The Future of Biodiversity in the Sierra Nevada through the Lake Tahoe Basin Looking Glass[1]

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The Sierra Nevada's biological distinction and diversity are almost as legendary as its spectacular peaks and beautiful granite landscapes. The Sierra Nevada is recognized as a zoogeographic region on the basis of the coincidence of species ranges (for example, Udvardy 1969, 1975; Welsh 1994). Udvardy (1969) defined the Sierra Nevada bioregion as bounded by the Great Basin to the north and east, the Mojave Desert to the south, and the Central Valley of California to the west. Welsh (1994) further delineated the Sierra Nevada into three latitudinal segments, recognizing shifts in species composition from north to south along the 650-kilometer north-south extent of the largest single mountain range in the contiguous United States.

Today, 493 terrestrial vertebrate species (California Department of Fish and Game 2003), 61 fish species and subspecies (Moyle and others 1996, USDA Forest Service 2001), and more than 2000 plant species (Storer and Usinger 1963) have portions or all of their geographic ranges within the bounds of the Sierra Nevada ecoregion. High levels of endemism contribute to the Sierra Nevada's biotic wealth: 13 terrestrial vertebrates (Graber 1996), 11 fish (Moyle and others 1996), and 405 vascular plant (Shevock 1996) species that are endemic to California occur only in the Sierra Nevada, and many more of the State's endemics have some part of their ranges in the Sierra Nevada. Concerns are mounting for the fate of biological diversity in the Sierra Nevada (Sierra Nevada Ecosystem Project (SNEP) 1996, USDA Forest Service 1998, California Legacy Project 2003). Although few vertebrate species are known to have been extirpated from the Sierra Nevada (Graber 1996), present-day species composition and richness may be misleading reflections of ecosystem conditions because of the time lag that often exists in measurable population response to changing environmental conditions.

Managing for sustainability in any type of system (ecological, social, or economic) requires maintaining diversity, variability, and redundancy (Berkes and others 2003). Biological diversity affects ecosystem processes, functions, and responses to disturbances (for example, fire), including the degree to which ecosystem services (for example, water yields and nutrient cycling) will be altered (for example, Lamotte 1983, Risser 1995, Kinzig and others 2001, Loreau and others 2002, Symstad and others 2003). In ecological systems, maintaining biological diversity at all levels of biological organization is an important step toward meeting the goal of sustainability.

Myriad past and present change agents, or stressors, have shaped Sierra Nevada ecosystems, including fire and fire suppression, grazing, logging, dams, development, recreation, air pollution, and climate change (Beesley 1996, Cahill and others 1996, Chang 1996, Duane 1996, McBride and others 1996, Momsen 1996, Stine 1996, Elliott-Fisk and others 1997, Lindström 2000, Millar this volume). Our understanding of the individual effects of these stressors on subsets of biota is growing (for example, Chang 1996); however, their combined

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effects on natural systems are virtually unknown. Human response to changing ecosystem conditions and services brings another level of complexity and uncertainty into the sustainability equation. In short, ecosystem response to stressors and the reciprocal response of people to changes in the ecosystem constitute coupled dynamic systems that are likely to exhibit new and adaptive behaviors (Gunderson and others 1995, Gunderson and Holling 2002).

A recent assessment of population trends over the past 50 years of vertebrate species in the Sierra Nevada (USDA Forest Service 2001a) found that approximately 50 percent (n = 210 species) of all terrestrial vertebrates and approximately 60 percent (n = 37 species) of all fish species were considered moderately to highly vulnerable to population loss, extirpation, or extinction. Such a large proportion of species with a precarious future suggests that the composition of biota in the Sierra Nevada, particularly vertebrates, may be unstable and susceptible to a change in state or may have already crossed a sustainability threshold. When environmental conditions change rapidly, as they have in the Sierra Nevada, populations of species can fall into a non-equilibrium state or "debt of extinctions" scenario (Hanski 1994, Tilman and others 1994, Hanski 1997). In such cases, even though environmental conditions can no longer support sustainable populations, populations of longer lived species will persist but decline steadily toward extinction as mortality exceeds recruitment. It is possible, even likely, that environmental conditions in the Sierra Nevada are approaching or have exceeded a threshold of sustainability for some species, and the extirpation of species from some or all of their ranges in the Sierra Nevada could affect substantive change in ecosystem dynamics and services (*fig. 1*). Insights into profitable approaches to maintaining biological diversity in the Sierra Nevada can be gained by examining the interaction of humans and nature in detail at a smaller spatial scale. The Lake Tahoe basin presents just such an opportunity.

