vireo huttoni	Hutton's vireo	33(6)	0.614	Arizona and California	Cicero and Johnson 1992
Strix occidentalis	Spotted owl	23(1)	0.55	Oregon, New Mexico, California	Barrowclough and Gutiérrez 1990
Empidonax hammondii	Hammond's flycatcher	36(16)	0.043	Western North America, including Sierra Nevada	Johnson and Marten 1991

[a] All species listed are native to (i.e., have summer and/or winter ranges in) the Sierra Nevada.

[b] The first two entries are based on dispersal data; all others are based on allozyme data. The number of loci assayed is followed by the number of polymorphic loci in the sample, in parentheses.

[c] F_{ST} is the amount of genetic differentiation among populations of a species.

its nesting distribution, including the southern Sierra Nevada, showed that only 4.3% of the genetic variation present (based on allozyme data) was distributed among populations (Johnson and Marten 1991). This indicates moderate to high genetic heterogeneity among populations, a pattern reflected in the bird's high degree of morphological homogeneity over its entire nesting distribution.

In general, bird species of the Sierra Nevada and elsewhere have low levels of individual genetic variation when sampled at a specific set of genes. For example, it is possible for a bird to have two forms of each gene; the number of times this occurs, averaged over all the genes sampled and all the individuals sampled in a population, leads to an estimate of the genetic variation in the average individual, a value referred to as observed heterozygosity. Observed heterozygosity values are available for some of the bird species (and from the same studies) listed in table 28.6: they are all low. Average observed heterozygosity for the Canada goose (Branta canadensis) is 0.051 (range: 0.031–0.083) (Van Wagner and Baker 1986); for the sage sparrow (Amphispiza belli) is 0.042 (range: 0.03–0.55) (Johnson and Marten 1992); for Hutton's vireo (Vireo huttoni) is 0.014 (Cicero and Johnson 1992); and for Hammond's flycatcher (Empidonax hammondii) is 0.026 (range: 0.012–0.039) (Johnson and Marten 1991).

Amounts and patterns of geographic variation in birds differ among studies using allozyme, mitochondrial DNA, and morphometric evidence. Usually, allozyme evidence is more conservative, perhaps because it is less influenced by the environment, showing less population structure than is suggested by the other two types of data. For example, the Canada goose (Branta canadensis) shows spectacular amounts of morphometric differentiation across its range, yet a rangewide isozyme study (including California samples) found very little population differentiation, as suggested by the low F_{ST} value of 0.065 (Van Wagner and Baker 1986). Similarly, in the northern flicker (Colaptes auratus), three subspecies are recognized in this widespread bird species, yet very little population differentiation is evident from an allozyme study ($F_{ST} = 0.098$) (Fletcher and Moore 1992). These allozyme values indicate much less population differentiation than that indicated by morphometrics.

To further understand these surprising differences, a third source of genetic material can be studied. It has been suggested (e.g., Zink and Dittman 1991) that, since mitochondrial DNA evolves more quickly than nuclear DNA, the former might be more likely to reveal geographic patterns of variation than the latter. Morphometric and allozyme data largely reflect products from nuclear DNA. However, among studies of birds of the Sierra Nevada, there appear to be more exceptions than trends in the relationships among patterns from mtDNA, morphometric, and allozyme studies. Two examples were presented previously of morphometric patterns that were not supported by allozyme variation. However, in a study of scrub jays (Aphelocoma coerulescens), Peterson (1991) found that the allozyme data agreed with the morphometric designation of five subspecies (and much gene flow among populations within subspecies). In a study of the brown towhee complex (Pipilo spp.), a group of four currently recognized species mainly inhabiting the southwestern United States, Zink and Dittman (1991) found that mtDNA and allozyme data revealed similar evolutionary and geographic patterns. Similarly, allozyme, morphometric, and mtDNA evidence showed strong and similar differentiation between two groups in samples of the sage sparrow complex (Amphispiza belli) taken from California and Nevada (Johnson and Marten 1992).

Mitochondrial DNA data do not necessarily reflect geographic patterns. For example, in a study of the chipping sparrow (Spizella passerina), a widespread migratory North American passerine species that also inhabits the Sierra Nevada, no geographic differentiation was observed in mitochondrial DNA at all, in spite of the fact that a large part of the range was sampled (Zink and Dittman 1993b). Thus, the three named subspecies for this sparrow have no support from mtDNA data. In fact, the lack of mtDNA geographic structure over relatively large distances is typical of several passerine bird species that inhabit areas that were recently glaciated (Zink 1994). In spite of considerable geographic variation in size and plumage color in the song sparrow (Melospiza melodia) across its continental U.S. range (including six California samples), mtDNA did not reveal any geographic structure (Zink and Dittman 1993a). Similarly, mitochondrial data from thirty-nine locales (including several in the Sierra Nevada) of the fox sparrow (Passerella iliaca) complex failed to show any geographic variation within four major taxonomic groupings, despite marked morphometric clines (i.e., gradual changes in species characteristics that parallel some geographic or environmental trend) within these groups (Zink 1994). In these cases, it has been postulated that isolation by distance has not been very important in shaping population genetic structure as measured by mitochondrial DNA. Rather, historical isolating events may be more important (Zink 1994).

In summary, most of the bird species in the Sierra Nevada for which there are genetic data show weak population differentiation based on allozyme data. Subspecies may be differentiated at the allozyme level if they have been isolated for a long time. Morphometric variation, even at the subspecies or rangewide level, is often not accompanied by allozyme or mitochondrial DNA variation. Together with information from limited captive-rearing studies, this may indicate that much morphometric variation does not have a genetic basis. Although the life history traits of mating system, pattern of dispersal, and migratory tendencies seem logically related to the amount and pattern of genetic information, there are too few empirical studies to verify these theories.

Reptiles and Amphibians

Of the approximately forty-six species of reptiles and thirty species of amphibians listed as occurring in the Sierra Nevada (Zeiner et al. 1988; Mark Jennings, e-mail communication with the authors, 1994), approximately half have genetic information available. Most of this information is on amphibians, particularly salamanders and frogs. Among reptiles, lizard species have been best studied genetically. Snakes appear to be the least well-studied group: except for some morphological and behavioral studies, there is virtually no genetic information for the twenty-seven snake species in the Sierran and proximal-Sierran regions (Zeiner et al. 1988). For amphibians and reptiles, it is interesting to note that, in general, the most common, widespread, and abundant species have been least studied, and the endemics and rare species have been studied most. This is postulated to be a consequence of both the current public focus (and associated funding opportunities) on rare or endangered species and the early distributional and morphological studies of the more common species, leaving only the less rewarding (genetic) increments of information to be gained.

Within the amphibian and reptile populations studied, genetic variability in allozymes is low to moderate (table 28.7). For example, recent studies (Wake and Yanev 1986; Wake et al. 1989) report that the invading population Ensatina eschscholtzii xanthoptica in the Sierra Nevada has the lowest heterozygosity of any population in the genus, in line with theoretical expectations. Heterozygosity values are generally less than 0.100. In addition, genetic differences among populations within some species of salamanders are often extremely high, sometimes approaching or exceeding genetic differences among related species (Hedgecock and Ayala 1974; Wake and Yanev 1986). Even in a species that occupies a limited area, such as the Inyo Mountains salamander (Batrachoseps campi), which occurs only in specific areas along a 32 km length of the Inyo Mountains, heterozygosity can vary somewhat from one population to another (its heterozygosity range is 0.04–0.08) (Yanev and Wake 1981). The limitation of these groups to moist, sometimes riparian habitats (Zeiner et al. 1988) restricts their dispersal and, consequently, gene flow between populations. This, along with extinction and recolonization with climatic fluctuations can result in random loss of genetic variability. Heterozygosities ranged from 0.01 to 0.09 among seventeen populations of the Pacific tree frog (Hyla regilla) (Case et al. 1975) and from 0.02 to 0.25 among sixteen populations of the lungless salamander (Ensatina eschscholtzii) (Wake and Yanev 1986). Differences in heterozygosity from one population to another are present, though to a lesser extent, in western frog species (Case 1978a, 1978b; Case et al. 1975).

Few studies have addressed genetic differentiation among Sierran populations of reptile or amphibian species. The available data, which are almost exclusively for amphibians, show a pattern of strong genetic differentiation among populations (table 28.8). In a study of nineteen populations of the lungless salamander (Ensatina eschscholtzii), including populations in the Sierra Nevada, Wake and Yanev (1986) noted “profound” allozymic differentiation among populations ($F_{ST} = 0.705$) (see also Jackman and Wake 1994; Wake et al. 1994). Similarly, a high level of genetic differentiation was demonstrated among populations of the Inyo Mountains salamander (Batrachoseps campi) (Yanev and Wake 1981). A high level of genetic differentiation exists among California populations of the black salamander (Aneides flavipunctatus), suggesting that there has been little gene flow among populations (since the Pliocene or late Pleistocene epochs) (Larson 1980). Another example

TABLE 28.7

Mean heterozygosity values for reptile and amphibian species of the Sierra Nevada.

Taxonomic Name	Common Name	Number of Loci	Heterozygosity[a]	Sampling Range	Reference
Amphibians					
Ambystoma macrodactylum	Long-toed salamander	21	0.066	Oregon and Idaho	Howard and Wallace 1981
Ambystoma tigrinum	Tiger salamander	32	0.055	California[b]	Shaffer 1984[c]
Aneides flavipunctatus	Black salamander	21	0.103	California	Larson 1980
Batrachoseps campi	Inyo Mountains salamander	33	0.060	Inyo Mountains, California	Yanev and Wake 1981
Ensatina eschscholtzii	Ensatina	26	0.112	California	Wake and Yanev 1986
Hydromantes brunus	Limestone salamander	18	0.180	Mariposa County, California[b]	Wake et al. 1978
Hydromantes platycephalus	Mount Lyell salamander	18	0.080	Tuolumne County, California[b]	Wake et al. 1978
Hydromantes shastae	Shasta salamander	18	0.080	Shasta Lake, California	Wake et al. 1978
Hyla regilla	Pacific tree frog	14	0.007–0.093	Oregon and California	Case et al. 1975
Rana aurora	Red-legged frog	15	0.039	California Coast Range	Case 1978a
Rana boylei	Foothill yellow-legged frog	15	0.038	California	Case 1978a
Rana boylei	Foothill yellow-legged frog	15	0.045	California	Case 1978b
Rana cascadae	Cascade frog	15	0.037	Lassen County, California	Case 1978a
Rana catesbeinana[d]	Bullfrog	15	0.000	California[b]	Case 1978a
Rana muscosa	Mountain yellow-legged frog	15	0.060	Sierra Nevada	Case 1978a
Rana muscosa	Mountain yellow-legged frog	15	0.070	Sierra Nevada	Case 1978b
Taricha torosa	California newt	18	0.094	Sierra Nevada	Hedgecock and Ayala 1974
Reptiles					
Anniella pulchra	California legless lizard	27	0.022	Coastal California	Bezy et al. 1977
Elgaria coerulea	Southern alligator lizard	34	0.063		Good 1988
Elgaria multicarinata	Northern alligator lizard	34	0.013		Good 1988
Elgaria panamintina	Panamint alligator lizard	34	0.015		Good 1988
Sceloporus graciosus	Sagebrush lizard	19	0.030	Five western states	Thompson and Sites 1986
Uta stansburiana	Side-blotched lizard	18	0.053	California	McKinney et al. 1972

[a] Heterozygosity is the proportion of heterozygous genotypes per locus per individual.
[b] One population.
[c] Recalculated in Shaffer and Breden 1989.
[d] Introduced from eastern United States.

of this trend is found in a widely occurring reptile species sampled outside of the Sierra Nevada. Thompson and Sites (1986) measured an average F_{ST} of 0.231 among western steppe populations of the sagebrush lizard (Sceloporus graciosus).

Little work has been done on genetic variation in morphological characteristics in Sierran populations of reptiles; most recent studies have been done on non-Sierran populations of the Pacific Coast. Seeliger (1945) surveyed morphological variation in the western pond turtle (Clemmys marmorata) and found that individuals in Sierra Nevadan populations had morphological characteristics that were intermediate to those in north coastal and south coastal areas of California. Although the genetic basis for these differences has not been established, such polymorphisms are the basis for further study. Bechtel and Whitecar (1983), in controlled breeding of Californian samples, have established inheritance of color patterns in the gopher snake (Pituophis melanoleucus). However, no studies have been done on the population structure or the ecological context of this variation in color pattern. In a study of geographic variation in feeding preferences in Californian populations of the terrestrial garter snake (Thamnophis elegans), Arnold (1980a, 1980b) established that differences between coastal and interior populations are inherited and affect feeding (or avoidance) responses to slugs, amphibians, and the toxic newts (Taricha spp.). Although Sierran populations were not included in the study, they do indicate adaptation to available food and suggest habitat-based population differences in Sierran garter snakes (as in Jennings et al. 1992). Sinervo and colleagues have done extensive work on physiological and biophysical genetics in lizards of the genera Uta and Sceloporus, comparing populations from contrasting environments in the western United States. They have found differences among species and among and within Oregon and southern California populations in thermal physiology and growth (Sinervo 1990; Sinervo and Adolph 1994); differences among and within Coast Range populations in the trade-offs between reproductive numbers, egg size, and survival (Sinervo et al. 1992, 1991); and heritability of running performance and leg and tail size (Tsuji et al. 1989).

Although population structure and gene flow are critical to genetic assessments of these species, it is not certain how the well-studied species groups may serve as models for the less-studied majority. There is little information on how life history traits might relate to fitness-relevant genetic variation, but this is considered to be a worthy topic for further research. Recent losses in amphibian populations require that Case's early work on frogs be reassessed and expanded. There is also very little information on local adaptation. Other high-priority research needs are comparisons of mitochondrial and nuclear DNA patterns to assess variation in sex-biased gene flow (as in Wade et al. 1994).

Fish

In the Sierra Nevada bioregion, there are approximately forty fish species native to the inland lakes and rivers, and another thirty or thirty-one species have been introduced (Moyle 1976). The overwhelming majority of genetic information (morphological, allozyme, and mtDNA) is for the commercially significant salmonid (family Salmonidae) species. Although only a few salmonid species are native to the Sierra Nevada (e.g., whitefish [Prosopium williamsoni], cutthroat trout [Oncorhynchus clarki], golden trout [O. mykiss whitei and O. mykiss aguabonita], and rainbow trout [O. mykiss]), several others are anadromous visitors (e.g., chinook salmon [Oncorhynchus tshawytscha], steelhead salmon [O. mykiss irideus], and Pacific lamprey [Lampetra tridentata]), and others have been introduced (e.g., brook trout [Salvelinus fontinalis], lake trout [Salvelinus namaycush], brown trout [Salmo trutta], and kokanee [Oncorhynchus nerka]). California, and to a lesser extent the Sierra Nevada, contains the southernmost populations of most of the anadromous fish of the Pacific coast of North America (Moyle 1994) and thus have the potential for harboring rare and/or genetically significant populations (Nielsen et al. 1994).

Of the life-history traits that most affect the amount and pattern of genetic variation in fish species, perhaps the most significant is the spawning migration typical of many of the species discussed here. Returning to their natal streams to reproduce would tend to restrict gene flow among the residents of various streams and thereby impose a certain geographic structure on genetic variation (e.g., Bartley et al. 1992).

Although species and subspecies designations in fish, like those in other taxa, have often relied heavily on morphometric characteristics, it has been suggested that the environment may play a larger role in determining phenotype in fish than in many other animal species (e.g., Allendorf et al. 1987). For example, certain physiological traits of fish (including indeterminate growth capacity, greater sensitivity to variation in temperature than other homoisothermic [cold-blooded] vertebrates, and greater flexibility in traits associated with reproductive success) may allow great phenotypic plasticity, thereby widening the potential gap between genetic and phenotypic variation.

In general, fish species of the Sierra Nevada for which there is some genetic information show rather low to moderate levels of within-population genetic variation and low levels of population differentiation (tables 28.9 and 28.10). In a review of eight salmonid taxa, Allendorf and Leary (1988) reported mean heterozygosity values of 0.013 to 0.095. The importance of within-population genetic variation is emphasized in studies comparing hatchery populations (which may have undergone a severe bottleneck—that is, may have been generated from a fairly small sample of the original population) with wild populations. In such cases (e.g., Bartley and Gall 1990), there is little evidence that hatchery populations have reduced amounts of genetic variation compared with natural populations. This suggests that if the species has low levels of genetic (or, at least, allozyme) variation in natural populations, this variation is not reduced significantly by taking a sample and using this as breeding stock.

However, the comparison of hatchery and wild trout and salmon populations in California shows different results when different genetic markers are used. With mitochondrial DNA (maternally inherited), there is an increase in diversity in hatchery stocks due to the introduction of geographically di-

TABLE 28.8

Population differentiation values (F_{ST}) for reptile and amphibian species of the Sierra Nevada.

Taxonomic Name	Common Name	Number of Loci	F_{ST}[a]	Sampling Range	Reference
Amphibians					
Ambystoma macrodactylum	Long-toed salamander	21	0.350	Oregon and Idaho	Howard and Wallace 1981
Aneides flavipunctatus	Black salamander	21	0.470	California	Larson 1980
Batrachoseps campi	Inyo Mountains salamander	33	0.470	Inyo Mountains, California	Yanev and Wake 1981
Ensatina eschscholtzii	Ensatina	26	0.705	California	Wake and Yanev 1986
Reptiles					
Sceloporus graciosus	Sagebrush lizard	19	0.231	Five western states	Thompson and Sites 1986

[a] F_{ST} is the amount of genetic differentiation among populations of a species.

TABLE 28.9

Mean (observed) heterozygosity values for fish species of the Sierra Nevada.

Taxonomic Name	Common Name	Number of Loci[a]	Heterozygosity[b]	Sampling Range	Reference
Oncorhynchus kisutch	Coho salmon	45(23)	0.027	Northern and central California	Bartley et al. 1992
Oncorhynchus tshawytscha	Chinook salmon	53(21)	0.038	Coastal and inland northern California	Bartley and Gall 1990
O. tshawytscha	Chinook salmon	78(47)	0.053	Northern California and southern Oregon	Gall et al. 1992
Gasterosteus aculeatus	Three-spined stickleback	18(7)	0.100	Northern California	Haglund et al. 1992
Catostomus tahoensis	Tahoe sucker	~60(12)	0.023	Pyramid Lake, Nevada	Buth et al. 1992
O. mykiss whitei	Golden trout	12(6)	0.134[c]	Southern Sierra Nevada	Gall et al. 1976
Oncorhynchus mykiss	Rainbow trout	32(24)	0.092	Northern and coastal California	Berg and Gall 1988

[a] Number of loci assayed is followed, in parentheses, by the number of loci polymorphic and scorable.
[b] Heterozygosity is the proportion of heterozygous genotypes per locus per individual.
[c] Excludes the heterozygosity estimate for the rainbow trout sample in the study.

vergent maternal lineages in the process of egg and fry transfers (Nielsen et al. 1994). With microsatellite DNA (paternally inherited), the opposite trend is noted, with hatchery rainbow trout in southern California showing greatly reduced levels of genetic diversity when compared with wild populations (J. L. Nielsen, Pacific Southwest Research Station, U.S. Forest Service, e-mail communication with the authors, 1995).

Probably the best studied of the western salmonids is the rainbow trout (Oncorhynchus mykiss). Although native to a relatively small range on the Pacific coast of Canada and the United States, including the Sierra Nevada, it has been distributed around the world, and its high commercial value has prompted genetic investigation, particularly on heritability of morphometric characteristics (e.g., Elvingson and Johansson 1993; Gjedrem 1992; Gjerde and Schaeffer 1989). Even within its native range, it displays a wide range of phenotypes, including being freshwater and anadromous, inhabiting great ranges in water temperature and flow rate, and even displaying some variation in chromosome number (Hershberger 1992). However, the extent to which the phenotypic variation is due to genetic variation is still under investigation.

Since we have only limited information on Sierra populations, we can gain insight by examining studies of the same species in nearby regions. In a study of thirty-two rainbow trout populations in Idaho, Oregon, and Washington, allozyme analysis revealed a high degree of polymorphism. The mean heterozygosity value of 0.059 is high for a salmonid (Allendorf 1975). A more recent study of coastal California rainbow trout populations (including several in the Sierra Nevada—for example, the Middle Fork of the Feather River) also revealed high levels of heterozygosity (Berg and Gall 1988). The mean heterozygosity value for these populations (0.092, table 28.9) is even higher than the estimate for the more northern populations. Analysis showed little evidence of geographic structuring in these populations and suggested moderate to high levels of gene flow (table 28.10). Although a few populations were distinguished by the presence of a few uncommon alleles, Berg and Gall (1988) suggested that this could be due to temporal fluctuations in allele frequencies rather than stable geographic structure.

Recent studies based on mitochondrial DNA and microsatellite alleles of the southern steelhead, the anadromous form of rainbow trout, show significant differences in genetic frequency among three biogeographic zones in California: northern, from Humboldt Bay to Gualala Point; cen-

TABLE 28.10

Genetic population structure (F_{ST}) for fish species of the Sierra Nevada.

Taxonomic Name	Common Name	Number of Loci[a]	F_{ST}	Sampling Range	Reference
Oncorhynchus kisutch	Coho salmon	45(23)	0.158[b]	Northern and central California	Bartley et al. 1992
Oncorhynchus tshawytscha	Chinook salmon	53(21)	0.177[b]	Coastal and inland northern California	Bartley and Gall 1990
O. tshawytscha	Chinook salmon	78(47)	0.106[b]	Northern California and southern Oregon	Gall et al. 1992
Gasterosteus aculeatus	Three-spined stickleback	18(7)	0.163	Western North America	Haglund et al. 1992
Oncorhynchus mykiss	Rainbow trout	32(24)	0.127	Northern and coastal California	Berg and Gall 1988

[a] Number of loci assayed is followed, in parentheses, by the number of loci scorable and polymorphic.
[b] Actually calculated as G_{ST}.

tral, from the Russian River to Point Sur; and southern, from San Simeon Point to Santa Monica Bay (Nielsen et al. 1994).

An allozyme study of thirty-five populations of chinook salmon (Oncorhynchus tshawytscha) from inland and coastal waters of California (including samples from the Yuba River, Bear Creek, Merced River, Stanislaus River, and Tuolumne River in the Sierra Nevada) revealed a mean heterozygosity value of 0.038, typical for salmonid species (table 28.9). The lowest heterozygosity values were found in the Klamath–Trinity River drainage (0.008–0.022), the authors speculating that this may be due to effects from relatively recent volcanic activity (Bartley and Gall 1990). Ash from volcanoes kills fish through suffocation and mechanical abrasion, thereby reducing population sizes and removing some of the naturally occurring genetic variation within populations. Somewhat higher population differentiation exists among these California populations ($F_{ST} = 0.177$) than has been reported in Alaska populations, the authors suggesting that this resulted from the longer time since glaciation in California. Further, although there is some evidence of coastal-inland genetic structuring in certain other salmonids, such as cutthroat and rainbow trout, there is no allozyme evidence for such a distinction in chinook salmon in California (Bartley and Gall 1990).

More population differentiation is observed in chinook salmon when mitochondrial DNA, rather than isozymes, is studied. Four groups in the Sacramento–San Joaquin Basin, which have historically been recognized as discrete units based on the seasonal distribution of their peak spawning times, were also recognized as genetically divergent based on mitochondrial data (Nielsen et al. 1994).

Two inland subspecies of the cutthroat trout are recognized as native to the Sierra Nevada, the Lahontan cutthroat (Oncorhynchus mykiss henshawi) and the Paiute cutthroat (O. m. seleneris). An allozyme study of populations within the range of the Lahontan subspecies in northeastern California and northern Nevada showed much population differentiation, with 45% of the observed allozyme variation accounted for as genic diversity among populations (Loudenslager and Gall 1980). This is unusual among Sierra Nevada fishes and not the standard pattern for cutthroat; other cutthroat subspecies show less population differentiation (Loudenslager and Gall 1980). The authors suggest that the population differentiation observed may be due to the fact that this subspecies inhabits the large lakes and headwater tributaries of the Humboldt, Truckee, Carson, and Walker Rivers, drainages that are presently isolated from one another. Further, since the final desiccation of glacial Lake Lahontan occurred 8000 years BP, the populations may have been isolated for a long time. More recent (unpublished) molecular studies of the Humboldt and Lahontan cutthroat trout populations show significant loss of genetic diversity in fragmented populations, regardless of geological time of isolation (J. L. Nielsen, e-mail communication with the authors, 1995).

Golden trout, endemic to the southern Sierra Nevada, has been the subject of recent genetic studies. Concern has focused on this species due to its extremely narrow range, human disturbance of its fragile habitat, and the high probability of hybridization between endemic goldens and rainbow trout, which have been introduced into significant portions of the golden's range, diluting and contaminating natural populations (Gall et al. 1976). Also, golden trout has been widely planted outside its native range. The estimate for mean heterozygosity for the two subspecies (S. a. aguabonita and S. a. whitei) is 0.134, indicating considerably more within-population allozyme diversity than most other studied fish species of the Sierra Nevada. Indeed, even the Cottonwood Creek population of S. a. aguabonita, which was a planted population started with only twelve or thirteen trout, has a high heterozygosity estimate (0.126) (Gall et al. 1976). The estimate for the two populations of S. a. whitei, while somewhat lower than the other populations (0.088), is still reflective of considerable genetic variation and leads the authors to suggest that the so-called "threatened" Little Kern golden trout "did not appear to be in immediate danger of extinction through lack of adaptive capability" (Gall et al. 1976).

Some genetic information is also available for the threespine stickleback (Gasterosteus aculeatus), a species with a widespread, circumboreal distribution that includes coastal California. It was introduced to some inland California waters, including the Mono Basin (Moyle 1976). A recent allozyme study of widespread populations in this species estimated the heterozygosity of the northern California sample to be 0.100, a value higher than that of most salmonid species and comparable to values for other teleosts (Haglund et al. 1992).

In summary, fish species of the Sierra Nevada show very modest levels of genetic variation within their populations. Although there is much apparent phenotypic variation within most species, a great deal of this may be due to environmental influences rather than genetic differences. In species that are anadromous or that occupy large river drainages, there is surprisingly little population differentiation. Striking counterexamples of much population differentiation occur in a few species that have been isolated in lakes or in nonconnected rivers for a long time. Most of the genetic studies on species of the Sierra Nevada are based on allozyme data, thereby limiting the opportunity to compare genetic patterns based on various different types of data. Fish introductions, transplants, and the release of hatchery-raised fish complicate the assessment of "natural" levels and patterns in genetic variation of fish species, perhaps more than in other taxonomic groups.

Insects

In the state of California, there are approximately 28,000 species of insects (Powell and Hogue 1979), many of them represented in the Sierra Nevada bioregion. In spite of their vast species representation, genetic information for this taxonomic group is both limited and sporadic (table 28.11). Most intraspe-

TABLE 28.11

Genetic population structure (F_{ST}) for insect species of the Sierra Nevada.

