

Chapter 6: Ecology and Biodiversity¹

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Introduction

The integrity of animal and plant communities serves as a critical measure of the effectiveness of policies designed to protect and restore ecosystem processes in the Lake Tahoe basin. The conservation of plants and animals in the Tahoe basin is utterly dependent on the conservation of its terrestrial and aquatic ecosystems; so, in many ways, the research agenda that follows builds on the other research described in this volume. Accordingly, successful integration of outcomes from research on water quality, air quality, and other natural attributes of the basin will contribute greatly to the recovery and persistence of biological diversity in the Tahoe basin.

A Lake Tahoe research agenda that considers biological diversity and ecological function is best based on data collected from across scientific disciplinary boundaries. In Tahoe's intensively managed forests, there is an immediate and keen interest in linking forest fuel treatments to changing soil conditions, vegetation composition and structure, and the status of wildlife populations at multiple trophic levels. That immediacy noted, the Lake Tahoe basin actually is home to remarkably few imperiled species; however, that could change in short order through well-intended land and resource management actions that lead to unanticipated species declines (Manley 2005). Little species-specific information is currently available to guide land use and resource planning should changed circumstances lead to new listings under federal or state endangered-species statutes.

A number of policies direct and define management objectives for biological diversity in the Lake Tahoe basin. The Lake Tahoe Environmental Improvement Program identifies multiple restoration actions that are expected to benefit wildlife. Documents supporting the Tahoe Regional Planning Compact (1969), namely the 1987 Regional Plan (see <http://www.trpa.org>), call out 20-year goals for wildlife and

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fish, and identify environmental thresholds, indicator measures of those thresholds (including species indicators), and species and communities of special concern. The National Forest Management Act (1976) directives pertain to plants and animals on the more than 70 percent of Tahoe basin lands under U.S. Department of Agriculture, Forest Service jurisdiction. The U.S. Department of the Interior, Fish and Wildlife Service implements focal activities associated with several wildlife, fish, and plant species on National Forest System lands in the basin. Provisions of the Migratory Bird Act pertain to the entirety of the Lake Tahoe basin. Stringent state lands and parks rules are enforced on both California and Nevada sides of the lake. And both federal and state wildlife agencies are able to implement prohibitive policies if a threatened or endangered species listing becomes necessary.

Despite a demonstrated concern, our understanding of nearly all aspects of Lake Tahoe's biodiversity—from species found in lakeside meadows, to those on alpine peaks above—is still rudimentary and would benefit greatly from implementation of the research agenda that follows. To varying degrees, management of all Tahoe basin ecosystems would be better informed by improved scientific knowledge about ecological characteristics, habitat associations, and species responses to management activities. Detailed status and management response information is available for very few species in the basin; and, in most management applications, it will be necessary to know the local status and responses to management given the unique configuration of wildlife habitats within the basin, and the basin's relative isolation from the larger forested landscape of the Sierra Nevada. To that end, this chapter identifies focal management issues, associated uncertainties, and key research questions that, if answered, would encourage effective, efficient, and accountable resource management designed to maintain and conserve biological diversity, ecological function, and ecosystem services. Research in the Lake Tahoe basin will be most effective when designed in a manner that both decreases resource risk and uncertainty by closing information gaps, and directly informs management. For example, a research program to address uncertainties about the effects of forest management on biological diversity might start with a description of site-scale response patterns of biological diversity to various environmental changes associated with forest management. This program also might take steps to apply those data to the development of management tools that:

- Apply that understanding to the basin as a whole to inform management about conditions throughout the Lake Tahoe basin.
- Identify system indicators that can be used to monitor progress toward management goals for forest ecosystems.

- Determine thresholds of species and community responses that can inform how and when management actions should respond to monitoring results.
- Provide evaluation tools that managers can use independently.
- Provide basic data to enhance management and policy development.

The ecology and biodiversity research agenda considers seven subthemes that represent various management activities and objectives: (1) old-growth and landscape management, (2) fire and fuels management, (3) special community management, (4) aquatic ecosystem restoration, (5) urbanization, (6) recreation, and (7) climate change. Within each subtheme, we provide a summary of issues and uncertainties and associated key research questions. The departure from historical conditions reflected in current ecosystem conditions in the basin presents many challenges to restoration. Most fundamental is the challenging fact that existing terrestrial and aquatic ecosystem conditions are unique in the history of the basin as are the current and projected future climate conditions. Thus, the objective of restoration is not to return these systems to an historical structure or composition, but rather to restore their biological diversity, function, and resilience. The key research questions span many types of information gaps including basic information gaps; effects and effectiveness of existing management approaches; models of past, current, and potential future conditions; and field and analysis tools to enhance the “toolbox” of methods available to managers to inform planning and decisionmaking.

The ecology and biodiversity research agenda highlights the interactions between native species and communities and natural and human-caused stressors that present the greatest ecological and social risk, and for which research can reduce management-related uncertainties. Conceptual models are provided that show the primary linkages between native species and communities as components of ecosystems and the factors that affect their condition, including human-caused stressors (figs. 6.1 and 6.2). The two conceptual models group subthemes that share most of the same components and drivers: terrestrial ecosystem subthemes (old-growth forests and fire and fuels management) (fig. 6.1), and primarily aquatic ecosystems subthemes (special communities and aquatic ecosystems) (fig. 6.2).