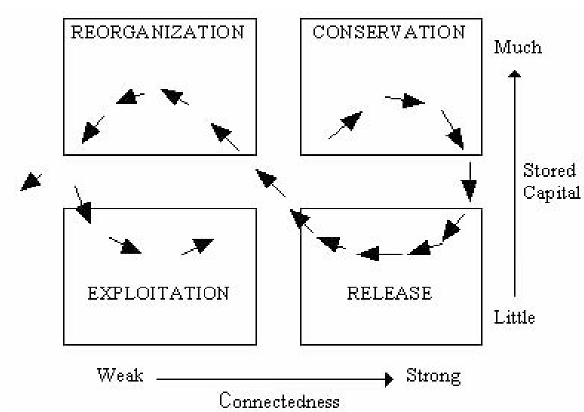

Figure 1— Holling's Cycle

Lake Tahoe as the Sentinel for Future Biodiversity

The same types and patterns of ecosystem degradation and alteration that are playing out throughout the Sierra Nevada are occurring in the Lake Tahoe basin. Coupled with high social value of the basin, Lake Tahoe can be viewed as a valuable portent for the fate of the Sierra Nevada. A recent Lake Tahoe Case study (Elliott-Fisk and others 1997) noted that the Lake Tahoe basin could serve in the discovery of solutions to conservation challenges facing the Sierra Nevada. Declining clarity in Lake Tahoe and a desire to maintain high environmental quality in the Lake Tahoe basin have summoned increasing attention to the fate of this area and resulted in many substantive actions, including the completion of multiple scientific assessments (Western Federal Regional Council Interagency Task Force 1979, Elliott-Fisk and others 1997, Murphy and Knopp 2000). A pivotal question is whether ecological knowledge and institutional commitment are sufficient to take effective action to sustain biological diversity and ecosystem integrity in the Lake Tahoe basin. If biodiversity cannot be sustained in the Lake Tahoe basin, perhaps it cannot be done in the Sierra Nevada. A closer look at a few of the ecological and social players in the Lake Tahoe theater will illustrate how we can study and learn from efforts to "save the lake."

Biological Diversity at Lake Tahoe

The 880–square-kilometer (88,000 hectares) Lake Tahoe basin cradles the largest alpine lake in North America, bounded by the Sierra Nevada crest on the west and the Carson Range on the east (Whitney 1979, Landauer 1996, Schaffer 1998). The Lake Tahoe basin has a high diversity of species, in part because of its location at the nexus of two major biogeographic provinces (the Sierra Nevada and the Great Basin; Udvardy 1969). The fault-block origin of the basin and its steep elevational gradient further diversifies the suite of ecosystems occurring in the basin, including a variety of ecologically significant areas, such as Pope Marsh, once a marsh of substantial extent in the Sierra Nevada; Grass Lake, Osgood Swamp, and Hell Hole, rare examples of bogs in the Sierra Nevada; the cushion plant community, an uncommon high-elevation shrub community adapted to alpine conditions; and deep-water plant beds in Lake Tahoe, a globally rare symbiotic plant community (Manley and others 2000). In addition to these exceptional ecosystem types, the basin also contains an array of more commonly occurring terrestrial and aquatic systems characteristic of lower montane, upper montane, subalpine, and alpine environments.

Human Disturbance: Recent Past and Present

The Lake Tahoe basin sustained perhaps the most intensive land use of any watershed in the Sierra Nevada during the height of commercial land uses that occurred throughout much of the range in the late 1800s and early 1900s. Past activities in the Lake Tahoe basin included clearcut logging of more than 50 percent of the basin and extensive grazing by sheep and cattle (Elliott-Fisk and others 1997, Lindström 2000). Intensive commercial use was followed by a century of fire exclusion, and, as throughout the Sierra Nevada, created an excess of dense, single-aged white fir stands with suppressed growth and high levels of mortality (Macomber and Woodcock 1994, McKelvey and others 1996, Elliott-Fisk and others 1997, Barbour and others 2002). Today, many stressors continue to shape the landscape (such as development, forest management, fire suppression, recreational use, declining air quality, and climate change), with fuel-reduction treatments becoming a prominent management activity (USDA Forest Service 2004) and recreation becoming a primary use of public lands in the basin, as throughout the Sierra Nevada. For example, National Forests in California host 28.7 million annual visitors (Anonymous 2002), and 3.1 million (13 percent) of them come to the Lake Tahoe basin (Kosis and others 2002)–the highest per annual visitation per unit area of any National Forest in California. Accordingly, Stewart (1996) identified Lake Tahoe as the single most important recreation component of the Sierra Nevada economy.