Taxonomic Name	Common Name	Number of Loci	F_{ST}	Sampling Range	Reference
Pieris rapae[a]	Cabbage butterfly	4	0.014	United States	Pashley et al. 1985
Cydia pomonella	Codling moth	4	0.066	Africa, Europe, U.S., Australia	Pashley 1980
Euphydryas chalcedona	Chalcedona checkerspot	8	0.090	Central California	McKechnie et al. 1975
Euphydryas editha	Checkerspot	8	0.118	Central California	McKechnie et al. 1975
Chrysomela aeneicollis	Montane leaf beetle	5	0.135	Sierra Nevada	Rank 1992
Coenonympha tullia	[Satyrine butterflies]	21	0.051	Northern California, southwestern Oregon, northern Nevada	Porter and Geiger 1988
Oeneis chryxus	[Satyrine butterflies]	16	0.081	Sierra Nevada	Porter and Shapiro 1989
Speyeria nokomis apacheana	Western seep fritillary	25	0.022	Sierra Nevada	Britten et al. 1994b

[a] Introduced species.

cific studies have been driven by human-interest factors such as health issues (e.g., mosquitoes), agricultural or forest crop concerns (e.g., budworms, bark beetles, and grasshoppers), or aesthetic interests (butterflies). For example, some studies have investigated genetic variation in response to pesticides in defoliating insect species (e.g., Choristoneura spp.) (Stock and Robertson 1980). A few species of particular phylogenetic interest or scientific value (e.g., fruit flies) have received considerable attention. Aquatic insects, including stoneflies, mayflies, and water striders, have received relatively little attention (White 1988).

Beyond the insects affecting health concerns and agricultural and timber production, and species of special interest, most insects have not been genetically studied, even at the species level. Thus, there are major gaps in the knowledge of intraspecific genetic variation. In particular, there is little genetic information for species with rare host plants. As there is much variation in breeding systems and other life history traits among insect species, and because the available genetic information is so sporadic, generalizations across these taxa are difficult.

Of those few insects of the Sierra Nevada that have been studied, the most common trend is for them to have genetic architectures displaying little population differentiation and high levels of gene flow among populations (table 28.11). In a study of twenty-one populations of a satyrine butterfly complex (Coenonympha tullia) in the northern Sierra Nevada, southwestern Oregon, and northern Nevada, Porter and Geiger (1988) found a high degree of polymorphism within populations but little interpopulation differentiation (mean F_{ST} = 0.051; 35%–59% polymorphic loci; expected heterozygosity = 13%–20%).

In an allozyme study of forty-one populations of the checkerspot butterfly (Euphydryas editha), little genetic variation was found among populations despite great geographic distances and ecological differences within the range of the species in the western United States (Baughman et al. 1990). An analysis of nineteen isozyme loci showed six major groupings, three of which have representative populations in the Sierra Nevada.

Considerable genetic research has been conducted on the bark beetles (family Scolytidae), largely owing to their destructive effects on pine forests in North America. More than 170 species of bark beetles occur in California (Powell and Hogue 1979), many of them in the Sierra Nevada. Until recently, most genetic research on bark beetles had been directed toward understanding the evolution of the various species (Hayes and Robertson 1992). Allozyme studies of the mountain pine beetle (Dendroctonus ponderosae) have revealed fairly high levels of heterozygosity (0.17 in a California population) and moderate differentiation among geographically separated populations (Stock et al. 1992). For both this species and the pine engraver (Ips pini), the observation has been that heterozygosity levels tend to be higher in populations that inhabit severe environmental conditions, a situation opposite to that found in coniferous trees.

Morphological, allozyme, and DNA data have recently been compared in one termite genus that is restricted to western North America, the dampwood termites (Zootermopsis spp.). Two of the three currently recognized extant species of this genus, Z. nevadensis and Z. angusticollis, are distributed sympatrically along the Pacific Coast from British Columbia to Baja California, Mexico, including the Sierra Nevada. Analysis of cuticular hydrocarbon (i.e., a phenotypic characteristic of unknown genetic basis) had been shown to distinctly identify all three species as well as to suggest two subspecies within Z. nevadensis (Korman et al. 1991). However, the two putative subspecies were not confirmed by allozyme differences. Allozyme variation within Z. nevadensis (expected heterozygosity 0.080), with samples included from the Sierra Nevada, was somewhat lower than that found in Z. angusticollis (expected heterozygosity 0.199) and close to an average reported for insects. More recent genetic studies, based on mitochondrial DNA, also showed slightly higher genetic variation within Z. angusticollis than within Z. nevadensis. Sierra Nevada samples for the latter species were included in this study. The several putative subspecies within Z. nevadensis, proposed on the basis of morphological data, were neither confirmed nor disputed by the mitochondrial data.

Of those species having been studied intraspecifically, genetic information has mainly been based on phenotypic or allozyme data, and the study objectives have most commonly been gene flow. However, studies of phenotypic variation often have not been genetically controlled and are usually confounded by environmental plasticity. Thus, it is uncertain how the allozyme data relate to genetic variation of adaptive significance. For the previously mentioned reasons, available gene-flow information is difficult to extrapolate to less-studied species. One possible generalization among insects is based on species mobility. Insects, like birds, can be considered to consist of two subgroups: one is colonial, highly specialized in its needs, and sedentary; the other is highly vagile and more generalized in resource utilization. In the former group, one would expect to find higher rates of inbreeding and endemism; in the latter, less. Few data exist, however, on insects in the Sierra Nevada to substantiate this.

In a direct examination of the relationship between vagility and population structure, Zera (1981) examined two species of water striders that differ in degree of winglessness. One species, Gerris remigis, has a widely distributed range, including the Sierra Nevada, and is nearly wingless. The other species, Limnoporus canaliculatus, occurs in the eastern United States and is wing-polymorphic. G. remigis, the wingless species, exhibited strong population structuring, fixation of alleles within populations, and relatively low heterozygosity within populations. The more vagile L. canaliculatus, in contrast, showed little population structuring and four times as much heterozygosity as G. remigis.

In summary, much of the genetic research on insects of the Sierra Nevada has been concerned with evolutionary history and species relationships. The relatively small number of species that have been genetically studied at the intraspecific level tend to show fairly high levels of genetic variation (e.g., high heterozygosity). The degree of population differentiation may be related to the migratory behavior and level of specialization of the species: species that are highly vagile and broadly associated with hosts might show less population differentiation than the converse.

Fungi

The number of fungal species in the Sierra Nevada cannot defensibly be estimated. This is a very large collection of species including the Basidomycota, Ascomycota, Zygomycota, and Chytridiomycota. Only a small fraction of the species in these groups have been studied genetically anywhere. Those that have been studied often have some economic importance (e.g., Armillaria [Basidomycota]) or have value as an experimental organism (e.g., Neurospora [Ascomycota]). Heritability estimates have been provided for some characteristics of an ectomycorrhizal fungus (Pisolithus tinctorius) that is beneficial to a commercially important tree species in the southeastern United States, slash pine (Pinus elliottii) (Rosado et al. 1994). In general, species in the Zygomycota and Chytridiomycota have received very little attention (Bruns et al. 1991), and taxa in general from the Sierra Nevada are scarcely even described, let alone studied, for intraspecific variation.

There may be more levels of intraspecific variation in fungal species than in other taxa. One reason relates to the biological species concept. This concept pertains to the definition of species based on reproductive barriers: individuals that can interbreed belong to the same species; those that can't belong to different species. This concept of a species doesn't fit fungal behavior well. There are often intersterility groups, or ISGs (groups in which the individuals from one group cannot reproduce sexually with individuals from another group), within fungal species that by definition could be classified as separate species. Other factors leading to potentially exceptional levels of within-species diversity relate to morphological or life history characteristics. For example, in endomycorrhizal fungi (Zygomycota), the mycelium can be partitioned morphologically and metabolically, the nuclei migrate, and germ tubes start new individuals that must adapt to host-soil conditions at the same or different locations. Somatic mutations have major consequences, since all cells of a fungal organism are totipotent (that is, each cell maintains the potential to develop into a complete organism). Accumulation of deleterious effects of these mutations can be averted if those nuclei are partitioned in nongerminating structures (Morton and Bentivenga 1994). There are potentially high rates of mutation in fungal species. For example, one race of wheat rust (Puccinia graminis) gave rise to more than fifty mutational variants during the 1960s (Burdon and Roelfs 1985b).

For these and other reasons, morphometric characters are seldom considered representative of genetic variation in fungal species. Often there may be very little variation in morphology within a species (Gardes et al. 1991; Otrosina et al. 1992). Alternatively, life cycle morphs complicate the study of intraspecific genetic variation by the examination of morphometric traits. For example, rust fungi—one of the largest groups of obligately parasitic plant pathogens—frequently produce five morphologically distinct spore stages and alternate between two unrelated plant hosts, making morphological identification difficult (Gardes and Bruns 1993).

Intraspecific genetic variation in fungal species is typically measured by DNA analysis, allozyme analysis, or virulence studies. (For a virulence study, fungal spores are collected and inoculated with the appropriate host plant. After remaining in conditions suitable for germination for a week or two, evidence of infection can be noted.) In some cases, the genetic patterns revealed by different methods are not consistent. For example, in a study of wheat rust (P. graminis) in Australia, a virulence analysis detected sixteen different races, while an isozyme survey detected no intraspecific variation (Burdon and Roelfs 1985b). In contrast, a study of eastern United States wheat rust that used these same two methods showed complementary patterns. The authors suggest that the difference may be due to life history characteristics. In the latter study, the populations had undergone sexual reproduction until the 1920s, when the alternate host, the barberry, was eradicated. The former (Australian) study was based on populations that had never possessed a functional sexual cycle (Burdon and Roelfs 1985b). A study using both isozyme and RFLP (i.e., fragments of DNA that indicate genetic differences based on how well they match a control library of DNA fragments) analysis of the fungal pathogen Rhizoctonia solani showed complementary genetic patterns, revealing five genetically distinct intraspecific groups (Liu and Sinclair 1992).

Genetic variability in plant pathogens has often been studied on a large geographic scale but seldom at the level of individual populations (McDonald and Martinez 1990). Since many fungal species occur worldwide, the scale of sampling can have significant consequences for the pattern of genetic variation observed. For example, in an isozyme study of wheat stem rust (Puccinia graminis) in thirteen countries, most of the alleles were widespread, yet the author observed that considerable variation could occur at more local levels (Burdon 1986). Indeed, in a hierarchical study (locations in field, stems within locations, lesions within a leaf, etc.) of a haploid fungus (Septoria tritici) sampled in one field near Davis, California, the authors found considerable genetic variation. The pattern observed was of a population highly subdivided into a mosaic of independent clones without significant migration between different locations in the field. The authors hypothesized that genetically diverse founding populations had provided the initial inoculum, and reproduction via asexual spores had resulted in localized clusters of clones. They concluded that most genetic variation in this fungal species may be distributed on a local, rather than broad, geographic scale (McDonald and Martinez 1990).

There are only a few examples of genetic studies based on samples of fungal species within the Sierra Nevada. An allozyme study has been conducted on the pathogen Heterobasidion annosum (= Fomus annosus), which causes root rot of coniferous tree species in temperate forests worldwide, including the Sierra Nevada. Two ISGs within this species have been described in North America. In the western United States the two groups occur sympatrically (i.e., in the same or overlapping areas) on a variety of host species. Samples from Oregon and California (including Yosemite National Park, Sequoia National Park, Plumas National Forest, etc.) showed isozyme patterns that largely concurred with the intersterility groups (Otrosina et al. 1992). Very few alleles were shared by the two groups, and the study results suggested that little or no gene flow occurs in nature between the two ISGs. Within each ISG there was a high degree of allele fixation. Given that there are differences in host preferences by the two ISGs, paleoecological factors that influence host species distributions may be major forces driving the genetic differentiation in this species.

An allozyme study of the western gall rust fungus (Pteridermium harknessii) in the western United States (including samples from the Sierra Nevada) showed considerable genetic variation (six of fifteen isozyme loci were polymorphic) (Vogler et al. 1991). Further, the isozyme profiles separated the samples into two distinct groups (“zymodemes”), each of which had a characteristic electrophoretic profile. Populations from both zymodemes were found in the Sierra Nevada, whereas only one of the zymodemes was found in the populations sampled in southern Oregon and coastal California. In forests in the Sierra Nevada where both zymodemes occurred, there was no evidence of gene flow between the two. Despite the great range in pine host species and the geographic area covered, most of the genetic variation in the fungus was between the zymodemes, with persistent heterozygosity in one group. Thus, this fungus presents a very different pattern of genetic variation than that of its pine hosts.

Another example of slow rates of gene flow is found in a study of the fungus that causes white pine blister rust (Cronartium ribicola), which infects North American white pines, including sugar pine (Pinus lambertiana). It is an introduced pathogen, probably arriving in western North America in about 1910. There is a major gene for resistance to the fungus in sugar pine (Kinloch 1992). However, a virulent race of the blister rust fungus has been discovered that can completely overcome the resistance normally conferred by the gene. This virulent race was first discovered in 1978 near Happy Camp in the Siskiyou Mountains of northern California. A virulence study by Kinloch and Dupper (1987) of samples of rust from Washington to California provided no evidence of the virulent race except in the vicinity of the initial discovery site. Thus, the authors concluded that if the gene is moving it is migrating slowly, and that possibly the fungus is largely inbreeding, thereby slowing the rate of gene flow.

In conclusion, based on the genetic studies reviewed, it seems that a primary factor in the amount and pattern of genetic variation in fungal species is the mode of reproduction. The presence or absence of intersterility groups, asexual or sexual reproduction, and time since cessation of sexual reproduction in currently asexual species or populations have all been found to have profound impacts on genetic variation.

Conclusions

The overview of genetic information for species of the Sierra Nevada highlights the fact that species have been studied sporadically, leaving large information gaps and making generalizations difficult. Certain groups have been well studied at the population level, often due to human-interest factors. Examples include salmonid fishes, plethodontid salamanders, butterflies, and commercially important forest tree species.

For many species, even basic taxonomic information or recent species-distribution maps are not available. Although some generalizations can be offered for the well-studied species concerning the relationship between genetic variation and geographic patterns or life history characteristics (e.g., low F_{ST} values for most but not all organisms studied at the population level), the sporadic information base makes it difficult to extrapolate these patterns to the unknown majority. One often-noted geographic trend at the SNEP Genetics Workshop was a stronger genetic relationship with elevation (i.e., an east-west trend) than with latitude. In terms of research needs, a common refrain was the need for more studies on gene flow and genetic structuring at the population level, prerequisites for understanding genetic processes and enabling better extrapolation and prediction. A common concern was the relative lack of information on adaptive variation. Because molecular markers are often employed in genetic studies, an important concern is the extent to which these markers reflect genetic variation of adaptive significance. There was much discussion about the conditions under which these data would reflect fitness-related genetic variation of particular interest to land management.

Patterns of Genetic Significance in the Sierra Nevada

In view of the need to set priorities for natural resource management, it is important not only to discuss the nature of genetic variation but also to attempt to define what is genetically significant. Such a definition addresses three issues: (1) What are attributes of significance? (2) What levels in the genetic continuum are significant? and (3) What is the physical scale or standard for defining genetic significance?

One set of attributes for significance includes genetic variation that is rare, rich, or representative (see Millar et al. 1996). Rarity implies those genetic entities that are unusual in some respect, often, but not always, in an ecological context. Examples include disjunct populations in an otherwise contiguous species, marginal populations, and organisms displaying unusual adaptations, such as those occupying unusual soil types or elevational extremes. Rarity can also be used to describe those entities that, while not necessarily rare in an ecological sense, are evolutionarily significant or phylogenetically rare. Examples could include monotypic species or those with unusual phylogenetic histories. Another type of rarity involves rare alleles or rare genotypes. In these cases, there may be a geographic or adaptive significance that is not associated with an obvious environmental gradient. Rarity, as it is used here, does not refer to any legal or policy-oriented interpretations.

Richness implies high levels of genetic diversity. Richness criteria can be applied at any level of genetic variation, from the levels at which it originates (DNA base pairs to individual genes to chromosomes to genotypes) to the levels at which it is manifested or structured (populations to subspecies to races). Richness is often associated with three arbitrary levels of organization: within populations, among populations, and among species. Although within the context of genetic significance it is desirable to understand richness at the population level or within populations, information is often not available to allow more than a definition of species richness. Hybrid zones are another example that frequently show a high degree of genetic richness.

Representativeness is perhaps the most significant type of genetic variation. Representative individuals or populations typify the genetic composition and structure (allelic and genotypic frequencies) of a reference group. Such a group most likely is the locally adapted ecotype but could be a race or subspecies. This concept is often discussed nongenetically at the plant community or vegetation association level, where one might refer to an area, for example, that is representative of the mixed conifer forest. Representative genetic variation reflects species structure, geographic subdivisions, and large-scale adaptiveness within species.

A second issue when considering genetic significance is the biological level under consideration. Genetic variation is a continuum, spanning the levels at which it originates (diversity among alleles, chromosomes, or individual genotypes) through those levels at which it can be manifested (i.e., within individuals, among individuals in a population, among individuals among various populations, among individuals in geographic or ecological regions, etc.). The value of one level of genetic variation to another—for example, the value of individual diversity to ecosystem health—is assumed but not well understood. The level at which an attribute is described more often reflects the level at which there is some current information rather than the level that is perhaps most responsible for the attribute. As such, attributes will most often be described as pertaining to the species complex, species, or population. It is also understood that genetic significance pertains to levels that are hierarchically arranged and natural in origin. Thus, human-vectored gene introductions, exotic species, and “contrived” ecosystems (e.g., Monterey pine “ecosystems” in New Zealand) all represent levels of genetic variation that lie outside the scope of this chapter.

The geographic domain or context within which to assess genetic significance must also be addressed. For the purposes of this chapter, genetic significance (rarity, richness, or representativeness) is assessed relative to the Sierra Nevada bioregion and, where possible, relative to watershed domains.

The sections that follow address genetic significance for each taxonomic group in response to two questions:

1. What are the key factors in this taxonomic group that contribute to geographic patterns of genetic variation?
2. What are some locations of genetic significance—by attribute and level?

TABLE 28.12

Key factors underlying geographic patterns of intraspecific genetic variation for conifers of the Sierra Nevada.

Priority[a]	Factor
1	East-west subdivision: this reflects climate, elevation, biogeographic history, soil moisture availability, and biotic interactions such as competition. (This is also a key factor for species-level diversity.)
2	Elevation (primary) and aspect (minor): from the north down to the Sierra National Forest on the east side and on the west side, respectively. Glacial history: from the Sierra National Forest south (Note: This distinction of key factors is due to a correlation between latitude and elevation.)
3	Glacial/tectonic history. (This is also a key factor for species-level diversity.)
4	Species-specific gene flow factors: barriers to or corridors for gene flow, e.g., riparian areas, mountains, canyons.
5	Unusual or modifying factors, e.g., rare substrate, aspect.

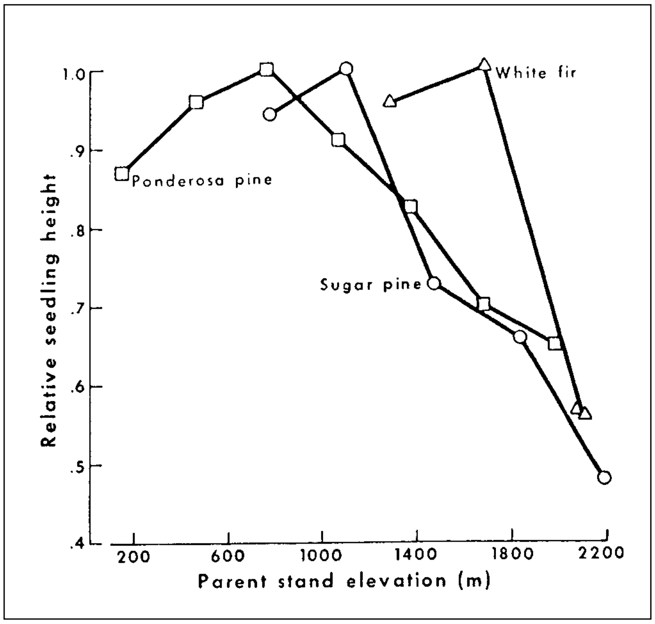
[a] 1 is the most influential factor, etc.

Plants

A relatively large database for commercial conifer tree species and some others supports generalizations regarding key factors that contribute to geographic patterns of genetic variation (table 28.12). The available data indicate that the most notable trend in intraspecific genetic variation in coniferous trees of the Sierra Nevada is an east-to-west transition. Rather than being related to one specific factor, this longitudinal pattern is related to several integrated factors, most notably elevation, and reflects changes in such ecosystem elements as climate (especially temperature and precipitation), soil moisture availability, biotic interactions, and biogeographic history. This east-west gradient of genetic variation has been revealed in several transect studies of such species as white fir (Abies concolor) (e.g., Hamrick 1976), sugar pine (Pinus lambertiana) (e.g., Harry et al. 1983), and ponderosa pine (P. ponderosa) (e.g., Conkle 1973). Seedlings from each of the species were collected along a transect along the western slope of the Sierra Nevada, encompassing an elevational range of approximately 2,100 m (7,000 ft). Seedlings were grown in a common-garden environment at a site near Placerville (about 800 m [2,640 ft]) and measured periodically. Height growth of seedlings after two years shows similar trends among the three species in the influence of source elevation (figure 28.1).

FIGURE 28.1

Influence of seed source elevation on two-year-old seedling height of sugar pine (Harry et al. 1983), ponderosa pine (Mirov et al. 1952), and white fir (Hamrick 1976) from an elevational transect in the Sierra Nevada. The common-garden study elevation is approximately 800 m. (From Harry et al. 1983.)



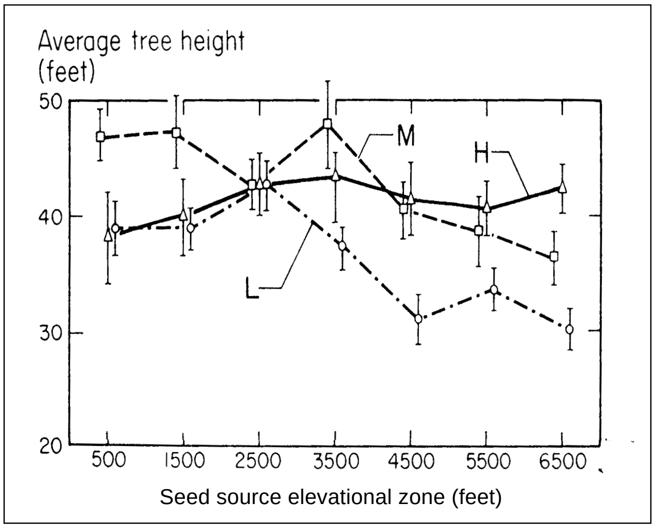


FIGURE 28.2

Height of ponderosa pine from a transect study, after twenty-nine years, at three common-garden sites differing in elevation: L = low elevation, 960 ft (about 300 m); M = middle elevation, 2,730 ft (about 800 m); and H = high elevation, 5,650 ft (about 1,700 m). (From Conkle 1973.)

This genetic relationship between tree height and source elevation is complex. The common-garden study just described was replicated with ponderosa pine at three sites of varying elevation. Conkle (1973) analyzed the results after twenty-nine years of growth and found evidence of genotype x environment interactions (figure 28.2). While height differences are relatively minor among seed sources at the high-elevation site, they vary dramatically among seed sources at the low-elevation site. Thus, the greatest risk in seed transfer is from high-elevation sites to low-elevation ones.

Multilocus analysis of allozyme data has confirmed these east-west trends for several species, including ponderosa pine,

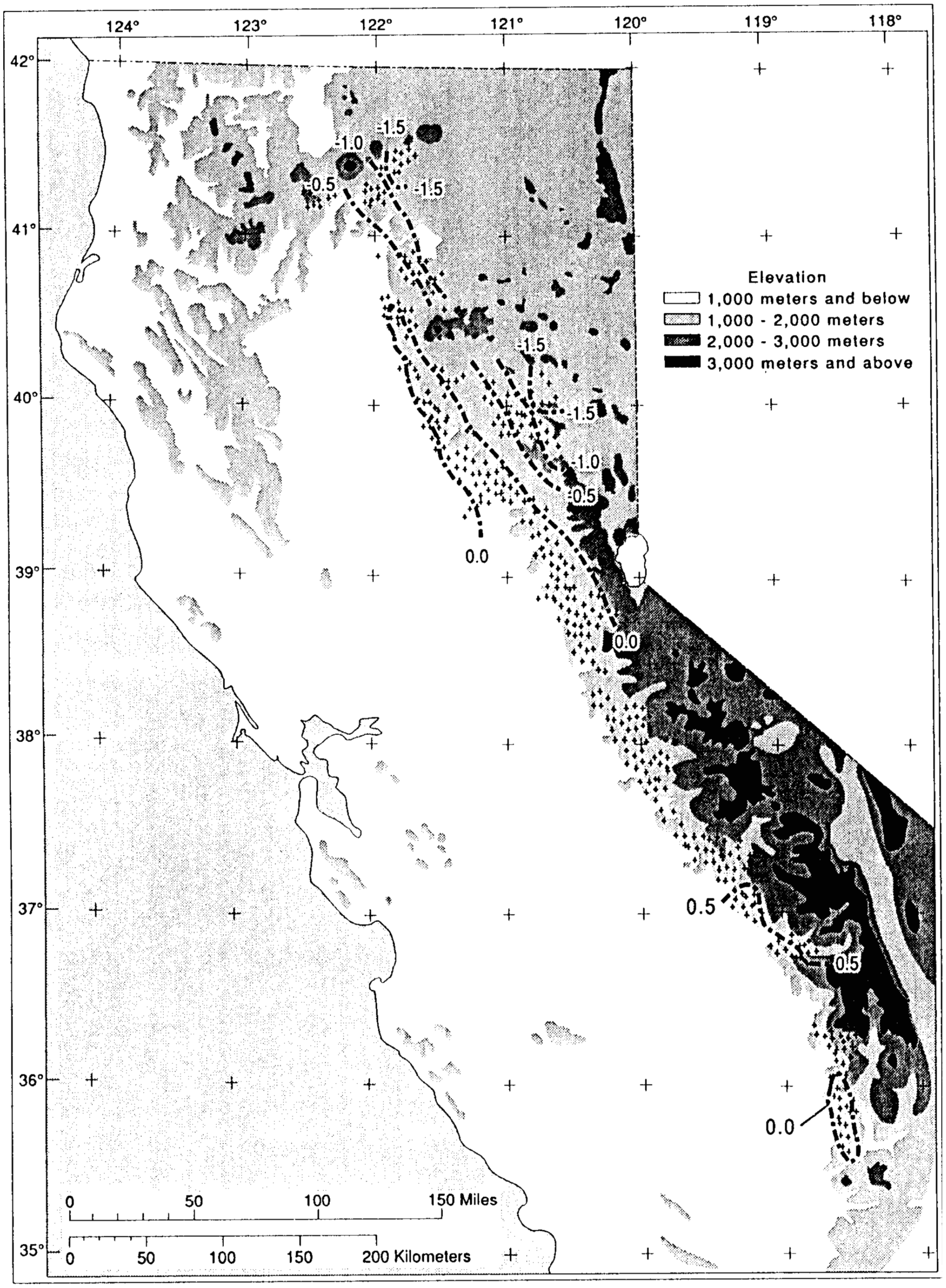


FIGURE 28.3

Multilocus contour plot of the first vector from a canonical trend-surface model for ponderosa pine. (From Westfall and Conkle 1992.)

in the Sierra Nevada (Westfall and Conkle 1992). Contour plots (based on the first canonical vector of a geographical trend-surface equation, $R^2 = 0.25$) for ponderosa pine show regions of similarity that are largely differentiated in an east-to-west direction (figure 28.3). When the next two vectors are added ($R^2 = 0.40$), elevation becomes more influential in determining the areas of genetic similarity (figure 28.4).

Geographic subdivisions recognizing these trends were proposed twenty-five years ago (Buck et al. 1970) and applied to seed transfer in commercially important conifers (figure 28.5) (Kitzmiller 1976). Subsequent common-garden and allozyme studies have modified the intitial geographic patterns and associated guidelines in minor ways. For example, latitudinal zones are now considered to be larger than those recommended originally, although the 152 m (500 ft) elevational zonation is confirmed by genetic studies (Kitzmiller 1990; J. H. Kitzmiller, Regional Office, U.S. Forest Service, conversation with R. D. Westfall, 1994).

A recent synthesis of allozyme and morphological (common-garden, early-expressed or juvenile traits) data for five

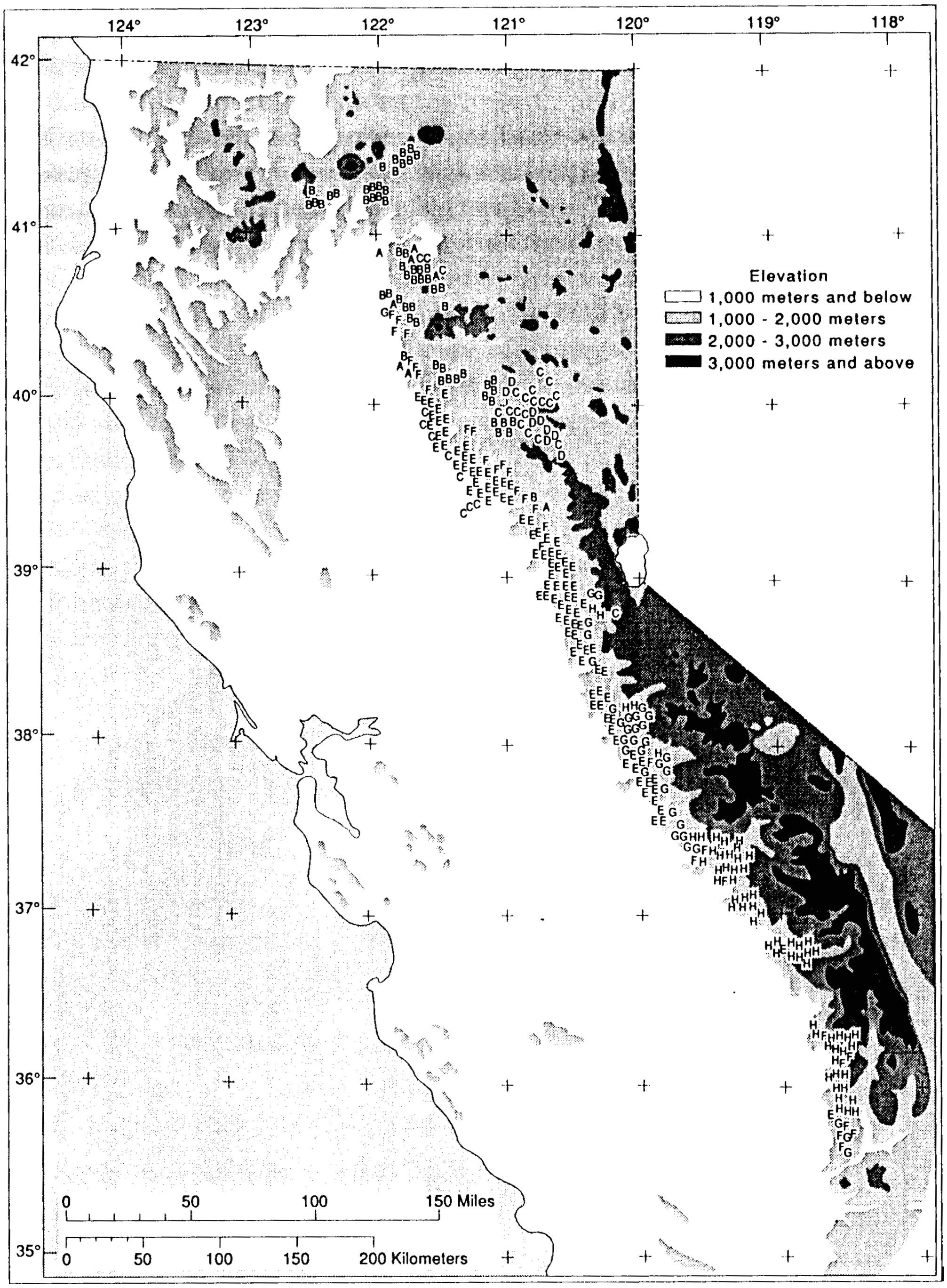


FIGURE 28.4

Multilocus contour class intervals of the first three vectors from a canonical trend-surface model for ponderosa pine. (From Westfall and Conkle 1992.)

commercial conifers in the Sierra Nevada (ponderosa pine, sugar pine, white fir, Douglas fir, and incense cedar) shows much agreement with the original patterns of geographic variation (Millar et al. 1991). Both types of data were evaluated according to the percentage change in genotypes along an elevational transect. This calculation provided an assessment of the risk in transferring genotypes in reforestation processes; expressed as the percentage change in genotypes per 1,000 ft of elevational change, this is an index of transfer risk (table 28.13). This analysis provided three conclusions. First, it confirmed that genetic variation in the Sierra Nevada for these species changes much more rapidly with elevation than with latitude (data for latitude are not presented here). Second, the northern low-elevation populations within species were genotypically similar to southern populations at higher elevations. Third, for this kind of risk analysis, allozyme and morphological data showed similar trends.

From the northern Sierra Nevada south to the Sierra National Forest, elevation appears to be the predominant factor affecting patterns in genetic variation; south of there, the patterns seem more reflective of glacial, topographic, and tectonic history than of elevation. These variables partition species differentiation more than known intraspecific variability. Factors reflecting corridors for or barriers to gene flow, such as riparian zones or mountain ranges, may be significant influences in the Sierra for speciation. Finally, some particular conditions, such as unusual soil types, may provide another level of genetic partitioning for some species (although there is little empirical data). Associations with serpentine soils have perhaps been best studied (e.g., P. sabiniana [Griffin 1965] and P. ponderosa [Jenkinson 1977]).

An extensive series of allozyme and common-garden studies for several commercial species has provided some insight regarding genetically (intraspecifically) rich areas for trees of the Sierra Nevada. First, examples of genetically rich areas are known from both spatially heterogeneous and homogeneous areas, indicating either that selection is not always the major force in shaping the genetic composition or that selective agents are not obvious. Second, for species with wide ranges, such as ponderosa pine, the highest levels of intraspecific genetic variation are found in the midsections of the major vegetation zones that they cross. Third, some species of this group exist at the boundaries of the major vegetation zones they traverse (e.g., seemingly localized populations of ponderosa pine exist above and below the mixed conifer forest type).

Table 28.14 presents some examples of species- and population-level genetic richness and rarity. These may occur at the margins of species ranges, as in the case of the unusual and northernmost population of giant sequoia (Sequoiadendron giganteum) in Placer County, California, which is distinct and low in genetic diversity relative to other giant sequoia populations (Fins and Libby 1982). Genetic variation within populations sometimes shows an increasing trend toward the south of a species' range. (This is discussed further in the section "Inferences of Genetic Significance.") For species whose

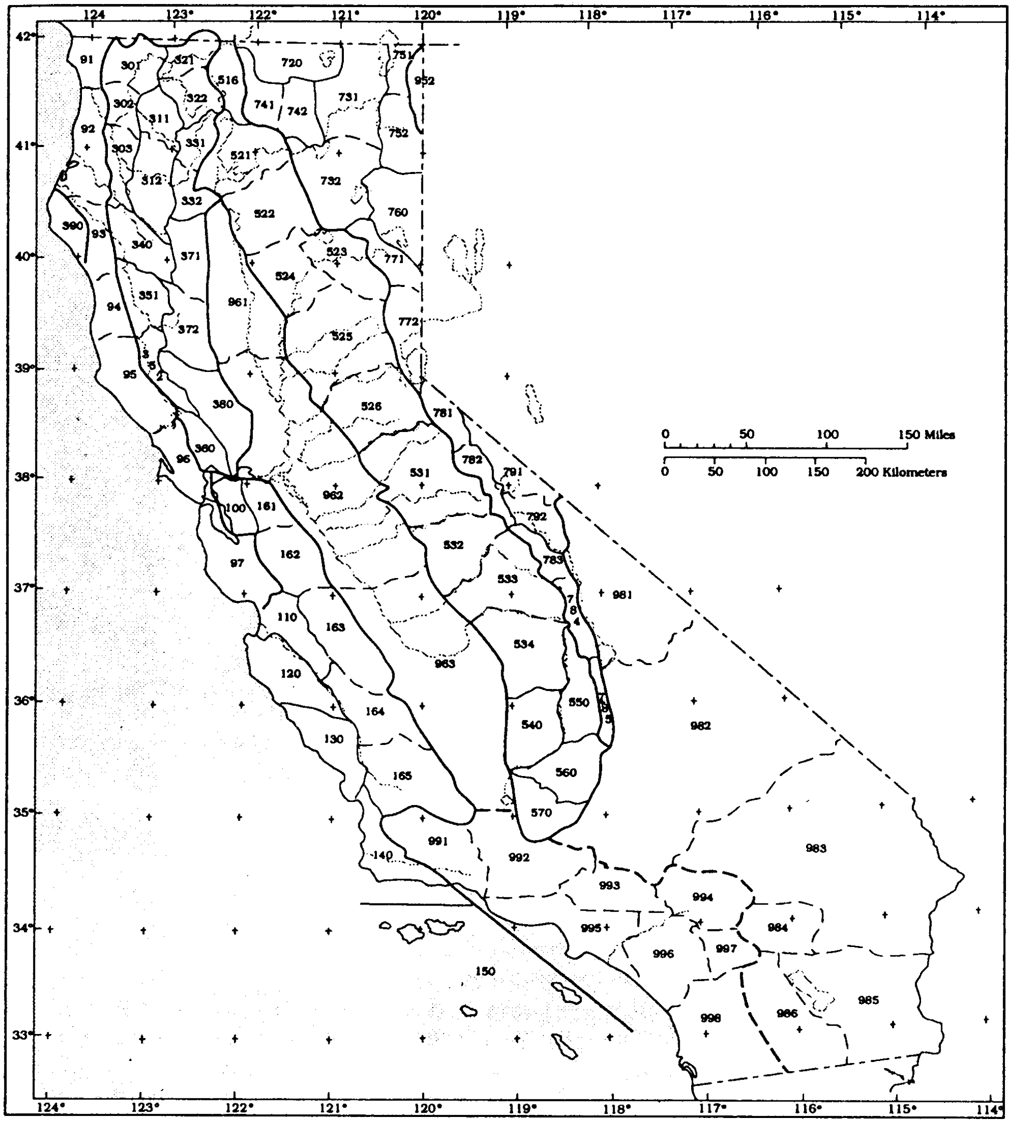


FIGURE 28.5

California tree seed zone map. (From Kitzmiller 1976.)

TABLE 28.13

Transfer risk index for elevation transfer of five central Sierran conifers.[a]

Species	Type of Data	Elevational Transfer Risk Index[b]
White fir	Allozyme	0.18
	Nursery	0.19
Ponderosa pine	Allozyme	0.25
	Nursery	0.20
Incense cedar	Allozyme	0.30
	Nursery	0.30
Sugar pine	Allozyme	0.35
	Nursery	0.27
Douglas fir	Allozyme	0.52

[a] From Millar et al. 1991.
[b] Transfer risk index is the proportion of genotypes in one population that do not match those present in another location. Risk is expressed here as proportion mismatched per 1,000 feet of elevational change.

ranges have their southern limits in the Sierra Nevada, these southernmost populations may be genetically rich or rare. One example of this pattern is found in western white pine (P. monticola) (Steinhoff et al. 1983). Throughout the northern part of its distribution, western white pine populations have a mean heterozygosity of 0.13 (with a range of 0.04–0.19). In its southern populations in the Sierra Nevada, the heterozygosity values range from 0.26 to 0.32. Sugar pine in the Sequoia National Forest exhibits high levels of allozyme diversity among populations; these high levels are not associated with elevation.

Genetic richness or rarity may occur at the convergence of major biophysical regions (e.g., the genetically rich, at the species and population levels, area of the Sierra Nevada–Cascade transition) and as unusual species compositions (e.g., the rich and rare Washoe–Jeffrey pine complex in the northeastern Sierra).

One example of a rare tree species that may be in the process of being assimilated into a more widespread species (ponderosa pine) is Washoe pine (P. washoensis) (Niebling and Conkle 1990). A high-elevation species, Washoe pine grows primarily in stands on the eastern edge of the Sierra Nevada and the western edge of the Great Basin. Only three populations are well documented, all of which are in the greater Sierra Nevada region—the Warner Mountains, Babbitt Peak, and Mount Rose.

TABLE 28.14

Some specific examples of genetically significant areas in the Sierra Nevada for trees.

Geographic Area or Subdivision	Genetic Attribute (and Genetic Level) of Significance
Northeastern Sierra: Washoe–Jeffrey pine complex	Rich and rare (species)
Plateau at Sierra-Modoc-Cascade convergence: ecotypes of many species, including red fir, white fir, ponderosa pine, and western juniper	Rich (species, ecotype)
Southern Sierra/Kern Plateau: rich in species of five-needled pines	Rich (species and population)
Southern Sierra: foxtail pine	Rare (population)
Placer County: giant sequoia	Rare (population)

Factors underlying genetic variation within other (i.e., nonconifer) plant species in the Sierra Nevada are more conjectural. Beyond the early reciprocal transplant/elevational transect studies of Clausen, Keck, and Hiesey (e.g., Clausen et al. 1948), little information exists on adaptive variation in native species. In a morphologically based common-garden study in Nassella, E. E. Knapp (1994) suggests that genetic differentiation is much more pronounced on an east-west gradient, from coastal to interior populations, than from north to south. This has been interpreted as a response to climatic patterns. However, this geographic pattern is based on analysis of widespread species; it is not known to what extent this pattern might hold true for more narrowly defined species or those specific to the Sierra Nevada. Rice and Mack (1991) have conducted a reciprocal transplant study of intermountain Bromus populations, finding lower performance of local populations at more mesic sites.

Ehleringer and colleagues have conducted a series of ecophysiological and genecological studies on a number of aridland species of the Great Basin and western deserts, some of which occur in the Sierra Nevada or at the montane-desert boundary. They have found water-use efficiency to be heritable (Schuster et al. 1992), to vary along climatic gradients (Comstock and Ehleringer 1992), and to vary among species (Evans and Ehleringer 1994), gender (Dawson and Ehleringer 1993), life history classes (Donovan and Ehleringer 1992), and life forms (Ehleringer et al. 1991). We expect that such information would be helpful in defining ecologically based genetic patterns in Sierran populations. Even with these patterns, the relationship between water-use efficiency and fitness is not a simple one (Donovan and Ehleringer 1994), and other physiological characteristics will have to be added.

In the absence of empirical data for nonconifer plant species, workshop participants proposed a more general approach to inferring the genetic structure of, and thereby recognizing representative genetic variation in, nontree plants, using a three-tiered decision-making key. The first level separates common or widespread plant species from rare species. Here, the idea of rarity is based on a structure proposed by Rabinowitz (1981), which uses the concept of "seven forms of rarity." Within common species, the next level involves describing various plant characteristics, such as gene flow, that will assist in deciding which model (in tier three) is more appropriate. The third level involves describing representative genetic variation based on the key factors of two models: a coarse-grained (regional) model or a fine-grained (local) model.

For common or widespread species, two main characteristics determine which model, local or regional, is more appropriate for structuring representative genetic variation. One of the most important characteristics is gene flow. There is much variation among widespread plant species in factors affecting gene flow, including breeding system, mode of reproduction (asexual, sexual, or mixed), and pollen and seed-dispersal systems. Gene flow is strongly related to genetic architecture and thus to the choice of a regional or local model for describing representative genetic variation. The second characteristic germane to the choice of model is the spatial pattern of population distribution. For example, continuous distributions might be most appropriately described with a regional model, while "patchy" or disjunct distributions might indicate a local model, even though the species range is broad.

For common species, different key factors (table 28.15) underly representative genetic variation in the local and regional models, a reflection of their relative scales. The regional model is mainly structured by climatic variables, both those correlated with east-west distance (e.g., temperature regime) and those correlated with north-south distance (e.g., day length). The local model is more finely structured by both physical (e.g., edaphic) and biotic (e.g., local patterns of competition) factors. In summary, then, two models or sets of factors have been hypothesized as descriptors for patterns of representative genetic variation in plants. The choice of which model is more appropriate will depend mainly on gene flow and the distribution characteristics of the plants. In some cases, such as a widespread species with much local differentiation, a mixed or hierarchical use of the models would be indicated.

In structuring representative genetic variation for rare or restricted plants, a Rabinowitz (1981) model for identifying rarity might be useful. For example, plants that are highly restricted in their distribution would have their resident site as the basis of representative genetic variation. For plants that are few in number but widely distributed (e.g., "sparse"), the factors underlying patterns in widespread or common species might be an appropriate way to structure their variation. For plants with intermediate numbers or distribution ranges, structuring by "specialized communities" might adequately capture their representative genetic variation.

Beyond the structuring of representative genetic variation, another issue is the occurrence and pattern of rare genetic variation. Although rarity in plants is difficult to illustrate geographically, there appear to be several correlates or indicators of rarity. First, rare species or populations often occur as edaphic endemics—for example, on gabbro and serpentine soils. More than a dozen serpentine endemics are known to exist in the Sierra Nevada (Kruckeberg 1987). Second, biogeographical history may point to rare forms—for example, nonglaciated refugia. Third, hybrid zones, at the species or population levels, may be areas of evolutionary significance. Finally, peripheral populations may have rare characteristics relative to more centrally located populations.

TABLE 28.15

Key factors underlying the structure of representative genetic variation for common or widespread (nonconifer) plant species in the Sierra Nevada, according to regional and local models.

Regional Model	Local Model
Elevational factors (primarily east-west gradient)	Physical factors
Temperature regime, growing season, etc.	Edaphic factors
Moisture, rain shadow effect, etc.	Aspect
	Slope
Latitudinal factors (primarily north-south gradient)	Biotic factors
Day length	Local herbivores and pathogens
Annual precipitation	Competitors

In conclusion, it is difficult to provide more detail or make specific recommendations with respect to describing or inferring significant genetic variation in nonconifer plants of the Sierra Nevada, because of the lack of information. Even detailed species-distribution maps with rough estimates of population sizes are unavailable. Hence, the workshop participants developed a more generalized approach to structuring variation within this taxonomic group, and we are not able to identify specific geographic areas of genetic significance other than for a few well-studied species.

Mammals

Areas or instances of rich or rare genetic variation are generally unknown for most mammalian species, due to the few genetic studies of Sierran populations. However, the well-studied pocket gopher (Thomomys bottae) provides some examples. In a study comparing cranial features and allozyme variation of samples from thirty-one geographic locations in eastern California, Smith and Patton (1988) report two areas of genetic significance in the Sierra Nevada. The first is on the northern and eastern shores of Owens Lake. Here, the gophers have allozyme similarity to other pocket gophers in the general area, yet have distinct cranial features. For all other gophers sampled in this study, allozyme and cranial data showed concordant patterns. The second unusual area is in the vicinity of Lone Pine. Here, evidence was noted of apparent intergradation (i.e., interbreeding with the result of hybrid progeny) between two of the three putative subspecies, T. perpes and T. melanotis.

Of special genetic interest may be subspecies that are peripheral isolates of more widespread species. Such populations may be centers for evolutionary change (W. Z. Lidicker, University of California, Berkeley, note to D. Rogers, September 1994). Examples of locations where such peripheral isolates of several species occur are the Kern River Plateau, Sierra Valley, and Mono Basin. Also, for at least one widespread mammal (Phenacomys intermedius, the heather vole), the main Sierran cordillera contains such an isolate.

Areas in which congeneric species or conspecific subspecies meet may represent another kind of genetic richness or uniqueness. For example, the ranges of the Columbian black-tailed deer (Odocoileus hemionus columbianus) and the Rocky Mountain mule deer (O. h. hemionus) meet in a narrow contact zone in the Sierra Nevada and Cascade Range (Cronin 1991).

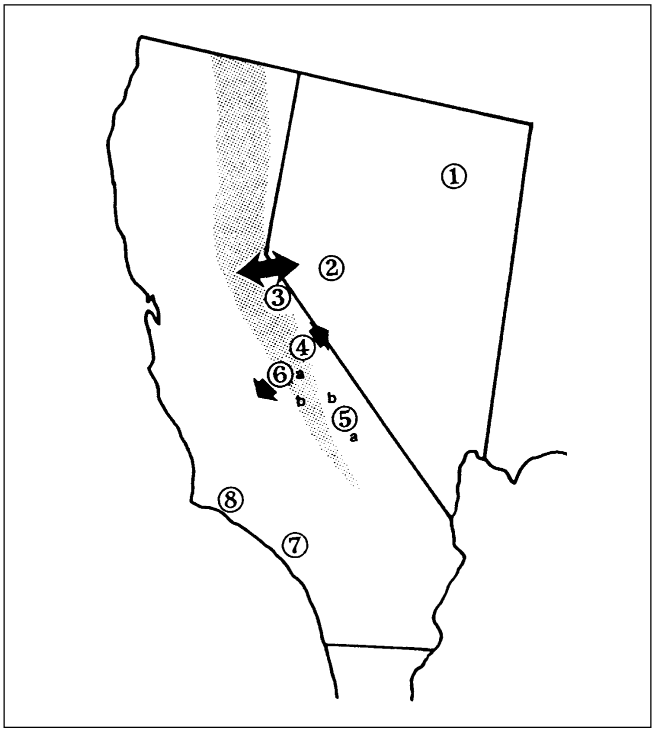
Overall, little genetic information is available that identifies factors underlying mammalian genetic patterns in the Sierra Nevada. With the exception of the pocket gopher, with its known population differentiation into six regions of the Sierra Nevada, most known geographic patterns reflect subspecies, rather than population, associations. At this level, most mammalian data support the major biogeographic subdivisions in the Sierra of east side and west side and north and south, with second-order structuring according to major vegetation type. Particularly strong and recurring patterns of subspecies divisions occur between east and west, both along mountain crests and in the foothills. Certain north-south divisions (e.g., south of Yosemite and south of Tahoe) are also described on the basis of phenotypic variation.

Birds

There is little evidence in the available literature of rare or endemic bird species in the Sierra Nevada. However, there are several examples of rich or unusual geographic areas with respect to avian genetics—areas that are implicated as hybrid zones among subspecies, as harboring multiple and non-interbreeding subspecies, or as being habitat for unusual populations or subspecies.

FIGURE 28.6

Probable areas of intersubspecific gene flow (arrows) in cowbirds *(Molothrus ater)* in the Sierra Nevada (shaded area). Number and letter designations refer to sampling sites. (From Fleischer et al. 1991.)



Two areas in the Sierra Nevada are probable corridors for gene flow between two subspecies of the brown-headed cowbird (Molothrus ater obscurus and M. a. artemisiae). This species is a relatively recent inhabitant of the Sierra Nevada, and contact between the two subspecies in the Sierra Nevada is even more recent, probably during the last twenty to fifty years. The subspecies M. a. artemisiae has historically inhabited the Great Basin, strictly east of the Sierra Nevada. The subspecies M. a. obscurus historically inhabited southern Arizona to Texas but has expanded its range gradually northward, initially invading southern California from the lower Colorado River in about 1900. Samples from ten sites in California and Nevada provided mitochondrial DNA evidence that gene flow is occurring between the two subspecies along the Sierran crest at two points: the Mammoth Lakes area and Lake Tahoe (figure 28.6) (Fleischer et al. 1991).

Two well-differentiated putative species of fox sparrow, Passerella megarhyncha and P. schistacea, appear to have a narrow zone of contact and hybridization along the interface of the Great Basin and the Sierra Nevada. Samples taken from the White Mountains, Warner Mountains, and Mono Lake show individuals from both groups as well as mitochondrial DNA evidence of hybridization. In this contact zone, and in the White Mountains in particular, there are a high number of unusual (mtDNA) haplotypes found nowhere else in the group of species collectively referred to as fox sparrows and apparently due to the genetic consequences of hybridization (Zink 1994).

In spite of the low level of population differentiation, on average, within sage sparrows (Amphispiza belli), there is a strongly differentiated population of sage sparrows (A. b. nevadensis) near Chalfant Valley. This population was discovered to have an unusually high frequency of a single unique allele in an allozyme study of twenty-two populations of the three subspecies in this complex in California and Nevada (Johnson and Marten 1992). The subspecies A. b. nevadensis is highly migratory. This general geographic area is also of interest as it is the only area where the ranges of two subspecies, A. b. nevadensis and A. b. canescens, meet (figure 28.7). The two subspecies are strongly differentiated on both morphological and isozyme data. No genetic evidence of hybridization has been found.

Although there is no direct evidence for this based on Sierra Nevada species, there is reason to believe that some elevation-related adaptations may be present in some of the species or subspecies that inhabit mountainous regions. Among finches, there is evidence of interspecific variation in blood properties related to elevation of native habitat. Rosy finches (Leucosticte arctoa), native to altitudes above 3,500 m (11,550 ft) have been shown to have much higher blood O_2 affinity than house finches (Carpodacus mexicanus), native to low altitudes, when both are measured at similar elevations (Clemens 1990).