Plant and Animal Populations

Manley and others (2000) examined historical changes in the composition of vertebrate species in the Lake Tahoe basin. Their findings revealed ecologically significant changes in species composition that echo those experienced throughout the Sierra Nevada. Changes in habitat and populations were evaluated across the span of four major time periods: Prehistoric Era (pre-1860), Comstock Era (from 1860 to 1900), Post-Comstock Era (from 1900 to 1960), and Urbanization Era (from 1960 to the present) (Lindström 2000). Terrestrial vertebrate species apparently lost over this time period include four bird, seven mammal, and one amphibian species, with four top carnivores among them (grizzly bear

[*Ursus arctos*], wolverine [*Gulo gulo*], Sierra Nevada red fox [*Vulpes vulpes necator*] and peregrine falcon [*Falco peregrinus*]). Nine bird, two mammal, and one amphibian species appear to have moved into the basin over the past 50 to 100 years, including one carnivore (California spotted owl, *Strix occidentalis occidentalis*), and five exotic species: wild turkey (*Meleagris gallopavo*), European starling (*Sturnus vulgaris*), rock dove (*Columba livia*), house sparrow (*Passer domesticus*), and bullfrog (*Rana catesbeiana*).

Although lack of data precluded Manley and others (2000) from conducting a complete analysis of changes in fish, invertebrate, and vascular plant species, the 102 exotic species from these three groups (16 fish, 2 invertebrate, and 84 vascular plant species) that are now known to occupy the basin have had demonstrated impacts on aquatic ecosystem diversity and integrity. For example, most fish species in the basin are exotic, and the introduction of exotic, predator lake trout (*Salvelinus namaycush*) contributed significantly, along with fishing pressure and habitat degradation, to the extirpation of the once prolific Lahonton cutthroat trout (*Onchorhynchus clarki henshawii*) (Reuter and Miller 2000). Some changes in species composition in the basin reflect Sierra Nevada–wide extirpations, but undoubtedly basin-specific ecosystem alterations contributed substantially to observed changes in species composition.

Forest Ecosystems

The ecological significance of vegetation changes invoked by past activities has not been fully examined, but it must be considerable given altered tree species composition, reduced vegetation complexity, decreased extent of old-growth forests, degraded biological diversity, increased risk of high-intensity wildfires, and altered ecosystem functions, such as water uptake, fuels, tree longevity, and decay characteristics. Historically, 2,100 to 8,000 acres burned annually in the basin through a combination of human and natural ignitions compared with fewer than 500 acres burned annually today through prescribed fire and wildfire (Manley and others 2000). Similarly, before intensive land use, an estimated 55 percent of the conifer forests in the basin were old growth (large-diameter trees, snags, and logs, and characteristic canopy cover and vertical layering [Franklin and Fites-Kaufman 1996]) in contrast to today's 5 percent old growth (Manley and others 2000, Barbour and others 2002). Today, old-growth forests in the basin differ from the uncut forests in the mid 1800s in that they have approximately four times the understory tree species density, which is composed of 200 to 300 percent more white fir and incense cedar, 50 percent less Jeffrey pine, and a 100- to 300-percent greater incidence of tree disease and mortality (Manley and others 2000, Barbour and others 2002). The younger age and simplified structure of these second-growth forests have a reduced diversity of habitat conditions to support populations of plants and animals, particularly species associated with old-growth forests.

Restoration of forest integrity in the Lake Tahoe basin will require managing forests to increase the proportion of the landscape in old-growth condition, mimicking historic fire regimes to the extent possible, and managing development, disturbance, and exotic species to restore biological diversity and ecological function. This challenge exists throughout the Sierra Nevada, and successful implementation will test the resolve of all involved on two fronts: it will require close collaboration between scientists and managers to create a vision of sustainable forest conditions and then design treatments to achieve them, and it will require the support of local communities to take on the burdens of short-term reductions in air quality, changes in esthetics, and risks of escaped fire.

Aquatic Ecosystems

Aquatic and associated riparian ecosystems provide resources that support a large number and wide variety of rare and common species (Graber 1996, Manley and others 2000), especially in areas with dry climates, such as the Lake Tahoe basin (Naiman and others

1993, Kondolf and others 1996). The basin also has a high diversity of aquatic ecosystem types; 17 aquatic ecosystems were identified in the Lake Tahoe basin by Manley and others (2000), including eight lentic types (lakes, ponds, bogs, wet meadows) and nine lotic types (streams, marshes, springs). Some of the rarest aquatic types, such as Lake Tahoe itself, the three bogs, Pope Marsh, and the Upper Truckee River, are considered ecologically significant areas and are considered keystone contributors to biological diversity in the basin.