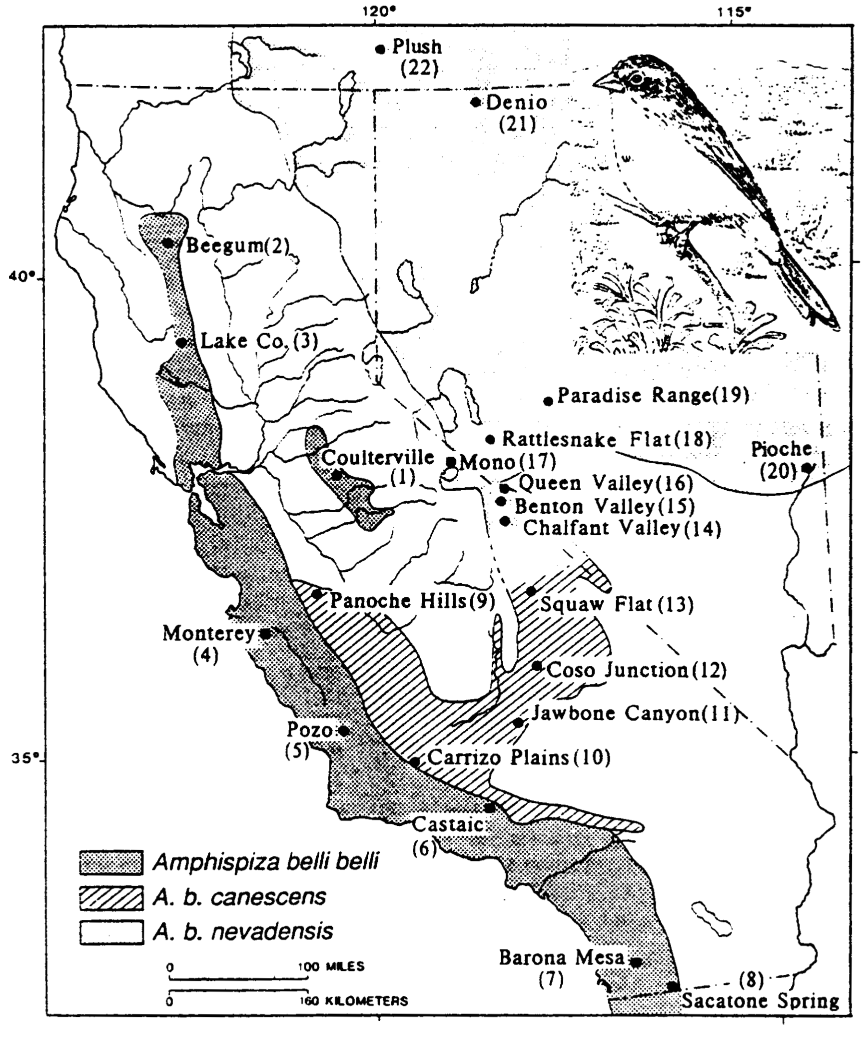


FIGURE 28.7

The known nesting distribution of the sage sparrow *(Amphispiza belli)*, showing the areas of contact between two subspecies *(A. b. canescens* and *A. b. nevadensis)* in the Sierra Nevada. (From Johnson and Marten 1992.)

Reptiles and Amphibians

Several life history characteristics pertain to the subject of genetic significance in reptiles and amphibians. First, amphibian species tend to hybridize (interspecifically) more than reptiles (e.g., Wake et al. 1978). As such, genetic richness in amphibians may be represented by hybrid zones more often than in reptiles. Second, due to the extreme phylogenetic ages of some reptile and amphibian lineages (i.e., relative to mammals), another attribute of genetic significance for this group is phylogenetic significance or age of lineage. For example, one species might be assigned more significance than another because it has no phylogenetic relatives or has fewer than the comparison species. Third, species that metamorphose may be more genetically variable, in general, than those that don't (Shaffer and Breden 1989).

For reptiles, the areas of highest species richness occur where the warm-adapted species from the south converge with the cool-adapted species from the north. Generally, they meet in areas in Kern and Tulare Counties, with the more southern species occupying the foothills and the more northern species the higher-elevation areas.

For amphibians, the notions of genetic significance are based largely on extensive salamander data. As such, there appears to be more species richness in the south for amphibians, with some notable ancient phylogenetic relicts in the Inyo Mountains and Kern Plateau. Indeed, the highest levels of species richness for salamanders in the state of California are in Kern County. (This is somewhat counterintuitive due to the moisture requirements of this taxonomic group.) Frogs are one exception to the pattern of southern species richness, with somewhat higher levels of species richness in the northwestern than the southwestern Sierra. Rare or highly restricted species occur not infrequently in the Sierra Nevada. Examples include the black toad (Bufo exsul), occurring only in Deep Springs Valley between the White and Inyo Mountains in Inyo County, and the Yosemite toad (Bufo canorus), restricted to the central high Sierra from El Dorado County south to near Kaiser Pass, Fresno County (Zeiner et al. 1988).

Table 28.16 lists key factors affecting the spatial structure of significant genetic variation for these three taxonomic groups in the Sierra Nevada. Because the most significant factors vary somewhat among, and even within, the three groups,

TABLE 28.16

Key factors underlying geographic patterns of intraspecific genetic variation for reptiles and amphibians in the Sierra Nevada (no priority inherent in presentation).

Elevation and its associated temperature regimes.
Rainfall, including seasonal and longer-term patterns of precipitation.
Snowpack, which reflects longer-term moisture availability.
Watershed boundaries—populations exist on cool, north-facing slopes, not on dry, south-facing slopes; thus, ridgetops demark areas of distinction.
Metapopulation structure as a result of habitat patchiness and life history.
Glaciation, which both forms a barrier and affects areas of recolonization.
Volcanism—important due to its effect as a barrier, its role in changing stream-flow patterns, its areas of multiple boundaries, and the effects (mainly inhospitable) of volcanic soils.
Tectonic effects—older phylogenetic lineages tend to reflect geological events to a greater extent than more recent species.
Edaphic/geological factors—e.g., rare populations of terrestrial salamanders in the Inyo Mountains occur in limestone creeks.

the order in which the factors are listed does not reflect priority. Elevation and its associated temperature regimes are understandably meaningful to this ectothermic group, and intraspecific genetic variation often shows elevational patterns. Moisture is another critical factor in patterns among and within species. Three major factors reflect moisture regime, and each may be correlated with intraspecific genetic variation. The first is precipitation; the second, snowpack; and the third, watershed boundaries. Not only do watershed boundaries have obvious gene-flow implications for fish, but ridgetops are often important (more so than stream bottoms) in influencing patterns of genetic differentiation within amphibian species (e.g., the Great Western Divide).

Elevation and moisture may be underlying factors in an apparent geographic trend of genetic variation in the Sierra Nevada. In some reptiles and amphibians, including plethodontid (lungless) salamanders, ranid (true) frogs, and iguanid lizards, greater population subdivision (among and within species) has been observed in the southern Sierra than in the northern Sierra. This trend appears to be independent of life history characteristics. From their extensive experience with Ensatina and other salamanders (e.g., Jackman and Wake 1994) and other amphibians, Wake and colleagues in the SNEP Genetics Workshop have proposed a preliminary and informal genetic zone map, whereby the subdivisions are at ridgetops between watersheds (figure 28.8). One difference between this map and the seed zone map that attempts to recognize genetic patterns in commercial tree species (figure 28.5) (Kitzmiller 1976) is the border definition. For trees, borders may often coincide with river boundaries, whereas for amphibians and reptiles, the ridgetops become more appropriate dividing lines. Part of the reason for this is that terrestrial amphibians are favored in the closed-canopy forests of north-facing slopes but are often excluded by the more open forests and chaparral on south-facing slopes. The ridgetops per se are thus not barriers, but they effectively mark barrier areas. Also, the map portrays the higher levels of interspecific and intraspecific genetic richness in the south, resulting in more zones in the south. Finally, high-elevation ridgetops have been excluded (blacked out) from the map due to the lack of amphibian and reptile species in these areas. Note that this map is intended only as an informal attempt at subdivision, for comparison with other taxonomic groups.

The distribution of moist sites creates what is known as a metapopulation structure, that is, local populations occupying habitat patches that are connected by occasional migration (Levins 1970; Hanski and Gilpin 1991). For example, the mountain yellow-legged frog, Rana muscosa, depends on large source populations to recolonize shallow ponds and marginal habitats, where the chance of local extinction is relatively high (Wake 1994).

Glaciation potentially affects patterns of genetic differentiation in two ways: first, it acts as a barrier to gene flow and second, it affects recolonization of previously glaciated areas. Some amphibian species, for example, still persist in the foothill areas of the Tuolumne and San Joaquin watersheds, reflecting ancient glacial effects.

Volcanism is another factor that influences genetic variation in various ways. Volcanic activity can result in barriers to gene flow and plays a role in changing stream-flow patterns, and volcanic soil is not conducive to maintaining certain (e.g., terrestrial amphibian) populations. A particularly important area of genetic differentiation defined by volcanic activity is the Sierra-Modoc-Cascade convergence.

The older phylogenetic lineages tend to reflect geological history, including tectonic factors, to a greater extent than the more recent lineages. Patterns of genetic differentiation in terrestrial amphibians tend to reflect tectonic history; examples of this occur in the southern Sierra. Some species are still established along major fault lines.

Finally, edaphic or geological factors such as the occurrence of limestone have important implications for certain species, especially those in the genus Hydromantes (e.g., H. brunus, a highly restricted species occurring along the Merced River in Mariposa County). Another example is the recently discovered populations of a (rare) terrestrial salamander (Batrachoseps campi) in the limestone creeks of the Inyo Mountains (Zeiner et al. 1988).

Fish

Many species of fish are endemic to the Sierra Nevada (see Moyle et al. 1996). The widespread species (especially those within drainages that reach the coast), however, may show little population differentiation, although they vary from moderate to high levels of gene flow. An isolated drainage system can completely arrest gene flow and thus contribute to population differentiation. The length of time of isolation of the Lahontan drainage system (on the California side) is perhaps responsible for its rich array of distinctive taxa, including the endemic Tahoe sucker (Catostomus tahoensis) and distinctive Lahontan forms of speckled dace (Rhinichthys osculus), tui chub (Gila bicolor), mountain sucker (Catostomus platyrhynchus), and cutthroat trout (Salmo clarki). Another well-known

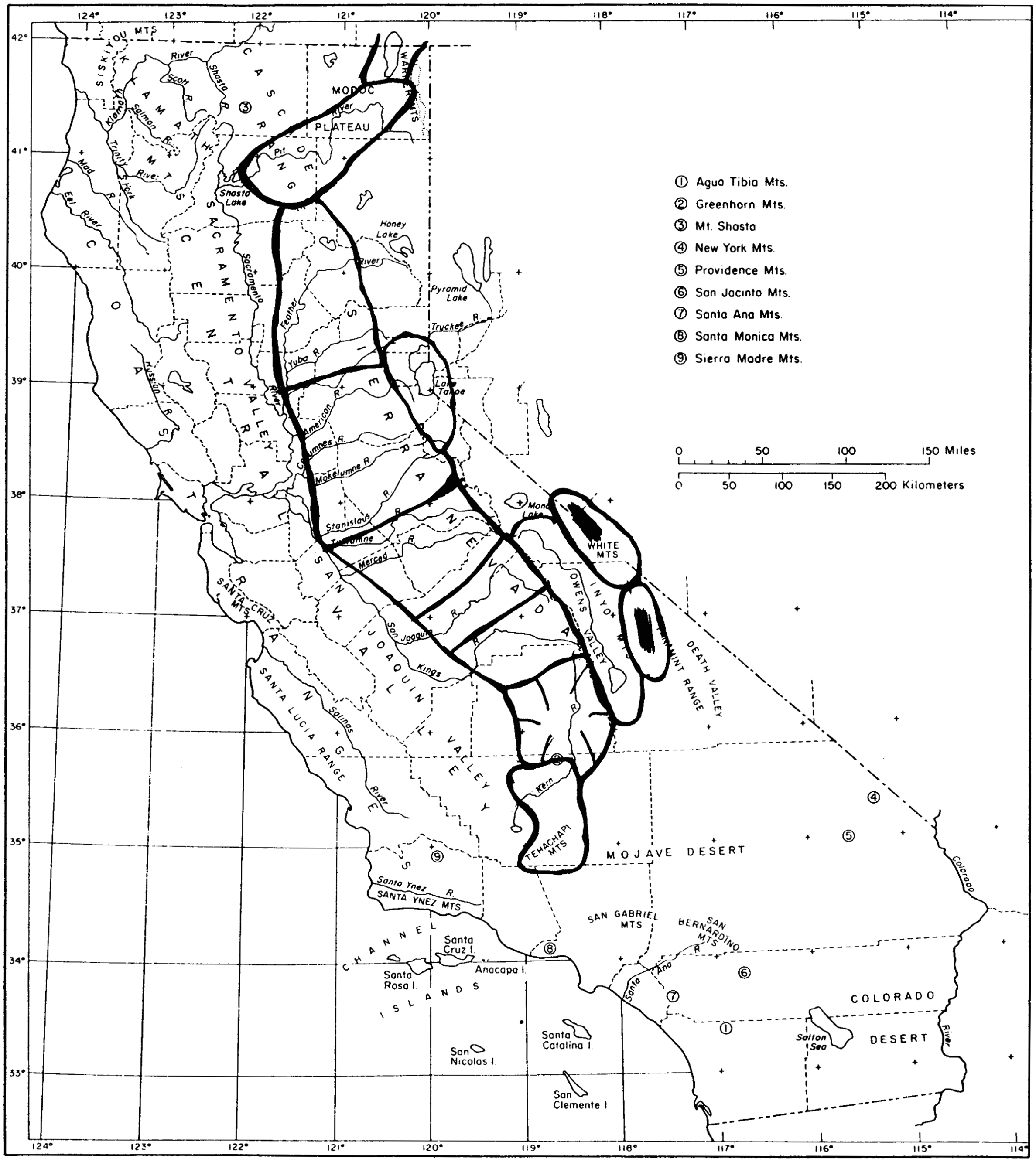


FIGURE 28.8

Patterns of geographic subdivision of significant genetic variation in reptiles and amphibians of the Sierra Nevada. Blackened areas on some ridgetops indicate areas with little or no occurrence of reptile or amphibian species. (From Wake 1994.)

example of a Sierran endemic is the golden trout, Oncorhynchus mykiss whitei, with its two known subspecies in the Kern River and Little Kern River drainages.

Levels of gene flow among migratory fish species are often high, and geographic patterns are weak. In a hierarchical study that considered the effects of regions (i.e., coastal versus inland), river drainages, rivers within drainages, and samples within rivers, Bartley and Gall (1990) found only weak geographic patterns in allozyme variation among thirty-five samples of chinook salmon (Oncorhynchus tshawytscha) from northern California, including the Sierra Nevada (F_{ST} = 0.177). Most of the among-population differentiation was due to river differences (within drainages), with drainages having the second greatest degree of differentiation. Very little was due to coastal versus inland location. This pattern was reinforced by the results of a more recent and extensive allozyme study, which included samples from Oregon and assayed a wider range of enzyme systems (Gall et al. 1992).

Genetic relationships between species and among populations within species of fish are often discussed in a geological context, the time since (physical or, occasionally, thermal) separation often being directly related to the amount of genetic variation. In most cases, the separation appears to have been due to natural events such as glaciers retreating or lakes receding. For example, the Lahontan drainage subspecies of the cutthroat trout (Salmo clarki henshawi) is considered to have differentiated not only from other subspecies but also among its populations, due to the length of time since the final desiccation of pluvial Lake Lahontan and the isolation of rivers (Loudenslager and Gall 1980).

A Californian, although non-Sierran, example illustrates a similar but more recent phenomenon based on human-mediated isolation. The construction of the Chabot Dam in Contra Costa County in 1875 and of the Upper San Leandro Reservoir in 1926 effectively isolated resident populations of steelhead trout (Oncorhynchus mykiss) in Redwood and Kaiser Creeks. A recent allozyme study suggests that not only have they been isolated long enough to have become differentiated from the coastal founding source, but, since they have not had an opportunity to hybridize with domestic trout (unlike the extant coastal populations), they represent a unique "pure" source of this species (Gall et al. 1990).

In addition to river drainages and geological events, which are interrelated, one other factor underlying genetic patterns in fish species of the Sierra Nevada may be the size of the river inhabited. For example, Bartley et al. (1992) found less geographic structuring in coho salmon in California than had been found in an earlier study of chinook salmon populations (Bartley and Gall 1990). One of the reasons the authors suggest for this difference is that coho salmon in California are restricted to smaller, less stable coastal streams, whereas chinook salmon inhabit larger inland rivers. The smaller and more unstable the stream, the greater the chance of "straying"—fish not returning to their natal streams to spawn—which results in more mixing of the gene pools. Thus, in general, smaller and less stable rivers would promote more gene flow between populations, resulting in less geographic structuring.

One final and specific factor that has been linked with geographic patterns of genetic variation in fish is selection for certain allele frequencies. Certain transferrin (TFN) genotypes (i.e., individuals with certain variations of the enzyme transferrin) have been shown to have increased resistance to bacterial kidney disease in specific stocks of coho salmon. A north-south cline in the frequency of the TFN-(103) allele was found to exist between samples of coho salmon from California and Oregon. The authors contend that "the fact that this cline exists, in spite of the homogenizing effects of stock transfers, may indicate a selective advantage for certain transferrin genotypes in California" (Bartley et al. 1992).

Insects

Due to the very limited database for this taxonomic group, much of the information provided regarding underlying factors and areas of genetic significance is inferential. The factor hypothetically expected to be the most important is the coevolutionary history with the host. (Often this is a host plant; in the case of insect parasitoids the host is another insect species.) Among insect species there are many examples of apparent coevolution with a host species. In such cases, genetic patterns of the insect species theoretically might reflect those of the host. Empirically, however, many cases of geographic variation in host affiliation are merely consequences of local host availability (Futuyma and Peterson 1985). For example, in an allozyme study of twelve populations of seven species of Ips bark beetles, including a population from the Sierra Nevada near Nevada City, California, no evidence was found of host race formation on the seven host pine species in the study. Beetles occupying the same or closely related pine species, or species with oleoresin similarity, did not show any greater genetic similarity than beetles on widely divergent host species (Cane et al. 1990). A similar conclusion was reached for a study of a montane willow leaf beetle (Chrysomela aeneicollis) in populations along three river drainages in the eastern Sierra Nevada (Rank 1992). The genetic composition of the beetles was homogeneous across both willow species hosts (Salix orestera and S. boothi). Thus, no evidence was found to suggest genetic divergence according to host species.

Examples of coevolution may be more common among the highly specialized, relatively sedentary subgroups of insects, which the species just mentioned do not exemplify. Examples include alpine grasshoppers (belonging to several families of Arthoptera), which are restricted to mountaintops, and the Euphilotes butterflies, with subspecies and population differentiation closely related to the phenology of their host plants, wild buckwheat (Eriogonum spp.).

Regardless of the paucity of genetic evidence for coevolution or host race formation in insects, the converse—genetic selection in the host by insect pressure—has been documented. The western pine beetle (Dendroctonus ponderosa) is one of the most destructive insect species attacking ponderosa pine in the western United States. Studies of ponderosa pine populations in northern California (including a Plumas County population) and southern Oregon showed monoterpene profiles (i.e., frequency distributions of the various monoterpenes present) that suggest a coevolutionary relationship between the tree and insect species. For example, the ponderosa pines in the Plumas County population and in other northern California populations, which have a continuous history of western pine beetle predation, are characterized by high concentrations of limonene relative to adjacent populations. Limonene is toxic to the western pine beetle (Sturgeon 1979). Populations without a history of predation have lower levels of limonene, suggesting that the beetle may have exerted selection pressure on its host species.

High-elevation ridges have been shown to be factors affecting gene flow in some insects of the Sierra Nevada. For example, allozyme analysis of populations of a montane willow leaf beetle (Chrysomela aeneicollis) in the eastern Sierra Nevada showed genetic subdivision among the three river drainages in which it was sampled (Big Pine Creek, Bishop Creek, and Rock Creek). The drainages are separated by high-elevation ridges. Although the F_{ST} among river drainages was only 0.135, this is higher than the F_{ST} values across broad geographic scales for many flying insects, including bark beetles (Drosophila spp.) and several lepidopterans (Rank 1992). Interestingly, although high-elevation ridges apparently are barriers to gene flow among populations, gene flow also does not occur through low-elevation connections. Although the drainages are connected by nearly continuous stands of willow at lower elevations, this is apparently unsuitable habitat for the beetle, and any gene flow that occurs among the populations occurs over the ridges instead of along the streams (Rank 1992). The low-elevation connections, however, occur outside of the Sierra, in very different habitat conditions.

Substrate or soil parent material has sometimes been suggested as a factor underlying genetic differentiation in insect species, but this is not upheld in genetic tests. Two alpine butterfly "species" endemic to the Sierra Nevada (Oeneis ivallda and O. chryxus stanislaus) occur on different substrates. In the southern Sierra, the lighter ivallda type occurs mainly on granitic substrates and the darker stanislaus type on andesite. However, in the northern Sierra, this relationship is less clear, with an increase in frequency of ivallda types but on a mainly andesite substrate. Porter and Shapiro (1989) found minor allozyme differentiation between these "species" (F_{ST} = 0.081), which are mainly characterized by wing color. They recommend classification of these two color types as a single species, given the lack of evidence for interruption of gene flow between them (figure 28.9).

One seldom-considered factor that is correlated with patterns of genetic variation in one insect species is time of day when populations are active, which is presumably related to ambient temperature. In some species, nested within spatial levels of variation is a genetically based temporal array of genotypes, as demonstrated in Colias butterflies (Watt et al. 1983). Samples from Tracy, California, and Gunnison, Colorado, showed correlations between flight patterns (e.g., time of day of flight initiation) and distinct allozyme patterns. It is not clear that similar phenomena occur in other systems (i.e., in other animals or in other loci not related to the flight muscle metabolism).

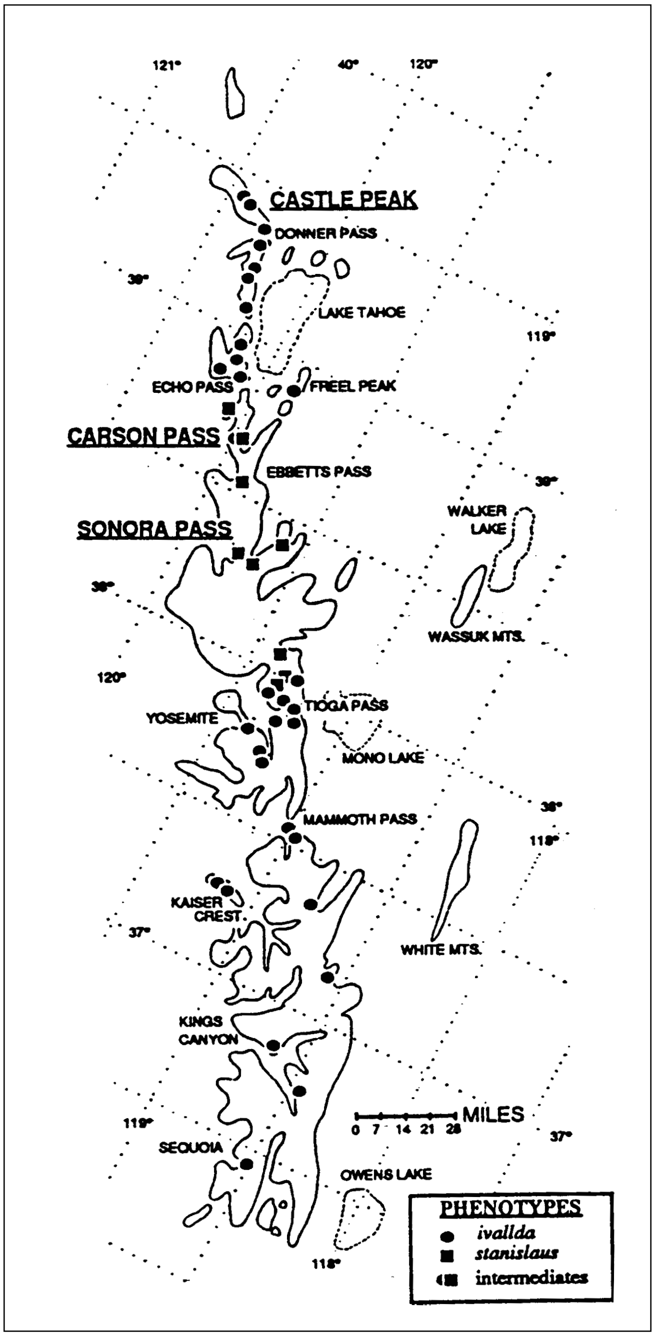


FIGURE 28.9

Distribution of alpine habitats in the Sierra Nevada with known localities of *Oeneis ivallda* and *O. chryxus stanislaus* (satyrine butterflies). Sampled populations are in the larger-sized font. (From Porter and Shapiro 1989.)

Two other geographic subdivisions or associations relate to representative genetic variation in Sierra Nevada insects. The first is the natural plant community, or biome. For example, three biotypes of Apodemia mormo occur in three distinct plant communities in the southeastern Sierra Nevada and the western Mojave Desert. They differ in the larval host plants to which each is adapted and may even deserve species status (Pratt and Ballmer 1991). The association between the insects and the plant communities may be related to natural selection. The second factor is the physiographic subdivisions within biomes (for example, a Sierra Nevada/Great Basin subdivision, or watershed subdivisions). The western seep fritillary (Speyeria nokomis apacheana) exists in small, isolated populations in the western Great Basin and eastern Sierra Nevada. Allozyme data suggest low levels of gene flow among populations, unique alleles in some (e.g., Round Valley), and mean population heterozygosity levels that are lower than those of other species in the same family (e.g., the heterozygosity of the Mono Lake population is 0.016) (Britten et al. 1994b). Genetic distances suggest major differentiation according to watershed areas and, to a lesser extent, east/west or Great Basin/Sierra Nevada differentiation. Here, the association between physiography and insect genetic variation may be due to barriers to gene flow.

Examples of areas of genetic significance in the Sierra Nevada (rich or rare) for insects are best represented in the literature by butterfly species—unusual populations, rare and endemic species, areas of hybridization, and so on. Genetically rich areas occur at the interface of the eastern Sierra and the Great Basin, where there is not only species richness but also much ecotypic and population differentiation. For example, two strongly differentiated congeneric butterfly species occur parapatrically at this interface. A population of Anthocharis sara sara, sampled at Sierra Valley, showed no evidence of gene exchange with A. sara stella sampled at Truckee, 40 km (24 mi) to the south (Geiger and Shapiro 1986). Sierra Valley is also the site of two sympatric congeneric butterfly species (Pontia protodice and P. occidentalis). Both species are highly vagile and abundant there and have apparently been in stable coexistence, without evidence of interbreeding, in Sierra Valley for more than ten years (Shapiro and Geiger 1986).

Another butterfly species, Limenitis lorquini weidemeyerii, a middle-elevation nymphalid butterfly, is restricted to montane riparian canyon habitats in the Great Basin and reaches its western distribution limits on the north shore of Mono Lake. Here, it hybridizes with the Sierran L. lorquini lorquini (Porter 1989).

Two sibling species of bark beetle, Jeffrey pine beetle and mountain pine beetle (Dendroctonus jeffreyi and D. ponderosae), have their main area of co-occurrence in the Sierra Nevada and an interesting population-level trend in the northeastern part of the bioregion. At Yuba Pass, the Jeffrey pine beetles showed markedly less allozyme diversity than other sampled populations of that species, and at nearby Sattley, the mountain pine beetles showed considerably more allozyme diversity than other sampled populations of that species (Higby and Stock 1982).

A hybrid zone within the giant silk moths (Saturniidae) has been studied at Monitor Pass in Alpine County (Collins 1984).

A lone population of the checkerspot butterfly (Euphydryas editha) near Big Meadow (Tulare County, California) was found to be genetically distinct from forty other sampled populations within the species range across the western United States (Baughman et al. 1990).

Numerous examples exist of butterfly species, semispecies or subspecies, endemic to the Sierra Nevada, including Phyciodes montana and Anthocharis stella (Shapiro 1992), and Oeneis ivallda and O. chryxus stanislaus (Porter and Shapiro 1989). For the latter two species, there is a genetically diverse area near Tioga Pass where an abrupt transition zone occurs between the two color types that distinguish the species. This zone has individuals spanning the full range in wing coloration among both species (Porter and Shapiro 1989) (figure 28.9). A specimen resembling Xyleborus californicus was found near Georgetown, California, in the late 1980s. This species may be either a recent introduction from South America or Southeast Asia or an extremely rare endemic species (Hobson and Bright 1994).

The gene-flow corridors provided by the transmontane rivers, such as the Pit and North Feather Rivers, are another example of species-rich areas. A complex cline involving three subspecies of the Coenonympha tullia group of satyrine butterflies (C. california, C. eryngii, and C. ampelos) occurs in the Pit River drainage (Porter and Geiger 1988). Rare species are often found on unusual soil types (e.g., serpentines) and on wetlands and bogs of Pleistocene origin.

Although introduced species may often have low genetic variation due to the bottleneck experienced during their introduction (e.g., Holocnemus pluchei) (Porter and Jakob 1990), the Sierra Nevada may hold unusual populations of these often widespread insect species. For example, the introduced European cabbage butterfly (Pieris rapae) was sampled over much of its current distribution in the United States. Although the species has existed for a longer time in the eastern United States (since about the 1860s), the eastern populations show little allozyme differentiation, while the population sample from Reno, Nevada, is distinctive (Vawter and Brussard 1984). Indeed, the western populations appear to have diverged not only from the eastern populations but also from one another. This genetic differentiation in the West is attributed to fragmentation of suitable habitat. The “suitable habitat” found in the West consists of agricultural or urban areas interspersed with inhospitable desert or montane natural areas.

In summary, the key factors underlying genetic differentiation due to natural selection in insects of the Sierra Nevada are, theoretically, coevolution with host plant species, climate, elevation, and substrate. However, there are few studies of such relationships and even fewer that confirm a genetic basis for the morphological differences observed. Differentiation due apparently to restriction of gene flow is more readily apparent, as in the case of populations differentiated due to ridgetops, geographic distance, or sedentary habit.

Fungi

The most important factor underlying patterns of genetic variation in fungal species, beyond life history characteristics, is theoretically the relationship with the plant host (M. Garbelotto, University of California, Berkeley, conversation with D. Rogers, September 1994). Implications based on this assumption have been made—for example, that forest pathogens are potentially more genetically diverse than fungi of domesticated crops and may have complex population structures that reflect the heterogeneity of their hosts and environments (Vogler et al. 1991). Studies documenting this pattern, however, are scarce.

Although there is no evidence from Sierra Nevada fungi for this relationship, an elegant study by Burdon and Roelfs (1985a) demonstrates a specific kind of host-pathogen relationship, namely, the genetic consequences of eradication of an alternate plant host. Wheat stem rust (Puccinia graminis) populations in the eastern United States have been asexually reproducing since the late 1930s, coincident with the eradication of the alternate plant host for this species, the common barberry. Populations from this area were compared with sexually reproducing populations (due to the presence of the barberry) from the Pacific Northwest. The two groups showed striking genetic differences, the sexual populations being more genetically diverse in all variables measured. The structure of genetic diversity between the two groups also differed. The sexual populations portrayed a pattern consistent with random mating, and isozyme alleles and virulence genes were unrelated. In contrast, the asexual populations were strongly subdivided along clonal lines, and there was close agreement between isozyme and virulence structure (Burdon and Roelfs 1985a).

Elevation and climate, paleohistory and recent history (mainly anthropogenic disturbances) are potentially important to fungal patterns (M. Garbelotto, conversation with D. Rogers, September 1994), although specific examples are rare. Substrate or parent material is likely to be important, especially for mycorrhizal fungi.

There is an interesting example of a genetic pattern in the western gall rust (Pteridermium harknessii) in the Sierra Nevada, for which there is no definitive underlying causation. In an area just east of Lake Tahoe, an allozyme analysis revealed two strongly differentiated forms of the fungus (called "zymodemes") that coexist without apparently interbreeding (figure 28.10). South of this area, populations of zymodeme II were found almost exclusively, while north and west of this area, zymodeme I was almost exclusively present. The authors interpreted this pattern, together with the lack of recombinant genotypes, to be indicative of asexual reproduction. However, the reason for the change from one zymodeme to the other in the Lake Tahoe area remains elusive (Vogler et al. 1991).

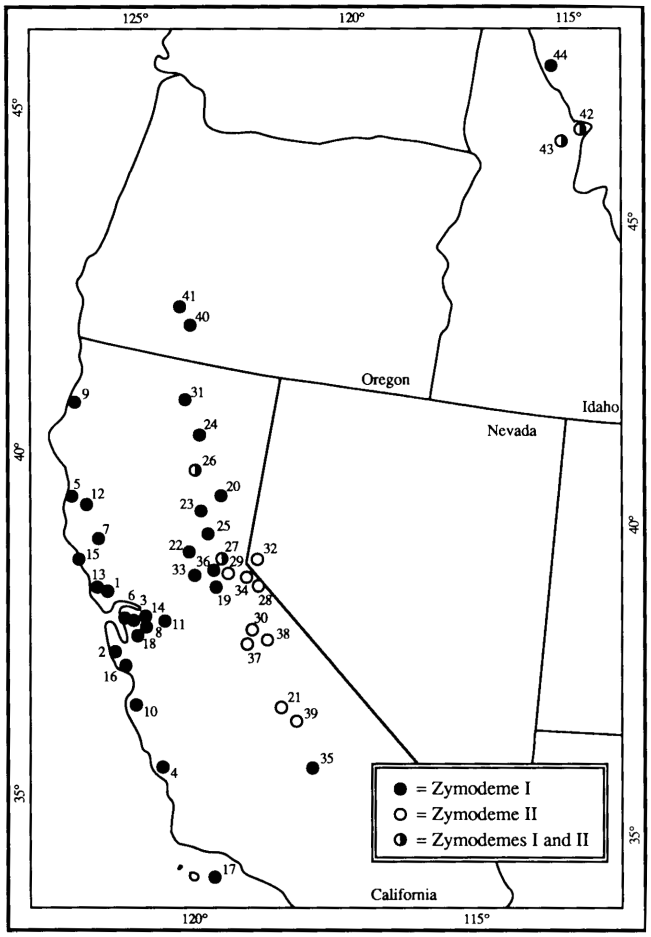


FIGURE 28.10

Geographic sources of *Pteridermium harknessii* isolates collected from the western United States. Numbers refer to collection sites. (From Vogler et al. 1991.)

Conclusions

Genetic significance is described by attributes of rarity, richness, and representative genetic variation, as well as other attributes. For example, some species may be highly valued due to their phylogenetic significance. Significant genetic variation is also described as that portion of the total variation that preserves evolutionary potential, which is theoretically defensible but nearly impossible to recognize. Furthermore, genetically significant units vary from the subpopulation to family level. Thus, both the attributes of genetic significance and the level at which they are described are closely interconnected and dependent on the overall (management or research) objective.

The ability to define areas of genetic significance in the Sierra Nevada is greatly hampered by the lack of information, even of range distributions, for many species and by the corresponding overrepresentation of a few species in the body of current knowledge. Key factors underlying genetic subdivisions vary among taxonomic groups, with perhaps the only generalization being that east-west gradients, with their associated temperature and elevational factors, are more determinant of genetic variation, in general, than the north-south gradients. However, even this generalization has caveats. For example, although there is an east-west dichotomy in species richness for amphibians, within the species-rich west side the structure of genetic variation more accurately reflects north-south factors.

The idea of constructing zones of representative genetic variation across the Sierra Nevada is challenged by differing constructs of genetic variation among the different taxonomic groups. For trees, and perhaps for amphibians, reptiles, and fish, the zoning concept is perhaps more easily approached, although there is a lack of concordance in zoning attributes between these two major groups. Trees seem most structured according to elevational and latitudinal differences, with zone boundaries defined by increments in these variables and by major topographic features. Amphibians are very influenced by montane barriers, and hence ridgetops are the most prominent genetic boundaries for this taxonomic group. For mammals and birds, and to some extent for insects, if zones were to be defined they would follow habitat or ecotone types. However, the zone concept has different or more restricted value here due to the importance of migration corridors. Thus, it is the edges as much as the centers of the zones that have significance with these latter groups. For fungal species, genetic structure is probably very finely scaled, making zones a less feasible management tool. Finally, with nontree plants, the available information is so restricted as to prevent generalizations concerning geographic patterns. Instead, areas of genetic significance are identified relative to life history characteristics. As more genetic information becomes available for more plant species, such geographic partitioning may be more feasible.

Inferences of Genetic Significance

For most species in the Sierra Nevada, there is currently little information or data that directly relate genetic diversity to adaptive significance. Genetic significance may be particularly germane to conservation and management as a means of establishing priorities. In the absence of such information, some idea of the extent and nature of genetic significance may be available from concepts based on correlations or associations that have generalized genetic variation within a certain context. These concepts are neither mutually exclusive nor necessarily independent of the need for genetic assessments. Rather, they are additional perspectives from which genetic structure, and thus significance, may be inferred. These concepts are, with a few exceptions, preliminary suggestions developed by workshop participants for the purposes of the current discussion.

Life Form and Life History Associations

Sufficient genetic information is available from taxa beyond the Sierra Nevada within certain taxonomic divisions (e.g., plants) for researchers to have realized correlations between the level and pattern of genetic variation and certain life form and life history characteristics (Hamrick and Godt 1990; Hamrick et al. 1992, 1979). This correlation has been investigated statistically for plants (Hamrick and Godt 1990). In a review of more than four hundred plant species, correlations were noted between amount and structure of genetic variation (as measured by allozymes) and such features as the species' geographic range, longevity, seed-dispersal mechanisms, and breeding system.

The relationship between allozyme variation and plant characteristics was investigated at three levels—genetic variation within the species as a whole, genetic variation among populations, and genetic variation within populations (tables 28.17–28.19). For example, widespread plant species tend to have greater amounts of allozyme variation than do narrowly distributed species (table 28.17). Long-lived perennials generally have higher levels of genetic variation than short-lived perennials. Breeding system is highly associated with gene flow: self-pollinating, or selfing, species tend to have relatively high amounts of variation among populations, while outcrossing species have relatively little. Population differentiation shows very different correlations (table 28.18). Selfing species have more population differentiation (i.e., more genetic variation among populations), in general, than do outcrossing, wind-pollinated species. Finally, the amount of genetic variation within plant populations shows a set of correlated traits that is similar, but not identical, to those correlated with species-level genetic variation (table 28.19). Widespread species again have higher levels of genetic variation within populations than do endemics; however, breeding system characteristics are even more highly correlated with within-population levels of variation than is geographic range. Mixed-mating, wind-pollinated species have considerably higher levels of genetic variation within populations than do selfing species.

For certain California tree species, a generalization has been noted concerning latitude and genetic variation within populations (Ledig 1987). Genetic variation within populations in the south of a species' range tends to be the highest, decreasing toward the north. A striking example of this trend occurs in a non-Sierran tree species, coulter pine (Pinus coulteri). In this species, heterozygosity increases from 0.11 in the northernmost populations near Mount Diablo, California, to 0.19

TABLE 28.17

Correlates with genetic variation within plant species.[a]

Trait[b]	Highest Level	Lowest Level
Geographic range	Widespread	Endemic
Life form	Long-lived, woody perennials	Short-lived perennials
Breeding system	Mixed mating, wind pollinated	Mixed mating, animal pollinated
Seed-dispersal mechanism	Attached	Explosive
Taxonomic status	Gymnosperms	Dicots
Regional distribution	Boreal-temperate	Tropical or temperate
Mode of reproduction	Sexual	Sexual and asexual
Successional status	Late successional	Mid successional

[a] Derived from Hamrick and Godt 1990.

[b] Traits are arranged in approximate order of their strength of correlation with genetic variation. Thus, geographic range is very strongly correlated with genetic variation within a species, but successional status is almost insignificant.

TABLE 28.18

Correlates with genetic variation among populations within plant species.[a]

Trait[b]	Highest Level	Lowest Level
Breeding system	Self-pollinated	Outcrossing, wind pollinated
Life form	Annuals	Long-lived, woody perennials
Seed-dispersal mechanism	Gravity dispersed	Gravity attached
Successional status	Early successional	Late successional
Taxonomic status	Dicots	Gymnosperms
Regional distribution	Temperate	Boreal-temperate

[a] Derived from Hamrick and Godt 1990.
[b] Traits are arranged in approximate order of their strength of correlation with genetic variation. Thus, breeding systems are very strongly correlated with genetic variation among populations, but regional distribution is not well associated.

TABLE 28.19

Correlates with genetic variation within populations of plant species.[a]

Trait[b]	Highest Level	Lowest Level
Breeding system	Mixed mating, wind pollinated	Self-pollinated
Geographic range	Widespread	Endemic
Life form	Long-lived, woody perennials	All others
Taxonomic status	Gymnosperms	Dicots
Seed-dispersal mechanisms	Attached	Explosive
Regional distribution	Boreal-temperate	Temperate or tropical
Successional status	Late successional	Early successional

[a] Derived from Hamrick and Godt 1990.
[b] Traits are arranged in approximate order of their strength of correlation with genetic variation. Thus, breeding systems and geographic range are very strongly correlated with genetic variation within populations, but successional status is only mildly related.

in the southernmost populations in Baja California (Ledig 1987). This pattern is also seen in such Sierran species as giant sequoia (Sequoiadendron giganteum), Jeffrey pine (P. jeffreyi), western white pine (P. monticola), sugar pine (P. lambertiana), and Douglas fir (Pseudotsuga menziesii). One explanation offered for this apparent trend is glacial history: as species migrated northward following glacial retreat, the new and more northerly populations might have arisen from only a small sample of the original species—those that dispersed and successfully colonized northward. This smaller sample would have contained only a fraction of the species' original gene pool. If the process was an iterative one, the populations migrating northward would have originated from a smaller and smaller gene pool sample, manifested today as lower levels of within-population genetic variation. Conversely, the southern populations would have been refugial, presumably harboring genetic diversity. Yet another possibility is selection rather than historic condition—that is, that higher temperatures and summer rainfall favor higher allelic diversity levels than in northern latitudes.

Similar correlations between life history characteristics and allozyme variation were noted (at the SNEP Genetics Workshop) for insects, on a more informal basis. For example, sedentary insects with strong host-plant relationships tend, or are expected, to show stronger differentiation among populations than highly vagile insects with less specialized trophic relationships (Shapiro 1994).

This type of generalization is useful in that life history characteristics such as breeding system and geographic range are known for some species and can often be inferred for others by field observations. However, there are some constraints and caveats in the application of this approach. Correlations with genetic variation are weak at best, may change across broad taxonomic groups, and, with the exception of plants, have either little direct evidence or have been entirely inferred on theoretical grounds for other groups. Further, the correlations have so far been demonstrated only for allozyme genetic variation and not other types. Thus, assessments are often inferred, and many exceptions to generalizations occur.

Evolutionarily Significant Units

Evolutionarily significant units (ESUs) were suggested not so much as a way of replacing genetic information with a proxy, but rather as a way of placing the emphasis on a different genetic measurement—that of genetic distance between populations or groups of populations, such as golden trout. One definition of an ESU is a historically isolated set of populations; the genetic criteria for recognizing an ESU are currently under discussion (e.g., Moritz 1994). The rationale is that the more historically isolated the groups, the more likely they are to have distinct genetic attributes and different evolutionary potential. Within this framework, an ESU could be a population, a group of populations, a species, or a grouping of species. For example, weakly differentiated species might be grouped together as an ESU; in contrast, strongly differentiated populations of one species might each be an ESU. This concept suggests a way to guide decisions about biodiversity protection. One does a phylogenetic analysis of genetic (e.g., allozyme or DNA sequences) and morphological data and than recognizes clusters of close relatives and progressively more distantly related forms (this has been called phylogenetic ranking in Moritz 1994). This helps inform decisions about conservation priorities; that is, when one must make choices, it may be more important to maintain major lineages, not necessarily all the minor phylogenetic branches.

This means of assessing (and valuing) genetic variation is attractive in that it recognizes the dynamic nature of gene pools; we want to conserve not only short-term adaptations but also longer-term evolutionary potentials. However, this assessment still requires species-specific genetic data and still relies on the same kinds (allozyme or DNA) of genetic measurements.

Environmental Correlates

As was discussed in previous sections, often an environmental variable (or variables) can be identified that correlates with patterns in genetic variation. Even in the absence of genetic data to confirm these patterns, there are some features, particularly geographic features that would tend to limit gene flow, that might at least be reasonably good indicators of population differentiation. For example, ridgetops have previously been discussed as presenting gene-flow barriers for some amphibian species, and thus genetic differentiation according to this geological feature could be expected. Similarly, fish populations in nonconnected river drainages might be predicted to be more strongly differentiated than those in continuous drainages. Much of this is inferential and has not been tested or confirmed, and many generalizations will occur.

Species Richness and Distribution Patterns

In lieu of species-specific genetic information, species richness provides some measure of biodiversity. Species diversity is not the primary focus of this chapter; however, genetic significance might be inferred to some extent not only by species presence but also by distribution patterns. For example, if the species tends to be distributed as disjunct populations, or if the area under consideration has marginal populations (i.e., populations that are near the edge or limits of the species' natural range), the populations might be more genetically distinct (as compared with midrange populations of a widespread, contiguously distributed species). For example, the dusky shrew (Sorex monticolus) is a widespread species, yet has two areas with isolated populations—one in the Sierra Nevada and one in the San Gabriel Mountains of southern California (Zeiner et al. 1990b). The fact that these populations are isolated might be used to infer genetic significance.

This approach to assessing genetic variation has the advantage of requiring only census data, rather than sampling and genetic analysis. The number of species expected within a given geographic area can usually be obtained from species range maps, which are readily available for most mammals, birds, fish, and trees, although to a lesser extent for nonwoody plants, insects, and fungi.

ASSESSMENT OF CONDITIONS AND TRENDS

Sources of Genetic Threats and Consequences

An essential step in linking the conservation of significant genetic diversity with management practices is the identification of threats to diversity. In this context, a threat could be defined as anything that potentially or actually reduces or changes genetic diversity by a significant amount relative to the standard in situ at any of the levels at which diversity is recognized, from genes through ecosystems. However, as there is a continuum from action to threat to consequence, it is often difficult to identify, with objectivity, the threat. For example, the following hypothetical sequence of events could occur: urban development, leading to population fragmentation, leading to an increase in inbreeding, leading to inbreeding depression, leading to a decrease in fitness, leading to population extinction. Urban development is an action, and population extinction is a potential genetic consequence, but a threat could be defined as any event from urban development through decrease in fitness, whereas a consequence could be any event from population fragmentation through population extinction.

The definition of genetic threat is further complicated by its interactive nature with the biological attributes involved. For example, if the taxon is already depauperate in genetic variation as a result of its evolutionary (e.g., Pinus resinosa, red pine) or recent (e.g., North American gypsy moth populations) history, then certain actions may not pose the same genetic threat as they would with a different, genetically diverse species. In other words, species context is very important in predicting whether imposed changes in genetic diversity are significant or not and whether they are potentially detrimental or not. Differences in genetic architecture among species help geneticists to determine which actions might be threats. For example, the importance of interpopulation gene flow would influence the likelihood of population fragmentation posing a threat. Further, the cumulative nature of threats means that some actions become threats only if they occur in concert with or compound other potential threats.

An obvious factor influencing the identification of threats is the amount of information available. Specific information on the amount and structure of genetic variation for a taxon, and the interrelationships between it and ecological processes, is almost never available. Even when genetic information is available, and a genetic consequence identified, the long- and short-term adaptive consequences are rarely clear. SNEP Genetics Workshop participants felt that an appropriate if conservative approach in the face of minimal empirical knowledge yet a strong theoretical foundation was to assume that detrimental effects on gene pools may occur when large changes in gene diversity are predicted.

Given the variability and subjectivity of defining threats and consequences, it is desirable to address the question, What constitutes an action that may significantly alter genetic diversity? by taxonomic group. This is done in the sections that follow. In addition, those taxa and geographic areas most implicated in the Sierra Nevada are identified to the extent they are known.

Management opportunities to mitigate threats and consequences become possible with the development of standards. Standards reflect the idea of a threshold: When does an activity become a problem? When is it time to take action? Like the concept of threats, standards are fraught with the problems of inadequate information, interactions and complexities in systems, arbitrariness, and subjectivity. Time lags between cause and effect, or action and threat, or threat and consequence, are a major issue. Genetic patterns, in particular, reflect conditions in the recent or distant past, further driving a wedge between present management options and future desirable conditions. Further, standards must somehow embrace the dynamic nature of populations and their genetic attributes (the natural ranges of genetic variation). The sections that follow address the issue of standards for each taxonomic group.

Commercial Tree Species

Spectrum of Actions Likely to Cause Major Changes in Native Gene Pools. While, as is the case with other taxonomic groups, the major threats to tree species in the Sierra Nevada are habitat loss and fragmentation, forest-management practices involving these species, particularly commercial conifers, have potential genetic effects across much of their native ranges in the Sierra Nevada. These potential management- and development-related actions and their consequences are presented in more detail in table 28.20. Mitigating actions that have been taken in forest-management programs are discussed in a later section. Potential consequences may be the result of cumulative effects of multiple concurrent or sequential actions. For example, depending on their implementation, commercial regeneration practices for pines and Douglas fir could have genetic consequences of inbreeding depression, outbreeding depression, reduction in genetic diversity, and/or alteration of genetic architecture, although these effects are undocumented.

Taxonomic Groups and Geographic Areas Involved. By virtue of their being harvested, bred, and planted, the commercial conifers that are the subject of intensive timber management are species that deservedly receive the most attention. Other conifers that are planted and harvested in operational forestry practices are also subject to activities that could potentially alter the gene pool. These include the mixed conifer species, yellow pines, and true firs in the Sierra Nevada (table 28.21). On U.S. Forest Service lands, all of these species are subject to rigorous genetic diversity standards developed to maintain broad adaptability and local adaptations. Some concerns remain that, although standards are in place, they might not be maintained adequately, due to local negligence, urgency, or practical operational realities. Since most of the genetic information available pertains to the commercial tree species, it is possible to be more specific about the nature of the activities used on these species and their consequences, as well as the specific populations and geo-

TABLE 28.20

Types of potential threats and their possible genetic consequences to trees in the Sierra Nevada.

Threat	Possible Genetic Consequences
Artificial-selection pressures	Conditions imposed on tree seedlings for regeneration and restoration efforts at the nursery may not prepare them for planting. Location (climate, soils) and management (soil moisture and fertility, freedom from competition, etc.) regimes at the nursery may not mimic natural selection pressures, leaving seedlings maladapted to the planting site.
Genetic bottlenecks	In out-planting programs, the amount of genetic variation in planted seedlings may be decreased relative to that expected in natural regeneration, due to the initial sampling procedures and subsequent selection in seed orchards and nurseries.
Inbreeding depression	Many tree species have outcrossing mating systems and are susceptible to inbreeding depression. Inbreeding may be a problem in seed collections from wild stands or from seed orchards, especially if not monitored or mitigated. The effects may not manifest themselves immediately in terms of mortality of inbreds, but lowered viability or fitness may occur. Thus, individuals with low fitness may be included in out-planting programs.
Introduction of maladapted genes	Primary introduction of maladapted genes may occur as the result of introducing inbred or nonadapted genotypes to a site. Secondary introduction may occur when the introduced trees reach reproductive maturity and begin combining with the local gene pool. “Outbreeding depression” in the hybrid generation may occur if the introduced genotypes were not adapted to the site or if the introgressed progeny have lower fitness due to hybridization of dissimilar genomes.
High-grading	Selection and removal of certain phenotypes or ecotypes, often the most fit or vigorously growing, known as high-grading, occurred historically on private and public lands but may now be largely controlled by forest practice standards. However, this may continue to be a consideration in some areas, especially where such standards are not in place or enforced. For example, in some “commercial” clear-cuts, trees of commercial size and quality are removed, leaving a small number of various defective and suppressed trees for stocking, seed production, and visual acceptance. Although these cuts may have higher visual acceptance, they likely are very dysgenic.
Attack by exotic insects and pathogens	If resistance to the insect or pathogen is found at very low frequencies in the host populations, as it is in the case of resistance in white pines to the white pine blister rust, then genetic diversity within the host population may be severely lowered, resembling a bottleneck process. Out-planting of nursery-grown stock may also contribute to this situation if the stock has been infected with nursery-found pathogens and serves as a vector to wild populations.
Introgression	In some cases, such as Washoe pine, naturally occurring but sparse or rare species may be in danger of being swamped by the more widespread and co-occurring species (in this case, Jeffrey pine) if the two hybridize. In the case of Washoe pine, some populations potentially at risk in this regard might be those that were apparently heavily logged in the early settlement period, such that population size (already small) shrank drastically in a short time.
Ecological displacement of native populations by introduced species	The introduced species, such as *Eucalyptus* spp., may cause displacement both by being a better short-term competitor for resources and by modifying the site so that it becomes less amenable to the original native species in the longer term.

graphic areas that may be most important to monitor. With less-studied tree species that are nonetheless targets of some kind of manipulative management (e.g., certain oak species), one of the main concerns, based on experience from commercial conifers, is the possibility of inappropriate management. For sparsely distributed species, for which we have little or no genetic information, a major concern is lack of genetic awareness in management or inappropriate genetic management that has relied on inferences from other, genetically dissimilar species.

Standards or Thresholds for Evaluating Effects. If quantitative standards were to be developed, they would have to apply to the genetic consequence (e.g., the allowable change in rate of inbreeding) rather than the threat (e.g., fragmentation), as the latter may be cumulative, qualitative, or not obvious, or may not be the source of the problem. However, due to the lag time between activity and genetic consequence, which is especially pronounced in long-lived species, basing standards on current genetic parameters may mean that action comes too late to mitigate some situations. Thus, it seems that a quantitative approach to standards is ill suited to this taxonomic group. Instead, qualitative statements about levels of tolerance within different species to various kinds of activities must be developed for individual cases. Tolerance could be further related to specific attributes or values such as within-population diversity or genetic architecture. Qualitative standards could then be developed based on the resilience that the value or attribute of interest has to the threat. Also, current and potential management activities could be described in terms of their likelihood of enhancing or lowering tolerance.

As an example, consider within-population genetic diversity for the commercial conifers. Potential threats (i.e., events that could lead to undesired genetic consequences) include severe wildfires, extended climatic extremes, loss of seed-dispersal agents, and excessive or inappropriate seed transfers. Depending on the number of threats at any time, a threat might be considered acceptable or unacceptable. Also, as more information becomes available, the relative nature of the threats (or specific levels of tolerance to each) may play a role in the decision-making process. Further, natural and management-provided processes that increase resilience can be identified and balanced with the perceived threat. In this example, resilience to loss of within-population diversity is provided by the relatively high frequency of reproductive effort in these species and by the relatively high levels of genetic information and its incorporation into management activities.