In the Sierra Nevada and the Lake Tahoe basin, aquatic and riparian environments have been highly altered over the past 150 years as a result of mining, dams, grazing, recreation, the introduction of exotic species, and urbanization (Kondolf and others 1996, Moyle 1996a, Elliott-Fisk and others 1997). A high and growing number of recreationists in the Lake Tahoe basin (Kosis and others 2002) may pose the most significant current and future risk to aquatic ecosystems. Recreational use can have numerous negative effects on the ecological integrity of aquatic ecosystems, such as bank erosion and compaction, loss of ground cover, pollution, introduction of exotic species, and harvest of native species.

Although aquatic ecosystems are currently managed with the intent of protection and restoration in the basin (TRPA 1982, TRPA 1986, USDA Forest Service 1988), the effects of past activities combined with increasing urbanization and recreation use have put aquatic and riparian ecosystems at risk of degradation. An evaluation of the status of aquatic ecosystems by Manley and others (2000) determined that most lentic ecosystems were at risk, primarily because of their rarity, and that protection from degradation of ecological integrity was not strong for any aquatic ecosystem in the basin. Aquatic conservation strategies can be an effective means of identifying problems and crafting solutions for large landscapes (for example, Forest Service 2003, 2004), and although their development and implementation have been proposed, they have not been adopted for the Sierra Nevada (Forest Service 1995, Moyle 1996b) and the Lake Tahoe basin (Murphy 2000).

Significant collaboration between scientists and managers is required to design, implement, and monitor aquatic conservation strategies (for example, Reese and others 2003). In the basin, conservation of aquatic and riparian biodiversity is complicated by a recent discovery that different taxa appear to exhibit different patterns of richness in riparian ecosystems (Manley 2000, Manley and others 2000). Specifically, Manley and others (2000) found that bird diversity was greatest at low elevations, mammal diversity was greatest at high elevations on the east side of the basin, and plant diversity was greatest at high elevations on the west side. It is likely that divergent spatial patterns of richness exist among taxonomic groups throughout the Sierra Nevada and that if concepts like aquatic diversity management areas (Moyle 1996b) are employed, they will need to encompass the broad taxonomic heterogeneity in diversity that exists across the larger landscape. The upcoming revision of the Tahoe Regional Plan by the Tahoe Regional Planning Agency and the Forest Service's Lake Tahoe Basin Management Unit may provide the momentum needed for the basin to design and implement the first aquatic conservation strategy in the Sierra Nevada.

Climate Change

In addition to direct anthropogenic and intrinsic processes at work in the Sierra Nevada, extrinsic factors are also acting on its ecosystems, with climate change being among the most significant (Millar this volume). Mountain ecosystems are key areas for monitoring and studying the effects of climate change on ecosystem composition, structure, and function (for example, Reasoner and others 2004). The extensive elevational range (greater than 1,000 meters) within the Lake Tahoe basin makes it a model laboratory for tracking environmental changes precipitated by climate change. Warming trends have the potential to change the distributions and interactions of many species in the basin. For example, species with limited elevational ranges in the basin, such as the western gray squirrel (*Sciurus* *griseus*; low-elevation associate), golden-mantled ground squirrel (*Spermophilus lateralis*; mid- to high-elevation associate), western meadowlark (*Sturnella neglecta*, low elevation associate), and winter wren (*Troglodytes troglodytes*; high-precipitation associate) are likely to be sensitive and respond measurably to changes in temperature and precipitation (Manley 2000).

Climate change has and will significantly shape ecosystems in the Sierra Nevada, with discernable effects within the short span of 150 years (Cahill and others 1996, Stine 1996, MVZ 2004, Millar this volume). Management plans and actions may need to have longer time frames to consider and account for changes in species distributions and populations that are at risk solely as a result of climate change. Broad-scale monitoring programs, such as the Forest Service's Multiple Species Inventory and Monitoring Protocol (Manley and Roth 2004, Manley and others 2004), will greatly inform us of climate change effects on biota by providing data on the distributions and abundances of species and communities along multiple environ-mental gradients. Such monitoring programs will help differentiate change resulting from management from that precipitated by climate change and other factors.