Other Plants

Spectrum of Actions Likely to Cause Major Changes in Native Gene Pools. Three main classes of events potentially pose serious threats to plant populations or species (table 28.22). The first is habitat destruction or degradation. Only events that are large or genetically significant relative to natural disturbances are considered here. These include alterations in natural cycles, including fire, hydrological, and mineral or nutrient cycles; land development and its associated effects; and human-initiated biotic disturbances such as exotic weed invasions and pesticide-driven loss of pollinators. The second inferred threat is genetic contamination, both within species as a result of inappropriate human movement of genetic material and between species due to hybridization with human-introduced exotics. The third threat is posed by activities that seriously fragment population structure, which can reduce effective population size and reduce gene flow. In the short term, such fragmentation may result in an increase in inbreeding depression. In the long term, genetic diversity in the population may be lost due to genetic drift (random loss of genetic diversity from a population due to sampling effects of small population size) and loss of exchange of genetic diversity. Potential threats become more serious when they either are widespread and cumulative or affect small populations of rare or sparse species. However, any consequences vary as a function of genetic architecture and breeding system.

TABLE 28.21

Examples of trees and tree habitats potentially at risk in the Sierra Nevada.

Taxa	Area and Threat
Sugar pine	Threatened throughout its range, particularly in areas where it is affected by both harvesting and white pine blister rust.
Whitebark pine, limber pine, other white pines	Possibly threatened in high-elevation areas by white pine blister rust. Resistance-oriented planting programs are less likely to reach these less-accessible sites. Also at risk in southern Sierra where (pine) species are common.
Giant sequoia	Historic harvest threatened some populations. Possible genetic consequences in areas where regeneration practices have involved transfer of seedlings among groves (populations). Potential inbreeding within isolated groves.
Ponderosa pine	Harvesting, water diversion, and regeneration practices threaten this species, particularly near urban areas, in low-elevation sites, and on private lands.
Oak species	Oak regeneration problems may result in changed genetic diversity.
Sargant cypress	At risk in west-central Sierra Nevada foothills, where urban encroachment has eliminated several isolated, disjunct populations.
Washoe pine	Especially at risk on Babbit Peak and Mount Rose, due to loss of habitat from wildfire and genetic swamping from ponderosa pine.
Riparian species	At the species level, willow and poplars throughout the Sierra Nevada are affected due to water diversion practices, loss of habitat, and lack of specific information on their patterns of genetic variation to guide restoration practices.

TABLE 28.22

Categorization of threats to plants in the Sierra Nevada.

Threat	Importance to Common Species	Importance to Rare Species
Habitat Destruction or Degradation Altered natural cycles (fire regimes, hydrological cycles, etc.) Human development • Erosion caused by road building or clear-cutting • Air pollution • Effects due to livestock presence Biotic disturbance (usually human caused) • Invasion by and competition from weeds • Presence of feral animals • Loss of pollinators • Introduction of new pests and pathogens	More important for genetically subdivided species (e.g., rare alleles may be lost from peripheral populations)	*Always Important!* (May be somewhat less important for "sparse" widespread species) Species extinction is more likely
Genetic Contamination Native species: both intraspecific and interspecific effects Exotics: interspecific hybridization (especially with exotic congeners)	Human-caused contamination more likely; usually results in loss of genetic architecture rather than extinction	Species extinction is more likely
Population Fragmentation Short term: increased inbreeding depression due to reduced effective population size Long term: loss of genetic diversity due to genetic drift Increased probability of local population extinction via demographic factors	Can be important, depending on breeding system and genetic architecture	Usually more important than in common species; impact depends on breeding system Species extinction is more likely

Taxonomic Groups Involved, Geographic Areas Affected, and Standards or Thresholds for Evaluating Effects. Due to the lack of genetic studies for many of the plant species in the Sierra Nevada, it is difficult to identify specific taxonomic groups or geographic areas that might be threatened. Also, because plants are a diverse taxonomic group in terms of distribution patterns and life history traits, species-specific interactions between these features and the threats will determine the consequences. Similarly, appropriate standards are hard to generalize, given the complexity of these interactions. Instead, a general approach to defining groups and areas at risk has been taken (table 28.23). Two factors, level of gene flow and spatial distribution, have been selected as being among the most important indicators of genetic consequence, given certain threats. Thus, according to the attributes of these two factors, the likely severity of genetic consequences is assessed relative to the threats listed in table 28.22. Those plant species that are most highly threatened, then, could be identified or conjectured according to their generalized patterns of gene flow and spatial distribution. Similarly, geographic areas that are most threatened could be projected by their high concordance of plants with certain spatial distributions. Standards are best approached as qualitative assessments of the likely severity of a consequence, given the species' features and type of threat.

Gene flow has been broadly classified according to only two levels: high and low. The level used here incorporates both intrapopulation and interpopulation gene flow. Spatial distribution of plants has been subdivided into four categories: common or widespread species and three types of rarity (e.g., few plants on few sites). The rarity categories have been based roughly on part of the classification system proposed by Rabinowitz (1981), with one important difference: adaptive processes or degree of habitat specificity have not been addressed here. They are another important layer of consideration affecting genetic consequences, but their inclusion was considered too complicated to accommodate here.

Several examples from table 28.23 illustrate these concepts. In general, habitat destruction has more severe consequences for species or populations with low levels of gene flow than for those with high levels. This assumption is based on the generalization that high levels of gene flow lead to more mixing of the species' gene pool, and loss of one population would probably not mean the loss of many unique alleles or a large portion of the total genetic diversity of the species. Conversely, low levels of gene flow are often associated with substantial local differentiation, and the loss of even one population might represent a loss of genetic diversity not found elsewhere in the species. Rare species, regardless of the type of rarity, are more likely to be affected by destruction of their habitat than are more common species, as any loss of habitat will represent a larger proportion of the total genetic diversity of a rare species.

The consequences of human-caused genetic contamination are more complicated. Here, the relationship between gene flow and consequence depends on levels of both intrapopu-

TABLE 28.23

Relationships between threats and consequences to plants in the Sierra Nevada.

	Severity of Consequences[a]				
		Spatial Distribution of Plants			
Genetic Threat	**Gene Flow[b]**	**Common**	**Few Plants/ Few Sites**	**Many Plants/ Few Sites**	**Few Plants/ Many Sites**
Habitat destruction or degradation (rapid removal of genotypes)	Low	**	*****	*****	***
	High	*	****	***	**
Human-caused genetic contamination[c]	Low	**	****	***	***
	High	*	****	***	***
Fragmentation—inbreeding depression	Low	*	****	***	**
	High	**	****	****	***
Fragmentation—genetic drift	Low	**	****	***	***
	High	*	****	**	**

[a] Rating system is based on degree of severity of consequence, from least (*) to most (*****) severe.

[b] Gene flow refers to both spatial and temporal gene flow and incorporates gene flow both within and among populations.

[c] For common plants, the consequences of genetic contamination are not so much a function of the biological situation as of the frequency of the threat. These plants are often the target of restoration or revegetation projects, so the threats are more common here, even if individually the consequences may not be severe. For rare species, the distinction between species with high and low gene flow is complicated here. The consequences will vary depending on the rate of interpopulation and intrapopulation gene flow, as well as other factors.

lation and interpopulation gene flow and other situation-specific factors (such as differences in gene frequencies between introduced and native groups, differences in number of breeding individuals, differences in adaptive capacities, etc.). For example, if a plant species possessed high levels of within-population gene flow, the introduced ("contaminating") genes might quickly circulate and swamp the natural diversity of a population; however, if the interpopulation levels of gene flow were low, the contamination would remain somewhat localized, mitigating the genetic consequence. Another aspect of genetic contamination is that common species are generally quite resilient to this type of threat. However, they are portrayed here as being subject to somewhat severe consequences, due to the frequency of occurrence of this type of threat. Common or widespread species are often used in restoration or revegetation efforts. Thus, while each individual event in itself may not have large consequences, the probabilities of ultimate genetic consequences may be additive.

The consequences of fragmentation should be considered in both short-term (inbreeding depression) and long-term (genetic drift) contexts. In the short term, species with low levels of gene flow might suffer fewer consequences than those with high levels. Low levels of gene flow are often associated with a largely inbreeding mating system, and thus there would be less likelihood of inbreeding depression. Conversely, outbreeding species would be more susceptible to inbreeding depression. If the species or population survived the short-term genetic consequences, it might be challenged by genetic drift. Here, the consequences would be felt more strongly in the species with inherently low levels of gene flow, which would remove or minimize any opportunities for bolstering levels of genetic diversity by incorporating pollen or seed from other populations.

One generalization that can be drawn from table 28.23 is that for habitat fragmentation, the main distinction in severity of consequences is between those species with few individuals and those with many. For habitat destruction, the major difference in consequences lies between species that are broadly distributed and those that are narrowly distributed (i.e., a function of spatial distribution).

Mammals

Spectrum of Actions Likely to Cause Major Changes in Native Gene Pools. Threats to mammalian species in the Sierra Nevada fall into five categories, four of which are anthropogenic. One general category includes management that generally fails to support wildlife habitat. This results from both misinformation (inappropriate use or interpretation of information, poor or inadequate studies, etc.) and lack of information (impediments to research, lack of specific information on genetic architecture of species, etc.). Often missing is the context for interpretation provided by long-term studies and those that help determine the relationship between common measures of genetic variation (e.g., heterozygosity and allozymes in general) and population fitness.

A second threat is change in natural metapopulation structure (i.e., the structure of the group of populations that interbreed, if only occasionally). Two aspects are important: fragmentation events that decrease gene flow among populations or that subdivide previously contiguous populations, and activities that connect previously disjunct populations, thereby increasing gene flow above normal levels. Severe fragmentation or habitat loss may prevent the occasional gene transfers that are critical to adaptations and long-term resilience.

A third type of threat is loss of migratory routes, including winter and summer habitats and elevational corridors. This is a critical concern for birds and mammals.

Competition and predation from exotics and gene swamping from nonlocal transplants are another major threat. Domestic grazing species, in particular, are major competitors with natural populations.

A fifth type of threat is disease. Although disease is a natural component of the ecosystem, populations that are already stressed may succumb to diseases that would not otherwise be significant. For example, the mountain sheep (Ovis canadensis), native to the southern Sierra Nevada and recently reintroduced into Inyo County and into the South Warner Wilderness of Modoc County, is extremely sensitive to disease. Diseases, particularly those transmitted from livestock, could likely be a major factor in the decline and loss of mountain sheep populations (Zeiner et al. 1990b). Loss of populations potentially leads to loss of ecotypic genetic variation in the species.

Taxonomic Groups Involved. The species most at risk are those with migratory patterns or highly specialized niches (riparian species, localized endemics, etc.) (table 28.24).

Geographic Areas Affected. Areas with easy access, lands where species and habitats have little protection, and areas of species richness are all identified as high-risk areas (table 28.24). Examples are the Sierra Valley and the Kern River Plateau. Also threatened are areas of significance to migratory species or aquatic-dependent species.

Standards or Thresholds for Evaluating Effects. In the absence of empirical data for defining standards to evaluate genetic threats in mammalian species of the Sierra Nevada, theoretical guidelines should be considered. If genetic parameters or proxies are to be used effectively to evaluate threats or as indicators of resilience or health, there must be a context within which to interpret them. There must be a temporal context, that is, knowledge of the normal or perhaps cyclical range of variation and how the parameters relate to demographic trends. There must also be a spatial context—a means of interpreting at the management unit level how local parameters relate to regional or larger-scale patterns and trends. Further, choices must be made as to which taxa can serve as representative units, as it is unrealistic to develop standards for every species. The information needed to establish such a context is not currently available. As such, it is perhaps most appropriate to discuss the approach to developing standards. At the community level, two aspects are important, monitoring and ecosystem indicator species.

An important initial step in monitoring the health of biotic communities is to inventory the community or communities within the management unit. Although the initial inventory is key, it is important to inventory regularly. After the broad-scale inventory, detailed monitoring should be provided for all indicator species (criteria for choosing these species are listed later). Minimum information collected for these species would include densities of local populations, numbers of local populations, and degree of genetic differentiation among populations, these three parameters providing some measure of metapopulation functioning. Other essential data include the appearance of new alleles and changes in the distribution of private alleles (i.e., alleles unique to a population). One or both of these could be a warning sign of disturbance. The point here is that changes in any of these features could indicate reason for concern and would eventually provide the connection, currently lacking, among threat, genetic consequence, and demographic consequence that would allow development of standards.

For choosing indicator species, an appropriate scale for reference might once again be a biotic community level or management unit. The number of species chosen will depend upon the complexity of the management unit. Choices should be locally appropriate.

SNEP Genetics Workshop participants suggested that representative or indicator species for a management unit include the following:

- Species with varying life history characteristics—short and long individual life spans, wide and narrow distributions, and so on
- Species representing various trophic levels
- Species that are strongly associated with the management unit (e.g., endemics)
- Keystone species
- Representative specialist and generalist species

TABLE 28.24

Taxonomic groups and geographic areas potentially most threatened in genetic diversity among vertebrate species of the Sierra Nevada.

Taxonomic Group	Threatened Taxa	Threatened Geographic Area
Amphibians	Terrestrial plethodontid salamanders (TPS), most native frogs and toads.	All areas where TPSs are found. The Kern River Plateau is *very* sensitive. All high-elevation areas of the Sierra Nevada, e.g., above 6,000 ft, and the southwestern Sierra Nevada at all elevations.
Birds	Neotropical migrants, aquatic-dependent species.	Migration stopover areas and staging areas.
Mammals	Bats, top carnivores, localized endemics, aquatic-dependent species.	Kern River Plateau, foothill areas, Sierra Valley, riparian areas.

- Species that are net transporters of nutrients and/or energy in or out of system (e.g., bats, certain fish)
- Species that opportunistically use the management unit and thus may help to monitor the health of the system
- Recent and ancient phylogenetic taxa
- Recent and historical residents
- Species that represent soil microfauna and microflora

Birds

Spectrum of Actions Likely to Cause Major Changes in Native Gene Pools. Given the high degree of gene flow observed in many bird species of the Sierra Nevada, an obvious genetic threat would be any action that resulted in the loss of natural metapopulation structure. Threats would be fragmentation events that decreased gene flow among populations or subdivided previously contiguous populations Severe fragmentation or habitat loss may prevent the occasional but critical gene transfers between metapopulations.

As most of the species in this bioregion are migratory, loss of migratory routes, including winter and summer habitats and elevational corridors, is a critical concern.

Activities that change the quality of habitat will have direct consequences for the resident bird species, although it is unclear whether these are detrimental, neutral, or beneficial. For example, chestnut-backed chickadees (Parus rufescens), prior to 1940, inhabited mainly coastal areas of northern and north-central California. Shortly after that time, they started to move inland, and today their distribution includes both their former range and much of the Sierra Nevada (Brennan and Morrison 1991). One explanation presented for this range expansion is that successional patterns following widespread logging in the Sierras caused an increase in the proportion of Douglas fir in the mixed conifer forest, which subsequently provided habitat favorable to chestnut-backed chickadees. Although in this case the range expansion of one bird species was apparently not accompanied by a range decrease in another, this is potentially a risk with such (management) activities.

Taxonomic Groups Involved. Taxa with very specific and narrow habitat requirements might be most threatened. Specific examples were not known by workshop participants (table 28.24).

Geographic Areas Affected. No specific examples are available.

Standards or Thresholds for Evaluating Effects. Little information is directly available from which to develop standards for evaluating genetic threats to avian species. A useful avian example exists, however, of a more general issue regarding the use of genetic information for evaluating threats. In 1990 an allozyme study was reported of seven populations of the spotted owl (Strix occidentalis), covering the three currently recognized subspecies from Oregon, California, and New Mexico (Barrowclough and Guttiérrez 1990). Twenty-three allozyme loci were scored; all were monomorphic for the two subspecies in Oregon and California, S. o. caurina and S. o. occidentalis. This implies both zero heterozygosity (for those loci) and no population differentiation between those subspecies based on these data. The New Mexico subspecies (S. o. lucida) was differentiated from the other two at only one polymorphic locus. However, in spite of the current conservation concerns regarding this species, the low heterozygosity values were not interpreted as evidence of a genetic risk or as evidence of higher than expected levels of inbreeding. Rather, it was suggested that the low values are the result of a historical bottleneck, low effective population sizes (small populations generally tend to have low levels of heterozygosity), and/or the inherently low levels of variation in many of the genes sampled in the study (across all species). The certain consequence of low heterozygosity values is that monitoring the species for genetically significant changes will be more difficult. Generally, this example illustrates that genetic information, like all other data, must be carefully interpreted within the proper biological context.

Reptiles and Amphibians

Spectrum of Actions Likely to Cause Major Changes in Native Gene Pools. The most significant threats to reptiles and amphibians in the Sierra Nevada are all related to direct (management) or indirect (e.g., urbanization and forest management) human effects. Population fragmentation and habitat loss not only result in direct removal of individuals or populations but also can have the secondary effect of increasing inbreeding depression. For terrestrial species, management activities are a threat to suitable habitat. Some specific examples of this type of threat are known for salamanders. Clear-cutting or the removal of significant and contiguous portions of the overstory on the western slopes in the Sierra Nevada is a serious threat to salamanders in areas where it dries the understory and substrate below adequate moisture levels. Similarly, controlled burns that are too intense, or severe wildfires, dry out even moisture-laden logs that otherwise could serve as temporary refugia for these species. Habitat improvement for other species, such as mammals, can pose a serious threat to amphibious species. For example, improving access for large-game mammals to a spring-fed pond in Sequoia National Forest destroyed the only known population of an undescribed species of Batrachoseps, a lungless salamander (Wake 1994).

Significant to amphibians are activities that have disrupted metapopulation phenomena. For example, Rana muscosa was once widespread in the Sierra Nevada, but its range has significantly contracted. Frogs have a natural metapopulation structure and depend on large source populations for recolonization of shallow ponds and marginal habitats, where local natural extinction rates are high. With the introduction of non-native trout into most large ponds and lakes of the high Sierra, the source populations have been devastated. Thus, local extinction continues to occur in the peripheral sites, but there is no recolonization, and the once-temporary absences become permanent extinctions. The situation may be even more extreme with Rana cascadae in the Lassen area (D. B. Wake, University of California, Berkeley, e-mail to the authors, 1995).

Introduced exotics are a threat to amphibians, primarily as predators. Non-native fishes have been stocked in most of the lakes in the Sierra Nevada, nearly all of which were previously fishless (Christenson 1977; R. A. Knapp 1994, 1996). Subsequently, fish dispersed throughout the streams that interconnect these lakes. Such introduced fishes appear to have nearly eliminated the mountain yellow-legged frog (Rana muscosa) where they co-occur (Bradford et al. 1993), and the same probably happened to R. boylei, Hyla regilla (Pacific tree frog), and Ambystoma macrodactylum. These eliminations are believed to have isolated many of the remaining populations of highly aquatic species such as R. muscosa (Bradford et al. 1993) and thus have been significant factors in causing habitat fragmentation and disruption of metapopulation structure, resulting in persistent local extinctions (D. B. Wake, e-mail to the authors, 1995).

In summary, urbanization activities such as land conversion, expansion of housing, development of recreation areas, road building, and dam construction are historical and continuing threats to reptiles and amphibians in the Sierra Nevada, causing habitat loss, disruption of metapopulation structure, and population fragmentation. More is known about the specific threats and consequences for amphibians than for reptiles, due to the void of genetic information for the latter group. Many of the most serious, current, and specific threats to amphibians (at least) can be categorized as management activities targeting nonamphibians without regard for amphibian habitat needs. Currently, the most profound human impacts on aquatic communities in the high Sierra appear to be related to historical and ongoing stocking of exotic fish species in high Sierra waters (Bradford et al. 1994).

Taxonomic Groups and Geographic Areas Involved. The lack of genetic information for many species makes it difficult to target specific taxonomic groups or geographic areas. However, it is known that some populations of plethodontid salamander species are threatened (table 28.24). The Kern River Plateau, because of its species richness, is an especially sensitive area; logging and other management or development activities threaten many species here.

Standards or Thresholds for Evaluating Effects. Again, due to the lack of information for many species and the complexity of genetic-ecosystem relationships, it is not currently possible, and perhaps not appropriate, to define quantitative standards. Natural patterns of genetic structure may provide some guidelines regarding the relative resilience of different taxonomic groups to various threats. For example, species with high levels of among-population diversity (e.g., high F_{ST} values) might be more resilient to the effects of fragmentation and inbreeding depression. The most appropriate approach to conserving genetic diversity in these taxa is to focus on protection of their habitat and the health of their biotic communities.

Fish

Spectrum of Actions Likely to Cause Major Changes in Native Gene Pools. Actions that potentially alter natural genetic levels and patterns of genetic variation in Sierra Nevada fish populations include natural phenomena, human activities affecting water flow and quality, introduction of non-native fish species, direct manipulation of native gene pools, and genetic technologies.

Natural if rare phenomena such as volcanic activity can indirectly reduce fish populations via suffocation and gill abrasion and perhaps have historically removed some fish species from waters in the Mono Lake basin (Moyle 1976). Volcanic activity can alter geographic structuring of genetic variation by increasing the incidence of straying (i.e., the change in water quality confuses fish and / or dissuades them from returning to their natal waters to spawn). For example, the high ash content of rivers near Mount Saint Helens increased straying in chinook salmon, as the fish tended to avoid ash-laden water (Bartley and Gall 1990).

Human activities that may affect water quality for fish and thus potentially affect genetic structure include hydraulic mining, water diversion projects, hydroelectric projects, roadbuilding, wildfire, and logging. Habitat degradation associated with these activities has been linked to the decline of populations of chinook salmon (Bartley and Gall 1990). These natural phenomena and human activities that degrade fish habitat have two main genetic impacts. First, fish population sizes decline rapidly, pushing the remaining populations through a genetic bottleneck with possible loss of genetic variation. Second, the decrease in water quality (e.g., from turbulence, mud slides, and volcanic ash) can alter natural migration patterns, thereby affecting geographic structure in genetic variation. Further, alteration of watercourses can bring previously isolated species or populations into contact with one another, causing artificial mixing of gene pools. For example, alteration of traditional salmon spawning routes after construction of Lewiston Dam on the Trinity River may have led to natural hybridization between chinook and coho salmon in Deadwood Creek, California (Bartley et al. 1990).

Introduced species potentially have many deleterious effects on genetic structure through their impacts on existing fish populations and habitats, including potentially displacing native species (e.g., Ferguson 1990). For example, introduced brook trout (Salvelinus fontinalis) and brown trout (Salmo trutta) are thought to have displaced many populations of bull trout (Salvelinus confluentus), a species that historically existed in the Upper Sacramento River drainage and is now thought to be extinct in California (Leary et al. 1993). Non-natives may also hybridize with native species, diluting native gene pools and perhaps reducing fitness due to the creation of sterile or less fit interspecific hybrids. Evidence from allozyme studies suggests that several golden trout (Oncorhynchus mykiss whitei) populations from the Little Kern River basin have hybridized with introduced rainbow trout (Oncorhynchus mykiss) (Gall et al. 1976).

Manipulation of native gene pools occurs through hatchery practices that do not recognize the importance of maintaining large founder population sizes, of keeping fish stock separate by location of origin, or of returning local populations to their origins. The use of nonlocal stock in hatcheries and the practice of transferring stock between populations potentially can reduce local levels of adaptation by swamping and hybridizing with native gene pools (called outbreeding depression, which is not empirically documented). Use of only a few founder fish in hatcheries acts as a genetic bottleneck, potentially reducing the amount of genetic variation in the subsequent populations. Inbreeding depression may become a threat when levels of genetic variability become reduced below naturally occurring levels. Evidence of inbreeding depression has been described for the well-studied rainbow trout, including increased mortality of eggs, alevins, and fry; decreased growth rate of fingerlings; and decreased body weight for adult rainbow trout (Gjedrem 1992).

Hatchery fish may also affect geographic structure in genetic variation due to increased straying. It is thought that hatchery-reared fish, in some cases, may be less imprinted on their natal river or stream than wild fish due to particular management practices in their hatchery environment. For example, the increased level of gene flow observed among chinook salmon populations in the San Joaquin–Sacramento River system has been interpreted as being at least partly due to the hatchery practices in this drainage. Hatchery-released fish may not have an opportunity to imprint properly, due to limited hatchery residence time and/or water differences between the hatchery and local areas. This may lead to increased straying, increased gene flow among populations, and consequent changes in genetic structure (Bartley and Gall 1990).

Genetic technologies present both an opportunity and a potential threat to natural patterns of genetic variation. Rainbow trout has had many extreme technologies successfully applied, such as chromosome manipulation (e.g., production of triploid fish), induction of androgenesis and gynogenesis (all-paternal and all-maternal inheritance, respectively), and gene transfers (Thorgaard 1992). This facility of fish in general, and the rapid increase in knowledge of the rainbow trout genome in particular, are potentially valuable for both research and commercial fisheries interests. However, uninformed or accidental release of manipulated stock could pose a new spectrum of genetic threats to native populations.

Taxonomic Groups and Geographic Areas Involved. The aforementioned threats to genetic variation in fish species are pervasive over the Sierra Nevada, although genetic effects have rarely been directly measured. The Little Kern River golden trout is one specific example. Evidence exists for hybridization between one subspecies, Oncorhynchus mykiss whitei, and rainbow trout in the Little Kern River (Gall et al. 1976). However, there are also apparently pure populations remaining in upper Soda Springs Creek and Deadman Creek, both apparently physically isolated from the introgressed populations and possessing high levels of within-population genetic variation (heterozygosity).

Standards or Thresholds for Evaluating Effects. Heterozygosity has been used as an indicator of adaptive potential. For example, in the previous description of the viability of golden trout populations, the resident levels of heterozygosity in the pure populations were interpreted (by the study authors) as indicative of adaptive capability (Gall et al. 1976). However, these allozyme data must be interpreted within their spatial and temporal context. There is some evidence that sampling methods in genetic studies may bias results due to naturally existing temporal variation in allele frequencies. Between the two sample periods of 1984–86 and 1987–88, Gall and colleagues (1992) found, for twelve allozyme loci, significant differences in allele frequencies among eighteen populations of chinook salmon. This suggests that fish populations have a genetic structure that may also be related to the season or year.

In general, the task of accumulating the desirable genetic baseline data for fish is perhaps more complicated than for many other taxa, due to the high degree of manipulation of natural populations prior to genetic sampling. This is well expressed in Bartley et al. 1992: “The excessive and often undocumented transplants of coho salmon throughout the Pacific Northwest may obscure natural patterns of genetic variability and make geographical identification of stock difficult.”

Insects

Spectrum of Actions Likely to Cause Major Changes in Native Gene Pools. The greatest potential threat to insects is the loss of habitat, leading to fragmentation of populations, loss of corridors for gene flow, and ultimately the alteration and loss of genetic variability. Although no direct studies on the effects of grazing have been done in the Sierra Nevada, habitat loss from trampling by grazing domestic sheep was implicated in the initial decline in populations of the Uncompahgre fritillary butterfly (Boloria acrocnema) in the Rocky Mountains (Britten et al. 1994a). This species, now limited to one population, is close to extinction. However, its intolerance of Holocene climates may have caused its demise anyway—it was already restricted to extremely cool, moist alpine slopes (A. M. Shapiro, University of California, Davis, e-mail to the authors, 1995).

A second, related threat is land-management activities that affect and alter forest successional stages. Many insect species are dependent on a particular seral stage. Management that affects the seral development or that arrests succession at a subsequent or earlier stage may lead to habitat loss or fragmentation. An example close to the Sierra Nevada is the apparent demise of the last population of an endangered butterfly species restricted to a Pacific Gas and Electric power line corridor in Mendocino County, California. Because the butterfly was federally listed (as threatened or endangered), the company was not allowed to cut vegetation in the corridor, and thus succession proceeded. The species was not well adapted to later successional stages, and, due to extreme fragmentation in its habitat, was not able to "escape" to a more favorable, earlier successional area. Thus, the population, and presumably the species, was driven to extinction by normal successional processes, in combination with fragmentation (Shapiro 1994). This relationship with a successional stage occurs in many butterfly species; in general, they are not adapted to old-growth habitats. Thus, successional processes might lead to genetic depletion and population extinction if seral diversity is not maintained at appropriate landscape scales and mixes.

A third potential threat may be the swamping of natural populations by human-associated new ecotypes of native (insect) species. Increasing in occurrence are ecotypes of native insect species that have adapted to feed on introduced (exotic) weeds. These are particularly prevalent in disturbed situations such as railway embankments and roadsides. As these ecotypes spread and contact the local native populations, they threaten to swamp them genetically, resulting in a loss in genetic variability that is relevant to the natural (herbaceous) host species. One example in northern California is the silvery-blue butterfly (Glaucopsyche lygdamus). It has a recently evolved, genetically distinct ecotype that feeds on introduced annual vetches (Shapiro 1995). This new ecotype has now spread to the point of contact with native populations that feed on native and local legumes. As such, the native populations may be threatened (Shapiro 1994). The same phenomenon is occurring independently in the northeastern United States in the same species (Dirig and Cryan 1991).

A fourth potential threat is overcollection by hobbyists. Distinctive phenotypes, especially in butterfly species, are sought and removed by sport and commercial collectors. The rarer the phenotype, the more avidly it is sought, and the larger the proportionate reduction in its species when it is removed. Once rare species or populations have been taxonomically recognized, they may be eligible for listing under state or federal legislation as threatened or endangered. However, this recognition may also increase their vulnerability to collectors. This phenomenon is associated with other charismatic species as well, including damselflies, tiger beetles, and longhorn beetles. Ladybugs are collected in great numbers in some forests by Laotians and other groups.

A fifth category of threat is posed by overuse or misuse of wide-spectrum biocides. For example, Bacillus thuringiensis (Bt) is a broad-spectrum biocide that is often employed against spruce budworm. However, it is an effective agent against all members of the Lepidoptera, and thus may kill all caterpillars in the application or drift area. Thus, its indiscriminate use could lead to losses of populations or races of nontarget species. While Bt provides a particularly striking example, this is a typical description of many biocides.

A last example of a type of threat that is particularly relevant to insects is the potential effects of homogenization of host species due to management activities. Standardizing, or reducing the amount of genetic variability within, host plant species (e.g., the use of standardized genotypes or clones in a forest regeneration effort) may be followed by depletion of genetic variability within the dependent insect species, although this is undocumented in the Sierra Nevada among native taxa.

Taxonomic Groups Involved. While data are not available to provide a comprehensive list of threatened species or populations for the Sierra Nevada, the Lycaenid butterflies possess the classic characteristics of a vulnerable taxon. These characteristics include having well-defined and local populations; in this case, ecotypes are differentiated according to host plants (A. M. Shapiro, e-mail to the authors, 1995). The life history characteristics of the ecotypes appear to coevolve with those of the host. The species are highly localized, specialized, and fragmented, and usually disperse only locally. They are thus vulnerable and cannot "escape" if threatened. Most of the endangered butterflies listed at either the state or federal level are members of the Lycaenidae (Arnold 1983a).

Other groups of insects may also be genetically threatened or vulnerable. These include taxa isolated on mountaintops, such as alpine grasshoppers and beetles. Parasitoids of narrow, specialist organisms are possibly threatened. Specialized roaches, such as wood roaches, might be vulnerable. Cave crickets and damselflies might also be included in this group of threatened species.

Geographic Areas Affected. For insects, three types of environments have high concentrations of potentially vulnerable organisms, from a genetic perspective. One is alpine environments, for example, the White Mountains. Insects in these environments tend to be restricted and unique, and small changes in climate or habitat threaten these organisms. Another is edaphic islands. The biota of islands of serpentine, gabbro, or Ione clay, and of sand dune areas of the Sierra Nevada, is potentially endangered. A third environment is riparian zones. Insect taxa may depend on these habitats as corridors for gene flow. Increasing fragmentation and isolation make their resident biota more vulnerable.

Another type of area that may be vulnerable for insects is described as a suture zone. This is an area consisting of multiple, overlapping hybrid or integration zones. Historically, they are often the result of refugial species meeting after expanding following major climatic shifts. These zones are often rich in unique genetic diversity due to these features of secondary contact and hybridization. Examples of this suture zone phenomenon in the Sierra Nevada include the Sierra Valley, Warner Mountains, riparian blend zones such as the Upper Feather and Pit River drainages, and parts of the Plumas National Forest (Collins 1984; Porter 1989; Porter and Geiger 1988; Shapiro and Nice n.d.).

There are several other examples of specific areas that, while not fitting the aforementioned generalizations, are host to apparently vulnerable organisms. The first is a low-elevation area of Oregon oak–juniper communities on Ball Mountain in Siskiyou County, California. This area supports a population of a butterfly that normally occupies only wet or even inundated meadows at moderate to high elevations (A. M. Shapiro, e-mail to the authors, 1994). Its existence on Ball Mountain is tenuous due to the dry summer condition of the area, and any additional stress might overwhelm the population's resilience. A second example of a threatened area is a specialized community on Goat Mountain in Colusa County, California. Here, a local population of the Mormon metalmark (Apodemia mormo) butterfly feeds on a local ecotype of wild buckwheat, Eriogonum wrightii. Similar situations may exist in the Sierra Nevada.

Standards or Thresholds for Evaluating Effects. Although specific and quantitative standards are beyond the scope of currently available data, several issues are germane to insects. First, it is unlikely that direct genetic data will suffice for developing insect standards. Because most insect sampling for genetic purposes is (currently) necessarily destructive, such studies for many species will not be undertaken, due to the rarity of many target taxa, legal protection of species, and the morality of such studies as electrophoresis when the interpretation and biological meaningfulness of the data are uncertain. At present, not enough is known about the correlation of insect population health with habitat attributes to suggest ecological or community-level proxies as a standard.

A second issue is historical sequence. Standards must be chosen so as to take into account the taxon's history. For example, low intraspecific variability would not necessarily be indicative of viability problems if that species had largely been inbreeding or homozygous for a long period of time. Fitness and viability problems are more likely to occur when there is a rapid depletion of genetic diversity, as occurs in an anthropogenic bottleneck process.

The challenge, then, is to develop standards based on trends and to have the means to examine trends in genetic attributes. One recently initiated approach with insects involves taking small samples from museum specimens, assaying them with PCR-based techniques (PCR, or polymerase chain reaction, is a means of detecting genetic variation with high sensitivity even in very small samples of DNA), and comparing the results with extant samples. One such project is currently underway in regions adjacent to the Sierra Nevada with an endangered species of butterfly, the Oregon silverspot (R. VanBuskirk, communication with the authors, 1995). This approach is not ideal, due to the limitations of museum specimens (i.e., they are few in number, are usually derived from a restricted geographic area, have the potential for being mislabeled, etc.) and the statistical challenges of comparing the historical and extant samples. However, at least qualitative results should be possible.

Plasticity is also problematic in developing standards. The role of environment in modulating phenotype may preclude the development of reliable morphological standards. For insects, the concern is the recognition of eco-phenotypes that may not have a genetic basis for differentiation. For example, silvering on the underside of hind wings in the fritillary butterflies is used for taxonomic classification. However, silvering is a highly plastic characteristic that may be greatly affected by humidity and have low heritability (Arnold 1983b, 1985; Hammond 1986).

Fungi

Relatively little information is available concerning specific effects to fungal species. This is partly a function of the general lack of (population-level) genetic information and partly due to the classification of some fungal species as pathogens. Their harmful nature to commercially significant plants has usually led to a desire to lower their populations, not conserve them. The so-called beneficial fungal species (e.g., mycorrhizae) are sometimes cultured domestically and cultivated as clones or races, making genetic variation in natural populations less of a concern. Nevertheless, it is possible that breeding commercial tree species with genes for resistance to fungal pathogens and incorporating these trees in large numbers in forests may have a negative impact on genetic variation in the target fungal species (e.g., the planting of sugar pine trees with a major gene for resistance to exotic white pine blister rust).

One fungal species that may suffer genetic consequences as a result of human activity is the edible and commercially valuable North American matsutake or tan oak mushroom (Tricholoma magnivelare). Although the possible genetic impacts are unknown at present, and ecological studies are only now underway, harvesting of this species in areas such as the Klamath National Forest has rapidly expanded since 1990 (Richards 1994). In recent years, the limited and traditional gathering of the mushrooms by local Native Americans and hobbyists has been outscaled by commercial harvesting (Richards 1996).

Recent and increasing attention has focused on the development of techniques to distinguish not only among fungal species but also among strains within species. These tools include random amplified polymorphic DNA (e.g., Garbelotto et al. 1993) and PCR in combination with RFLP and/or sequencing techniques (e.g., Gardes et al. 1991).

Assessment Conclusions

Because of the nature of genetic variation, its measure, and interpretation, it is extremely difficult to arrive at firm synoptic conclusions about threats to genetic diversity in the Sierra Nevada. Nevertheless, several specific issues can be singled out as being of high priority, and several others are general categories of concern.

Severe Wildfire

SNEP assessments clearly indicate the changed nature of fire regimes over the last century in the Sierra Nevada (see McKelvey et al. 1996). The risk of severe fires is higher than during any other period that has been evaluated in the Holocene. Large, stand-replacing fires such as are likely now present significant risks to gene pools of forest trees and plant communities, with direct and indirect consequences to other plants and animals that live in them.

Habitat Alteration

For most taxonomic groups, the major known threats to genetic diversity are habitat destruction, degradation, and fragmentation. These not only result in direct losses of genetic structural diversity at the population level, but also change genetic processes (gene flow, selection), affect effective population sizes, and contribute to changes in genetically based fitness. Habitat alteration and loss have both trickle-down and trickle-up effects, in that lower-level genetic diversity is affected (within and among individuals and within and among populations) and there are potential effects to species viability. Although we have not emphasized in this chapter the assessment of which geographic and taxonomic locations are most affected by habitat alteration in the Sierra Nevada, information from other chapters confirms that high-priority areas would be the foothill zone on the west slope, several of the trans-Sierran corridors (especially in the central Sierra Nevada), and scattered locations of concentrated development elsewhere.

Silviculture

Management actions that are extensive across the landscape yet intensive in manipulating individuals and populations have the greatest potential for direct and significant genetic effects. As such, silvicultural activities, including tree improvement programs, operational forest regeneration (artificial and natural), and timber harvest, potentially affect the gene pools of target species. Fortunately tree improvement programs in the Sierra Nevada (both public and private cooperatives) have long used sophisticated and ecologically appropriate genetic diversity and genetic conservation guidelines. Similarly, in operational forest regeneration, most federal, state, and local regulations regarding genetic diversity in planting have high standards and are backed by significant amounts of research. Seed banks for public and private reforestation exist that maintain high standards for seed origin and genetic diversity. These programs, which have histories dating back several decades in the Sierra Nevada, serve as models for other taxa where similar activities occur (e.g., fish stocking).

Although these programs and guidelines are genetically sophisticated and widely practiced throughout the Sierran forests, there is room for implementation error. For instance, about half of the trees planted by the U.S. Forest Service in the Sierra Nevada are in unanticipated plantations in areas burned by forest fire (Landram 1996). The seed banking program of the U.S. Forest Service bases the quantity of seeds it procures and stores primarily on a determination of planting needs. National forests are required to maintain a ten-year supply of seed for the relevant seed zones (the actual supply quantity varies from 5 to 12 years, depending on species and zone). This supply is based on estimates of planting needs determined from harvest plans and an estimation of the amount of seed needed for replanting following wildfires. Since national forests must pay for cold storage space and periodic seed testing, there is no incentive to maintain extra quantities to handle exigencies of severe and large wildfire. After large wildfires occur, there is often pressure internally in the agencies, as well as from the public, to reforest rapidly. If local and appropriate seed is not in the seed bank, the pressure to use seeds from nonlocal seed zones, low-diversity seed lots, or old seed collections may be high, despite the awareness of seed-transfer and genetic diversity guidelines. In practice, when local seed is not available, seed from adjacent zones is sought (as directed by policy), and consultations with geneticists occur when transfers are necessary.

Also important is the fact that seed is collected on national forests primarily from the timber forest types, and primarily from the commercial tree species, although this has been changing in recent years. Ability to reforest high-elevation, high-stress sites or noncommercial species within timber zones would be hampered by inadequate seed supplies.

Research studies are inconclusive about the long-term genetic consequences to commercial tree species of timber harvest, as well as about the ecological and evolutionary significance of those consequences. Nevertheless, traditional silvicultural practices, which were designed primarily to maximize growth of the target species, tended to result in spatial patterns of harvest and live-tree retention that acted in concert with genetic conservation guidelines. By contrast, some new forestry practices, which combine fiber production with ecological stewardship for wildlife and nontimber species, may have potential for dysgenic genetic effects on the native timber species. For instance, leaving clumps of trees, especially suppressed individuals (as, for example, for wildlife protection), may promote inbreeding or lowered fitness if the members of the clumps are related, as they appear to be. Similarly, leaving large, isolated live individuals as snag recruits or perch trees may lead to inbred seed if these act as seed sources. On a case-by-case basis, these effects are probably minor relative to background natural genetic diversity, although cumulative effects should be considered.

A specific taxon of concern in this regard is sugar pine. Although a well-funded and genetically sophisticated program exists for developing and out-planting sugar pine that is resistant to white pine blister rust, there has been limited recognition of the genetic consequences of the current federal harvest practices for the species. At present, known resistant old-growth sugar pines are not cut, but susceptible trees may be harvested, and in areas where resistance is unknown, harvest proceeds without genetic testing. Although leaving resistant trees and harvesting susceptible ones may seem genetically appropriate, it causes a significant loss of genetic diversity in traits other than the resistance loci and may seriously impede sugar pine's ability to pass through the pending blister rust bottleneck (Millar et al. in press). In the case of sugar pine, all mature trees should be left unharvested, especially in areas where the rust is not presently a major problem, unless the reasons for harvest are carefully evaluated and justified.

Ecological Restoration

Although tree improvement and regeneration programs have followed genetic diversity guidelines for decades, practitioners of ecological restoration have only recently become aware of genetic concerns in planting (Millar and Libby 1989). Although many programs focus on restoring correct native species, an understanding of the appropriate genetic material within species, its origin, diversity, and collection, is missing from many programs. Thus, genetic contamination problems may be more severe than if exotic species had been planted. The significance of this genetic threat in the Sierra Nevada is lowest in projects of ecological community restoration (primarily because in the Sierra Nevada such projects are highly limited in number and extent and are conducted by knowledgeable users) and highest in postfire erosion control projects. These frequently involve grass species and occasionally forb mixes. Although exotic grasses (especially ryegrass) were previously used routinely, native grasses are increasingly becoming favored. There is often little understanding of the potential genetic consequences of planting seeds of native species but unknown (often commercial nursery) origin. Further, even where there is awareness, the lower cost of commercial seeds (of unknown origin and diversity) compared to that of local, custom-picked seeds and the pressure to plant rapidly following a fire encourage the use of inappropriate genetic stock. Similar situations may arise in watershed restoration projects, where the genetic implications of activities are often not considered or evaluated.

Fish Management

Management of fish species and genetic diversity within species in the Sierra Nevada is done in a way that potentially disrupts many native gene pools. Fish raised in hatcheries and introduced into native Sierran waters are not managed to maintain or promote natural genetic architecture. Selection is for endurance and resilience to both hatchery conditions and a wide range of natural conditions, regardless of native genetic architecture. The introduction of hatchery, nonlocal, and genetically altered genetic stocks of native fish species has had the direct effect of creating conditions—and of continuing to create the potential—for intraspecific hybridization, gene contamination, and gene pool degradation. Indirectly, the introduction of exotic fishes has enormous effects on biodiversity through the displacement of native fish species as well as through impacts on aquatic invertebrates and amphibia, which affect gene pools through loss of populations (i.e., the introduction of exotic fishes is another example of habitat alteration).

Range Improvement

Similar to fish management, although of lesser effect in the Sierra Nevada, is the direction and intent of range improvement projects. In past decades, range shrubs, particularly bitterbrush, were widely planted in Great Basin areas (on the Sierra Nevada border) to improve rangelands for cattle. Germ plasm of these shrubs was almost invariably nonlocal, often from distant states. Some stock was derived from shrub improvement programs, which genetically bred stock for tolerance to wide conditions and resistance to stress and disease, but which did not promote maintenance of native genetic architecture. Thus, very little shrub germ plasm planted in the past derives from local seed zones or follows genetic diversity guidelines that maintain native genetic structure. More recently, shrubs have been planted to enhance wildlife habitat. These projects are increasingly falling under seed-transfer and genetic diversity guidelines similar to those of tree regeneration programs, with the result that native local seeds are now being collected and planted in many instances.

Exotic Pathogens

Exotic pathogens create direct and indirect genetic threats in the Sierra Nevada. White pine blister rust is fatal to sugar pines that carry the susceptible gene. The resistant gene exists in very low frequencies naturally in sugar pine; thus, the pending bottleneck from the disease epidemic will have significant and pervasive genetic effects throughout sugar pine's range in the Sierra Nevada. In other taxa and disease situations, resistance, if it exists at all, is often not simply inherited but is a combination of genetic and environmental effects. Indirect genetic effects occur when populations are so devastated as to drastically decline in size or become extirpated. An example is the exotic pathogen that moves from domestic to native bighorn sheep (which are being reintroduced into the Sierra Nevada) (see Kinney 1996). This pathogen causes a disease that is extremely serious and usually fatal to bighorn sheep, exterminating entire populations, with consequent genetic impacts.

Taxon-Specific Issues

In addition to the high-priority issues just described, there are many activities that have serious effects on specific taxa in the Sierra Nevada. Examples of these include the sport collecting of butterflies, the harvesting of special forest products (especially mushrooms and other fungi, ladybugs, lichens, etc.) (see Richards 1996), the use of biocides with wide action against native insects, and forest-health practices whose goals are to reduce or eliminate populations of native insects and pathogens. Beyond these, indirect impacts on the gene pools of specific taxa are numerous and are categorized with those that alter habitats of specific taxa. Examples include the effects of fire suppression on plant species whose seeds require fire for germination, the decline of amphibians due to the stocking of exotic fish, the displacement of native grasses by exotic perennials, the decline of taxa that depend on old-growth habitat, and so on.

Land Management

The specific activities listed in the previous sections soon grade into the comprehensive set of human activities that have some effect on gene pools. As we have noted before, most human-mediated (as well as natural) activities have some genetic consequences. The question is not whether we create genetic change but which effects are significant enough to be worthy of altering our behavior. In general, there has been a pervasive lack of awareness of the potential (theoretically inferred) genetic consequences of land management, from local practices to regional landscape plans. Levels of genetic awareness, evaluation, prescription, mitigation, monitoring, and restoration have generally been very low in public and private management, and they have been concentrated in a few land-use programs (e.g., tree regeneration). Although it is broadly recognized that most management actions have effects on wildlife, there are few instances where environmental analyses—for instance in National Environmental Policy Act (NEPA) contexts—have considered genetic effects. Land-management agencies do not place geneticists broadly throughout the Sierra Nevada, and genetic knowledge is usually centralized (e.g., with tree improvement headquarters) or resides within silvicultural staffs, where it is focused mostly on the already established genetic management programs of commercial timber species.

What is needed is a general awareness that genetic consequences must be considered and evaluated for land-management activities in general, and a framework and strategy for doing so. It is not enough to lump these concerns under general biodiversity evaluation, since this often takes into account only immediate effects on the population or species viability of a few indicator species.

The identification of taxa most at risk in the Sierra Nevada is difficult, due to the lack of specific genetic information for most species. Because the threatened taxa are widely distributed, there are few trends that point to specific geographic areas that are most threatened. For certain taxa, for which there is considerable genetic information, it may be possible to define genetic standards, such as levels of inbreeding. However, as the interpretation of genetic measures is very much affected by species' characteristics (mating system, genetic architecture, etc.), standards would be difficult to generalize. At a minimum, they would need to be structured according to basic life history characteristics. In general, taxa and their resident levels and patterns of genetic diversity and evolutionary potential are best protected by standards aimed at the biotic community level. For many species, standards based on genetic parameters (e.g., levels of heterozygosity) may be ineffective and misleading due to the time lag between threat and the genetic consequence. Addressing the following two basic needs would assist in the development of either standards or alternative approaches to risk assessments:

1. There is a need for research into the relationships between genetic parameters and the fitness of a species, and for inspecting such relationships for patterns related to life history characteristics.
2. There is a need to establish long-term monitoring programs that are systematically organized. Information on normal ranges of variation (both spatial and temporal) is essential to the development of biotic standards.

MANAGEMENT OPTIONS FOR GENETIC CONSERVATION

Although genetic effects due to land use, land management, and other human-mediated actions (e.g., air pollution) occur pervasively in plant, animal, and fungal populations of the Sierra Nevada, we cannot hope to, nor is there reason to, directly manage the entire Sierra Nevada gene pool. One responsibility of genetic conservation policy is to reduce the scope to one that is manageable. Management actions most likely to have significant genetic consequences can be prioritized, allowing management attention to be effectively focused. Certain taxa, actions, and situations are more likely to result in undesired genetic consequences than others. Thus, we recognize that (1) time and money are not available—nor is it practical—to gather genetic information that would allow all management decisions to be made wisely or defensibly; (2) in some taxa and conditions, a little genetic information incorrectly interpreted is actually misleading; ecological commonsense, knowledge of life histories and past land use, and application of sound genetic reasoning are best; and (3) some actions are more significant than others in their genetic consequences and ecological impacts; conservation efforts should be tailored to focus on high priorities but to be aware of detrimental genetic consequences both averted and caused. Baseline standards that broadly maintain the health of diverse taxa and promote the maintenance of the ecological process will provide a safety net for maintaining genetic diversity.

The following sections briefly summarize specific ongoing programs in the Sierra Nevada that address genetic diversity management and give general guidelines for genetic conservation as well as strategic approaches for integrating genetic diversity perspectives into regional planning, landscape analysis, and project implementation.

Existing Genetic Management Programs and Guidelines for Genetic Conservation

Outside of research, the longest ongoing operational program in the Sierra Nevada with direct genetic resource management and conservation objectives is the Tree Improvement and Regeneration Program of the U.S. Forest Service (Kitzmiller 1976, 1990) and cooperators in the state (the California Department of Forestry and Fire Protection) and the timber industry. The focus of the genetic conservation aspects of this program traditionally was on a small number of commercial forest tree species, at two levels: intensive tree breeding (the high-level program) and operational forest regeneration following timber harvest (the base-level program). The geographic scope is federal lands for the Forest Service program and state and private lands on which timber harvest has occurred for the other cooperators.

Within the high-level program, genetic conservation efforts traditionally were directed at maintaining broad genetic adaptedness and natural levels of genetic diversity within the families being bred for increased fiber production and other desired traits for the wood industry. This approach was counter to the prevailing agricultural and animal husbandry models, in which pedigrees were iteratively bred for reduced genetic diversity, favoring the desired traits in homogeneous lines (monocultures). It was recognized early in forest genetics that populations that lack diversity would not be stable in long-lived species and under the uncontrollable and highly variable environments and climates of natural forestlands. Diversity is maintained in the improved lineages in several ways while they are being bred for desired traits: breeding zones are used to develop locally adapted improved strains (Kitzmiller 1976), whereby parents are chosen from within certain areas of the Sierra, breeding is among parents only from within a zone, and improved progeny are out-planted within the same zone as their parents. Selection in the intensive tree improvement program is for a mix of traits, focusing on general adaptability of trees and retention of diversity. Improved stock developed in this way takes many years to become available and, with one notable exception, has not yet contributed to production of seed for regeneration in forestlands in the Sierra Nevada.

The exception in the level of production is the Blister Rust Resistance Program for sugar pine undertaken by the U.S. Forest Service and cooperators. Research on genetic resistance to white pine blister rust caused by Cronartium ribicola (Kinloch 1992) has transferred in the last decade to intensive operational resistance breeding. Although the target for breeding sugar pines is more focused on genetic resistance than in the general tree improvement program, the philosophy of maintaining and selecting general adaptedness and of maintaining adherence to local breeding zones remains. This program is highly productive and produces a large annual volume of resistant (having major gene resistance) sugar pines. Other landowners (industrial forest owners and state forestry) cooperate in similar resistance breeding of sugar pine for their land.

Much more extensive in its effects on lands and forests in the Sierra Nevada is the base-level program of the Forest Service tree improvement program (and its analogs in the state program) (Kitzmiller 1976, 1990). The base-level program is basically a genetic conservation approach integrated into operational forest regeneration and plantation management activities. The key elements are a focus on maintaining adaptedness, local genetic variation, and high genetic diversity while applying mild selection for desirable tree and stand traits (Kitzmiller 1990). This is accomplished through use of the seed zone map discussed previously (Buck et al. 1970; Kitzmiller 1976, 1990), which defines zones of genetic structure (presumably adaptedness) throughout California. Seed transfer, collection, and stock management guidelines maintain local and broad genetic diversity throughout the reforestation program, from selecting trees for seed collection through nursery operations and plantation management to out-planting.

This program, and similar ones throughout the timber industry and agencies, traditionally focused only on commercial tree species and had little influence on other aspects of land management or land use that might have genetic consequences. More recently, the tree improvement programs throughout the Forest Service have been broadened in scope to include all wildland taxa and any situations involving genetic management (Hessel 1992). The strategic plan focuses on developing policies for genetic adaptability, guidelines for genetic reserves, genetic policies for rare and endangered taxa, and management strategies for maintaining natural genetic diversity. In California, the former tree improvement program just described has thus expanded to become the Genetic Resource Management Program for the Forest Service Pacific Southwest region (Kitzmiller 1993), serving all aspects of genetic concerns in ecosystem management for Forest Service programs of the Sierra Nevada.

The Pacific Southwest (PSW) region of the Forest Service, at the recommendation of the PSW Genetic Resource Management Program, developed and issued a directive, Use of Native Vegetative Material on National Forests, and Genetic Guidelines for Native Plant Collections (Stewart 1993), that extends the genetic approach in the area of tree improvement and regeneration to all activities that deploy seeds or nursery stock into wildland situations.