A Weave of Wildland and Human Ecosystems

The role of local communities and society in the conservation of biological diversity is significant. Urban and wildland ecosystems are interwoven throughout much of the Sierra Nevada (for example, McBride and others 1996), including Lake Tahoe (Nechodom and others 2000), with various environmental effects, such as reduced tree density, lower canopy cover, and increased incidence of exotic plant species in forested environments (McBride and others 1996). The Lake Tahoe basin has acute urban-wildland interface challenges because of concordance of landscape complexity, high visitor/resident ratio, demand for outdoor recreational opportunities, risk of high-intensity fire, and socioeconomic stakes given high property values and regional dependence on tourism (Elliott-Fisk and others 1997, Nechodom and others 2000). Highly enmeshed wildland and human-dominated environments can stymie the use of some effective forest management tools that are needed to maintain and restore ecosystem integrity. For example, the reintroduction of fire has been identified as essential to restoring forest health in all recent assessments of the Lake Tahoe basin (Elliott-Fisk and others 1997, Manley and others 2000), as well as throughout the Sierra Nevada (Weatherspoon 1996, USDA Forest Service 2001c, USDA Forest Service 2004); however, smoke from prescribed fires obscures the basin's world-class views and can be a health concern for some individuals. Similarly, domestic dogs, both on- and off-leash, can affect the reproductive success and survivorship of many wildlife species (Knight and Cole 1995); yet, walking and running with dogs on- and off-leash is so common in the basin that it is considered part of the Lake Tahoe "lifestyle." Thus, although Lake Tahoe resources are valued by many, it will be likely difficult to garner local support for inconveniences associated with some critical conservation and management activities.

Concomitant with the allochthonous human-nature interactions occurring in the basin are also complex feedback loops operating between the basin and surrounding communities. As land prices climb in the basin, surrounding areas, such as Truckee and the Carson Valley, are experiencing rapid population growth, and these populations are increasing visitation and human impacts in the basin (Elliott-Fisk and others 1997). Similarly, as the Sacramento metropolitan area grows, so does the population of the adjacent foothills of the Sierra Nevada (Duane 1996), forming a burgeoning recreating public just one hour's drive from Lake Tahoe. The complex, adaptive nature of ecosystems (Levin 1998) presents challenges in meeting sustainability objectives in light of increasing human pressures that, if ignored or underestimated, put the future of biological diversity and sustainability in the Lake Tahoe basin and the Sierra Nevada in peril. Levin (1999a) offers eight commandments for environmental management that recognize the pivotal interplay between human and natural systems: (1) reduce uncertainty, (2) expect surprise, (3) maintain heterogeneity, (4) sustain modularity, (5) preserve redundancy, (6) tighten feedback loops, (7) build trust, and (8) do unto others as you would have them do unto you. Revision of the Tahoe Regional Plan in 2007 will serve as an important benchmark to discern whether incentives to conserve and restore terrestrial and aquatic ecosystems are great enough to overcome information gaps, institutional barriers, and competing social values.

The Path Ahead for Biological Diversity in the Sierra Nevada

The Lake Tahoe basin has to contend with every primary stressor that currently acts on the Sierra Nevada resources, and in many cases, they are present in the extreme. The effects of past activities in the Sierra Nevada are now part of the fabric of current-day ecosystems. The gauntlet of successes and failures to understand and manifest sustainable, resilient ecosystem conditions in the Lake Tahoe basin will inform a course toward sustainability throughout the Sierra Nevada. Management approaches, including narratives of desired conditions, should reflect the fact that, as Levin (1992) articulated, "Ecosystems are assemblages of interacting components…. The essential constant is change: the balance of Nature describes a system far from equilibrium, alternating between periods of relative stasis and dramatic change." Thus, our vision of biological diversity for the Sierra Nevada must be as dynamic as the factors acting on it, and management actions intended to achieve or maintain desired conditions for biological diversity need to recognize all agents of change as part of the management equation.

Experimentation, learning, and adaptation are the keys to sustainability (Holling 1978, Lee 1993, Janssen and Carpenter 1999). Institutions play an important role in the success of efforts to achieve ecosystem sustainability. Levin (1999b) argues that, "[we] need to build flexible, adaptive institutions, and recognizing the essential hegemony of individual decisions as cornerstones of effective management plans." "Command-and-control" approaches to management that neglect intrinsic cycles of natural and social systems (Holling and Meffe 1996, Carpenter and others 1999) are inadequate to the task of achieving ecological sustainability and biodiversity conservation. Exploratory and adaptive approaches to management have the greatest potential to generate solutions for harmonizing management with natural forces and for maintaining ecosystem resiliency, biological diversity, and the services they provide (Carpenter and others 1999, Levin 1999b, Yorque and others 2002).

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