Another component of the PSW Genetic Resource Management Program is the National Forest Genetic Electrophoresis Laboratory (Kitzmiller 1990; USFS 1994). Established in 1988, it was created to generate genetic information rapidly to support timber management programs, using biochemical and molecular genetic markers. In recent years, this laboratory has also expanded to focus on the assessment of genetic variation in all aspects of ecosystem management, including genetic analyses pertinent to the management of rare and endangered plants, ecological restoration, and postfire reclamation.

Given the relatively long history of genetic conservation in tree improvement and timber programs, genetic management issues have been slow to be incorporated into other programs and activities where genetic manipulation is explicit or implicit. The community concerned with ecological restoration has been the most active in considering genetic guidelines. In the last several years, the California Native Grass Association has developed guidelines similar to those described for trees (California Native Grass Association 1993), emphasizing use of native species and local germ plasm for all grass planting. Although conceptually these guidelines were developed from genetic theory and experience in forest genetics, increasing study of grass genetics is allowing the refinement specific to native grass taxa (Knapp and Rice 1994a). Similarly, as genetic studies expand for other Sierra Nevada taxa that may be threatened genetically, specific guidelines are being developed, as in the case of oaks (Millar et al. 1990a; Millar and Guinon 1990).

Several programs specifically focused on genetic aspects of Sierra Nevada wildland taxa are excluded from the scope of this chapter, as they address genetic manipulation and breeding with goals that do not include maintenance of native genetic diversity. These programs occur, for instance, in range shrub and browse species improvement programs and in sport fishery programs. Genetic manipulation focuses on developing strains that are genetically resistant to disease or to specific environmental challenges (e.g., to mine spoils or hatchery environments), but maintenance of local, native diversity is not a prerequisite goal.

At a broader level, several general policies apply to Sierra Nevada activities and impose forest and wildland management guidelines that implicitly include genetic conservation measures. The National Forest Management Act of 1976 contains specific language to maintain native diversity on national forests of the United States. This has been interpreted primarily at the species and community level (e.g., ensuring that reforestation restores the same mix of species as was in the forest prior to harvest), although it would be a natural extension to direct this language to genetic diversity within species. The California Forest Practice Act, which includes strong regulatory action for reforestation, has a genetic policy that applies to “commercial species from a local seed source or a seed source which the registered professional forester determines will produce trees physiologically suited for the area involved.” Several California regional agency regulations advocate the use of native species and local germ plasm in reintroduction or restoration projects (e.g., the National Park Service and the Soil Conservation Service), but little detail is given and the guidelines are very general.

Broader still are guidelines on how to incorporate genetic considerations into ecological restoration and reintroduction in general. These do not focus specifically on Sierra Nevada situations or taxa but are applicable to these specific conservation situations. Examples include Falk and Holsinger 1991, Falk et al. 1995, and Millar and Libby 1989. Similarly, both general approaches (Cheatham et al. 1977) and specific approaches (Millar et al. 1993, 1991; Wilson 1990) have been developed that have been applied to Sierra Nevada situations (Millar et al. 1996). Many papers provide examples of specific programs and general guidelines on genetic conservation, which would apply to the diverse situations in the Sierra Nevada (Falk and Holsinger 1991; Falk et al. 1995; Millar 1993; Millar et al. 1990b; Millar and Westfall 1992; Schonewald-Cox et al. 1983).

Genetics in Policy Criteria, Standards, and Monitoring

Only a few examples exist of instances in which genetic policy or guidelines have been developed systematically for land management and land use across a set of specific ecosystems (e.g., Crow et al. 1994, for Chequamegon and Nicolet National Forests, Wisconsin). In the Pacific Northwest, as a project of the president’s forest plan, a model framework for genetic conservation planning is being developed to guide genetic management of forest resources. This project is just beginning and will focus primarily on forest trees. The PSW region of the U.S. Forest Service recently developed a conceptual framework for California national forests that provides an analysis process for implementing ecosystem management (Manley et al. 1995). As part of the analytical process, genetic diversity is considered a key ecosystem element with specific environmental indicators to be addressed at hierarchical domains of landscape scale. This process is intended to guide ecosystem management throughout the national forests of the Sierra Nevada (e.g., see Millar 1996) and provides a valuable analytical approach for incorporating genetic considerations into land-management planning and project implementation.

Based on our review of literature and survey of geneticists working on California taxa, we find genetic information lacking for most species in the Sierra Nevada. This situation is likely to remain in the future, with specific groups of taxa or occasional rare or high-interest species receiving specific study. Where we do have empirical information, we find few generalities emerging, except occasionally within closely related or ecologically similar taxa. As an attempt to provide guidance on how to manage genetic diversity in the face of diverse situations and genetic architectures and of limited empirical knowledge about most genetic architectures but strong theoretical foundations, we offer the following approaches for incorporating genetic concerns into land use and management.

Theoretical Standards for Genetic Management

The following standard and corollary for genetic management derive from population-genetic theory, based on a goal of maintaining locally adapted genetic diversity, short-term population viability, and long-term species sustainability (adaptability and resilience). In most cases, it is explicit that we do not have direct information on these variables, are unable to provide numeric baseline values for these standards, and must respond via proxies, preventative actions, inferences, and so on (see “Best Management Practices” later in this chapter). We propose the following single primary standard, along with the corollary standards listed after it.

Maintain natural levels of genetic diversity and genetic process at local to regional scales (individual to subspecies to species diversity). Natural levels are defined in an appropriate historical context, with the understanding that population and species extinction and creation, as well as other abrupt and gradual changes in gene pools, occur as an integral part of evolution. Some change is expected and appropriate; other levels and types of change are undesired.

- Avoid significant losses in genetic diversity. At the local level, avoid reductions in population sizes that would result in inbreeding depression or declines in viability that would lead to increased probabilities of population extinction.
  - Avoid losses of genes known or suspected to confer resistance to insects or pathogens, especially to exotic pests.
  - At the landscape and regional level, avoid losses in ecotypic, racial, or subspecies diversity.
- Avoid incorporating nonlocal genes into natural populations or disrupting genotypic combinations adapted to local environments. Through either direct effects on viability or indirect effects on coadapted gene complexes, genes that have not evolved locally or gene combinations novel to a population may lead to declines in individual, and thus population, viability. Avoid unnatural intraspecific or interspecific hybridizations.
- Promote natural levels and patterns of genetic process, including gene flow, natural selection, and drift (e.g., stochastic effects).
- Promote natural spatial patterns of genetic architecture, from local to regional levels.

Management Activities of Highest Concern

Generally, activities of greatest concern are those that significantly add individuals to or remove individuals from natural populations or areas adjacent to natural populations; activities that translocate individuals among locations; and activities that directly and significantly affect sex ratios, number of breeding individuals, fecundity, population establishment, viability of individuals, or mortality of different age classes in natural populations.

Specifically, the following management activities or situations involve manipulations that potentially have significant genetic consequences:

Timber harvest

Tree, shrub, or grass breeding

Wildlife habitat improvement

Land settlement

Fire suppression

Ecological restoration

Fish and other wildlife reintroductions

Forest tree planting

Air and water pollution

Recreation projects

Livestock (including wild horse) grazing

Range improvement

Habitat conversion

Prescribed and “unnatural” wildfire

Reclamation

Fish and other wildlife stocking control

Forest-health control

Biological control

Watershed restoration

Road and dam construction

Best Management Practices (BMPs)

Despite defensible theoretical standards (given earlier), it is usually impossible in practice to determine how much genetic diversity is enough or when changes in diversity are significant. Even monitoring and adaptive management approaches are difficult, due to the difficulties of successfully partitioning genetic effects from other ecological factors. Thus, except in obvious cases, it is rarely practical to determine whether standards are being met or violated. The conservative approach is to rely on preventative policy through BMPs.

Two approaches are suggested—coarse and fine filter. Coarse-filter approaches apply when no major changes in the standards are anticipated and/or none of the management activities listed in the previous section are implicated. Coarse-filter approaches focus on maintaining species, habitat, and community integrity, such as plant and animal species composition, vegetation structure and fragmentation, and disturbance regimes. The assumption is that the maintenance of these functioning systems maintains the genetic standard.

When specific management activities occur that may cause significant changes in the theoretical standards, fine-filter (intensive or case-specific) approaches are needed. Because management actions vary so much, and because of the many different effects on genetic diversity, these cases should be handled individually, with specific guidelines determined by a genetics specialist.

For fine-filter situations, some general guidelines or criteria pertain, with many exceptions:

1. When introducing individuals into natural habitats (through tree planting; plant, fish, or animal reintroductions; wildlife habitat or range improvement; reclamation; biological control; etc.):
    - Maintain local native germ plasm. Use germ plasm from donor populations that are geographically close and ecologically similar to those of the introduction site. The meaning of local depends on the species and context, but is related to the size of genetic neighborhoods, selection gradients, and historic events. Specific detailed guidelines ("transfer rules") have been developed for some taxa.
    - Collect donor germ plasm from local populations that are also relatively large, viable, uncontaminated (by nonlocal genotypes of the same species or interspecific hybridization), and healthy.
    - Do not use germ plasm of uncertified origin. (This guideline is exceptionally defensible.)
    - Maintain natural sex ratios and demographically appropriate age-class structures.
    - Maintain high effective population sizes through the germ plasm collection-to-introduction phases. Within the guidelines listed here, maximize the number and diversity of distinct founding genotypes, and maintain equal contributions from each donor individual through to the out-planting or introduction phase. No general rules exist (although detailed guidelines for specific taxa are available) except that larger is safer.
    - Introduce healthy founders; avoid, when possible, introducing disease with founders.
    - Favor rapid early population growth.
    - Choose introduction sites that match the habitat requirements of the species (both physical and ecological, e.g., metapopulation structure).
    - Avoid sites surrounded by or adjacent to (i.e., within significant gene-flow distance of) populations of nonlocal genotypes or races of the same species capable of contaminating the introduced populations. If necessary to accomplish this, flag the area for special concern.
    - Choose sites that are geographically large enough to accommodate large effective population sizes, unless metapopulation structure suggests otherwise.
    - Minimize inbreeding (in species that naturally outbreed) by maintaining large population sizes, minimizing relatedness in founders (avoid using clones), equalizing sex ratios, maintaining age-class stocking, and maximizing diversity (within above standards).
    - Promote reproduction and dispersal through the maintenance of ecological functioning; that is, favor natural pollinators, seed dispersers, corridors, disturbance regimes, and habitat availability (safe sites) for sexually reproducing species.
    - For asexually reproducing species, maintain high numbers of clones, as they will determine the amount and distribution of resident genetic diversity.
2. When removing individuals from natural populations (through timber harvest, fishing [native species], livestock grazing, stocking control, prescribed fire, etc.):
    - Avoid significant reductions in effective population size (i.e., reductions that bring the population size below naturally expected Ne's) (e.g., significant reductions in census number of individuals, unequal sex ratios, unequal contributions from parents, unequal numbers of offspring, drastically fluctuating population sizes).
    - Avoid actions that may lead to unnatural changes in mating systems (e.g., isolated seed trees or clumps of leave trees [trees left standing following harvest] may promote inbreeding; none of the new silvicultural or prescribed fire practices have been evaluated in this regard).
    - Avoid actions that may lead to increases in undesired intraspecific or interspecific hybridization (e.g., changes in gene-flow corridors, fragmentation).
    - Mimic natural structural patterns (spatial distributions, age-class distributions, etc.) and processes, especially disturbance regimes.
    - Mimic natural patterns and intervals of mortality.
    - Mimic inferred natural selection regimes.
3. When monitoring: Because of the nature of measuring genetic diversity and the difficulty of interpreting its significance, genetic monitoring has not been—and is unlikely to become—a routine activity in Sierra Nevada ecosystems. Rather, genetic monitoring remains somewhat of a research, or at least highly specialized, activity. Incorrect or misleading interpretations based on genetic analysis of,

for example, monitoring of marker genes could lead to imprudent management or policy.

In some cases, however, where a genetic researcher or specialist can be involved (e.g., from the National Forest Genetic Electrophoresis Laboratory), it will be useful to monitor specific aspects of genetic diversity and genetic attributes directly and plan management accordingly.

Because of these limitations, SNEP Genetics Workshop participants and geneticists generally are advocating more reliance on management decisions inferred from sound genetic theory rather than relying on the monitoring of direct genetic trends. Genetic data (i.e., direct monitoring) provide supplemental tools to inform monitoring.

A more generalized monitoring approach relying on combined empirical and theoretical insights could be as follows: Monitor levels and trends of overall genetic diversity in the population of concern, together with other proxy data, to interpret genetic status. Proxies may be ecological traits that would otherwise be part of habitat monitoring, such as demographic attributes and life history parameters of population growth and viability. If results from the monitoring of these traits indicate a population decline or significant drop in viability, and allelic or genotypic diversity similarly has dropped significantly, then it is possible that genetic factors have contributed to the decline and should be addressed. Conversely, if overall levels of genetic diversity are maintained or increase, and the population is viable and healthy, it can conservatively be assumed that genetic diversity is adequate. Abrupt changes in allele frequencies (i.e., the appearance of unique alleles) may indicate gene contamination or interspecific hybridization and should be followed by careful inspection of neighboring populations.

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APPENDIX 28.1

Population Genetic Studies for Plant Species Native to the Sierra Nevada

Taxon	Type of study[1]	Sampling range	Source/author(s)
PLANTS			
Trees			
Gymnosperms			
Abies concolor	M[a]	Elev. transect, Eldorado Co.	Hamrick (1976)
	M[a]	Range-wide, including SN	Hamrick & Libby (1972); Libby et al (1980) PSW Region Genetic Regeneration Program (n.d.)
	M[a]	Northern & central SN	Jenkinson (n.d.-b)
	A[a]	Northern & central SN	Westfall and Conkle (1992)
A. magnifica	B	Sierra Nevada	Zavarin et al. (1978)
	M[a]	Northern & central SN	Sorensen et al. (1990) Jenkinson (n.d.-b)
Calocedrus decurrens	A & M[a]	Includes Sierran populations	Harry (1984)
	M[a]	Includes Sierran populations	Rogers et al. (1994)
Cupressus spp.		Includes Sierran species	Millar and Delany (n.d.)
Juniperus osteosperma	B*		Adams (1994)
Pinus albicaulis	A*		Furnier et al. (1987)
	B	Rangewide, including SN	Zavarin et al. (1991)
P. attenuata	A	Includes Sierran populations	Strauss and Conkle (1986)
	A & M[a]	Includes Sierran populations	Strauss (1987)
	A	Rangewide, including SN	Millar et al. (1988)
	D	Includes Sierran populations	Hong et al. (1993); Strauss et al. (1993)
P. balfouriana	B & M	Rangewide, including SN	Snajberk et al. (1979)
	M	Rangewide, including SN	Mastrogiuseppe (1972); Mastrogiuseppe and Mastrogiuseppe (1980)
P. contorta	M & P	Rangewide, including SN	Critchfield (1956)
P. flexilis	A*		Schuster et al. (1989)
	B	Rangewide, including SN	Zavarin (1993)
P. jeffreyi	A	CA, including SN	Furnier and Adams (1986)
	A	Mono Co.	Millar et al. (1993)
P. lambertiana	A	Rangewide, including SN	Conkle (n.d.)
	A[a]	Sierra Nevada	Westfall and Conkle (1992)
	M[a]	Elevational transect	Harry et al. (1983)
	M[a]	Rangewide, including SN	Jenkinson (n.d.-a)
	M[a]	Northern SN	Kitzmiller and Stover (in press)
P. longaeva	B & M	Includes Californian populations	Zavarin et al. (1982)
P. monophylla	A	Includes Californian populations	Delany (n.d.)
	B	California	Smith and Preisler (1988)
	B	Includes Californian populations	Zavarin et al. (1990a)
P. monticola	A	Rangewide, including SN	Steinhoff et al. (1983)
	B	Rangewide, including SN	Zavarin et al. (1990b)
	D*		White (1990)
P. ponderosa	A & M	Includes Sierran population	Linhart et al. (1989)
	M	Includes Sierran population	Grant et al. (1989)
	P	Includes Sierran population	Monson and Grant (1989)
	A[a]	Sierra Nevada	Westfall and Conkle (1992) PSW Region Genetic Resources Program n.d.
	M[a]	Elevational transect	Conkle (1973)
	M[a]	Sierra Nevada	Westfall et al. (n.d.)
P. sabiniana	M		Griffin (1965)
P. washoensis	A	California and Oregon	Niebling and Conkle (1990)

continued

Taxon	Type of study[1]	Sampling range	Source/author(s)
Pseudotsuga menziesii	A^{a}	Sierra Nevada	Westfall and Conkle (1992)
	M^{a}*		Campbell (1986)
	M^{a}	Northern SN	N. Sierra Tree Improvement Assoc. (n.d)
Sequoiadendron gigantea	A & M^{a}	Sierra Nevada	Fins and Libby (1982)
	M	Sierra Nevada	Mahalovich (1985)
Taxus brevifolia	A & B	Rangewide (in USFS locations), includes SN	Doede et al. (1995)
Angiosperms			
Acer negundo	P*		Dawson and Ehleringer (1993)
Salix spp.	A	Includes Sierran spp.	Brunsfeld et al. (1991);
	D		Brunsfeld et al. (1992)
Populus tremuloides	A*		Jelinski and Cheliak (1992)
	D*		Rogstad et al. (1991); Chong et al. (1994)
P. trichocarpa	M^{a}*		Rogers et al. (1989); Dunlap et al. (1994)
	P*		Dunlap et al. (1993)
Quercus chrysolepsis			Riggs?
Q. douglasii	A	Rangewide, including SN	Millar et al. (1990)
Q. kelloggii			Riggs?
Q. wislizenii	A*		Nason et al. (1992)
	B	Includes SN	Dodd et al. (1993)
Non-Tree Angiosperms			
Achillea	M^{a}	Sierran populations	Clausen et al. (1948)
Agastache spp.	A	Includes Sierran species	Vogelmann and Gastony (1987)
Antennaria corymbosa	A	Sierran populations	Bayer (1988)
A. media	A		Bayer (1989b)
A. rosa	A		Bayer (1989a; 1990);
Arctostaphylos spp.	M	Yosemite	Ball et al. (1983)
	A	Yosemite	Ellstrand et al. (1987)
A. mewukka	M & M^{b}	Sierra Nevada	Schierenbeck et al. (1992)
Arabis holbolellii	A & M^{2}*		Roy (1993)
Artemisia spp.	M^{b}	Includes Sierran species	McArthur et al. (1981)
A. tridenatat	M/P*		Meyer et al (1990); Meyer and Monson (1991)
	B & M*		Freeman et al. (1991)
Aquilegia spp.	D	Sierra Nevada	Hodges and Arnold (1994)
Bromus carinatus	M		Luedke (as cited at SNEP wksp)
	M^{a}	Includes Sierran populations	Flowers and Rice (1994)
B. tectorum	A	Includes Sierran populations	Novak et al. (1991)
	M^{a}*		Rice and Mack (1991a; 1991b; 1991c)
Calamagrostis canadensis	A*		MacDonald and Lieffers (1991)
Calchortus spp.	P	Includes Sierran spp.	Fiedler (1985)
	M	Includes Sierran spp.	Ness (1989)
	A	Includes Sierran spp.	Ness et al. (1990)
Calycadenia	D & M/M^{b}	Includes Sierran spp.	Baldwin (1993)
Carpenteria californica	A & M		Clines (1994)
Ceanothus			
Clarkia spp.	M	Includes Sierran spp.	Vasek (1977)
	M		Baldwin (as cited at SNEP wksp)
	A	Includes Sierran spp.	Smith-Huerta (1986); Holsinger and Gottlieb (1988)
C. speciosa	A	Kern Co.	Soltis and Bloom (1986)
Danthonia californica	A	Includes Sierran populations	Knapp and Rice (1994a)
Elymus glaucus	A	Includes Sierran populations	Knapp and Rice (1995)
Eriastrum densifolium	M	Includes Sierran populations	Patterson and Tanowitz (1989)
Eriophyllum confertiflorum	M^{b}	Includes Sierran populations	Mooring (1994)
Hymenoclea salsola	P*		Comstock and Ehleringer (1992)
Ipomopsis aggregata	A	Includes Sierran populations	Wolf et al. (1991); Wolf and Soltis (1992)
Lewisia spp.	A	Sierra Nevada	Carroll et al. (n.d.)
Lithophragma spp.	D	Includes Sierran spp.	Soltis et al. (1992)
Lupinus	M		Harding (as cited at SNEP wksp)
Plantago	M		Stebbins (as cited at SNEP wksp)
Nassella pulchra	M & A	Includes Sierran populations	Knapp and Rice (1994b)
Polemonium	M		Pritchet (as cited at SNEP wksp)
Potentilla	M		Knapp, Rice (as cited, SNEP wksp)
Stephanomeria spp.	B	Includes Sierran spp.	Bohm and Gottlieb (1989)
Scutellaria bolanderi	A	Includes Sierran populations	Olmstead (1990)
S. californica	A	Includes Sierran populations	Olmstead (1990)
S. nana	A	Includes Sierran populations	Olmstead (1990)
S. siphocampyloides	A	Includes Sierran populations	Olmstead (1990)
Tellima grandiflora	D	Includes Sierran population	Soltis et al. (1991)
Vulpia microstachys	M	Includes Sierran populations	Kannenberg and Allard (1967) Allard and Kannenberg (1968)
Wyethia	A, M		Ayers (as cited at SNEP wksp)

Taxon	Type of study[1]	Sampling range	Source/author(s)
Ferns			
Cheilanthes gracillima	A	Includes Sierran populations	Soltis et al. (1989)
Polystichum spp.	A*		Soltis et al. (1990)
ANIMALS			
Mammals			
Tadarida brasilliensis	A	SW US (not including SN)	Svobda et al. (1985)
	A	SW US (not including SN)	McCracken et al. (1994)
Marmota flaviventris	A	East R.Valley, CO	Schwartz and Armitage (1980)
Thomomys bottae	A	SW U.S.A., including SN	Patton and Yang (1977)
	A	Lower Colorado River	Smith and Patton (1980)
	A & M	California, including SN	Patton and Smith (1990)
	D[3]	Not given (single sample)	Hafner et al. (1994)
Dipodomys agilis	A	Western U.S.A.	Johnson and Selander (1971)
D. deserti	A	Western U.S.A.	Johnson and Selander (1971)
D. heermanni	A	Western U.S.A.	Johnson and Selander (1971)
D. merriami	A	Western U.S.A.	Johnson and Selander (1971)
D. microps	A	Western U.S.A.	Johnson and Selander (1971)
	A	Butte Co.	Patton et al. (1976)
D. nitratoides	A	Western U.S.A.,	Johnson and Selander (1971)
D. ordii	A	Western U.S.A.	Johnson and Selander (1971)
D. panamintinus	A	Western U.S.A., including SN	Johnson and Selander (1971)
	A	Kern Co.	Patton et al. (1976)
Peromyscus maniculatus	A	U.S.A. & Canada, including SN	Avise et al. (1979)
	D	U.S.A. & Canada, including SN	Lansman et al. (1983)
	D	U.S.A. & Canada, including SN	Neigel and Avise (1993)
	M	Arizona & Nevada	Thompson (1990)
P. californicus	A	Coastal CA, Northern Baja CA and foothills of SN	Smith (1979)
Onychomys spp.	D	Western, including CA populations	Riddle et al. (1990)
Microtus californicus	A	Calif. coast range	Bowen (1982)
	M		Lidicker and Ostfeld (1991)
Canus latrans	A	Zoo	Fisher et al. (1976)
	A[4]	Not known	Wayne and O'Brien (1987)
C. latrans	D	Southern Calif.	Roy et al. (1994)
Vulpes macrotis	A	Western U.S.A., including SN	Dragoo et al. (1990)
Ursus americana	A	Yosemite NP	Manlove et al. (1980)
	D	E & NW US	Cronin et al. (1991a)
Martes americana	A	Wyoming	Mitton and Raphael (1990)
Odocileus hemionus hemionus	A*	Colorado	Scribner et al. (1991)
	A & D	Western US	Cronin (1991)
		Montana	Cronin et al. (1991b)
	A	Western US (including SN)	Derr (1991)
	D	Western US	Cronin (1992)
O. h. columbianus	A & D	AK & OR, US; BC, Canada	Cronin (1991)
	A	California (one population)	Derr (1991)
	D	Pacific Coast	Cronin (1992)
Amphibians			
Ambystoma macrodactylum	A*	Oregon and Idaho	Howard and Wallace (1981)
A. tigrinum	A[4]	California	Shaffer (1984)
Aneides flavipunctatus	A & M	California	Larson (1980)
A. lugubris		Sierra Nevada	Jackman (n.d.)
Batrachoseps campi	A	Inyo Mountains, CA	Yanev and Wake (1981)
Other *Batrachosep* spp		S. Sierra Nevada	Yanev 1978
Elgaria		Sierra Nevada	Good (1988)
Ensatina eschsholtzii	A	California, including SN	Wake and Yanev (1986) Jackman and Wake (1994) Wake et al. (1989)
Hydromantes brunus	A	Mariposa Co., California	Wake et al. (1978)
H. platycephalus	A	Toulumne Co., California	Wake et al. (1978)
H. shastae	A	Shasta Lake, California	Wake et al. (1978)
Hyla regilla	A	Oregon and CA	Case et al. (1975)
Rana aurora	A	Californian coastal ranges	Case (1978a)
R. boylei	A	California	Case (1978a)
R. boylei	A	California	Case (1978b)
R. cascadae	A	Lassen County, California	Case (1978a)
R. catesbeinana	A	California	Case (1978a)
R. muscosa	A	Sierra Nevada	Case (1978a)
R. muscosa	A	Sierra Nevada	Case (1978b)
Taricha torosa	A	Sierra Nevada	Hedgecock and Ayala (1974) Tan (1995)

continued

Taxon	Type of study[1]	Sampling range	Source/author(s)
Reptiles			
Anniella pulchra	A	Coastal CA	Bezy et al. (1977)
Elgaria coerulea	A		Good (1988)
E. multicarinata	A		Good (1988)
E. panamintina	A		Good (1988)
Sceloporus graciosus	A*	Five western states	Thompson and Sites (1986)
Suaromalus obesus	D*	Southwestern deserts	Lamb et al. (1992)
Uta stansburiana	A	California	McKinney et al. (1972)
Xerobates agassizi	D	Southwestern deserts	Lamb et al. (1989)

[1] Type of study:
M = morphological (morphological and/or phenological characteristics) data; M^a = based on common-garden studies (and therefore NOT including plasticity); M^b = based on cytological data.
A = allozyme data, single-locus data analysis; A^a = allozyme data analyzed as multi-locus phenotypes.
B = biochemical data.
D = DNA data (RFLP, RAPD or PCR-based).
P = physiological studies.
[2] Infections by pathogens.
[3] Host-parasite systematics.
[4] Systematic study
Data include samples taken from the Sierra Nevada, unless otherwise indicated.An asterisk (*) indicates that samples were mostly or entirely outside of the Sierra Nevada portion of the species' range.

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Back to CD-ROM Table of Contents