The subthemes identified in the ecology and biodiversity theme area represent focal elements for management planning and action in the Lake Tahoe basin (figs. 6.1 and 6.2). The core components are those shared by most biological systems (e.g., species composition and abundance, vegetation structure), with differences expressed in the specifics of the components (such as associated species). The primary drivers of the condition of components also are often shared, given that human activities are pervasive and affect many biological components. Secondary

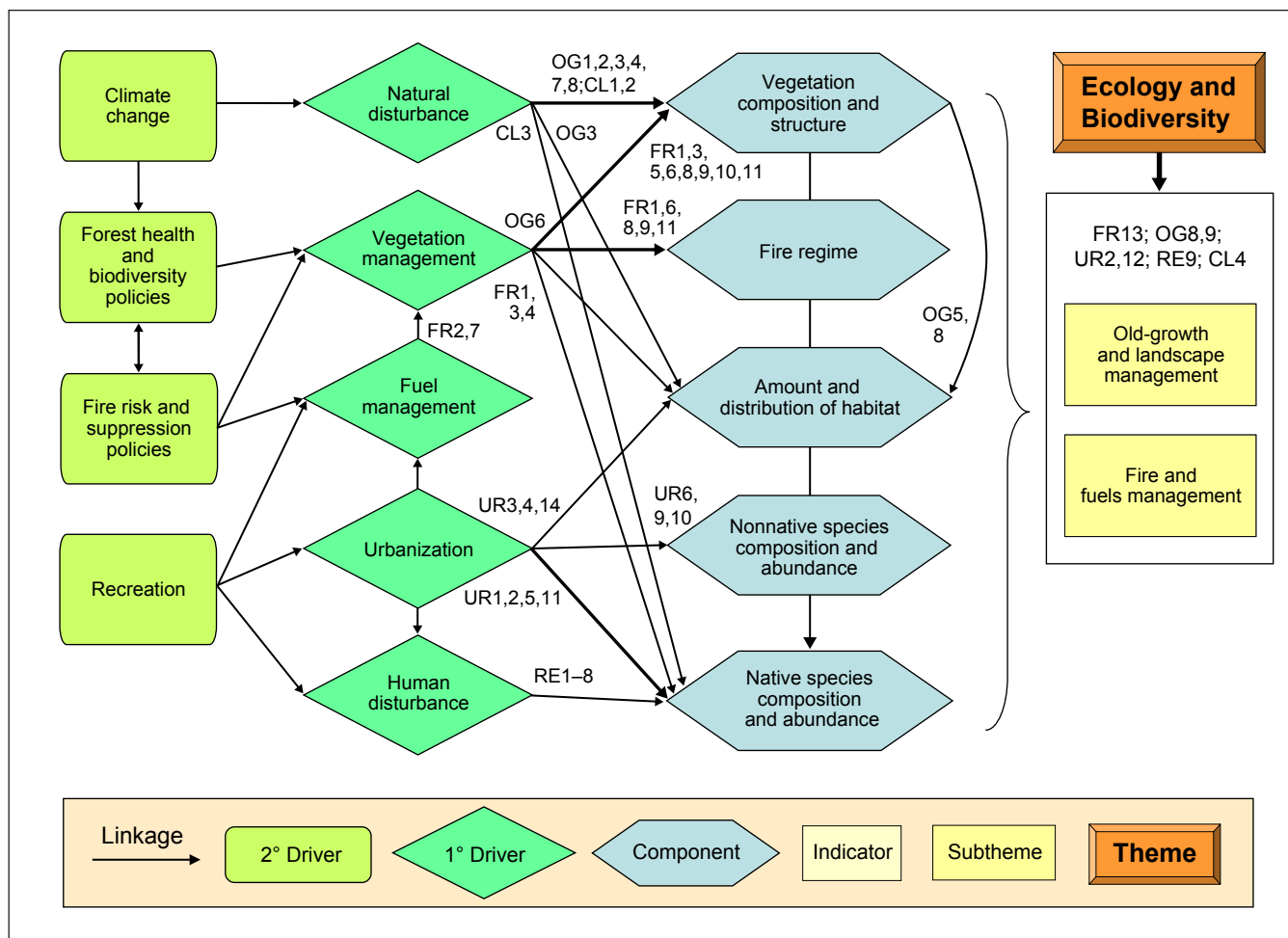


Figure 6.1—Conceptual model of the terrestrial ecosystem subthemes in the Ecology and Biodiversity theme. Identified are the primary components of terrestrial ecosystems in the Lake Tahoe basin, the natural and human-caused phenomena that affect their conditions, and the focus of research questions in the theme area, which are based on management concern and uncertainty. Thick arrows indicate especially important linkages between drivers and components. Research needs are indicated by alphanumeric symbols (e.g., CL3, OG3) and correspond to the descriptions presented later in the chapter.

drivers are typically external, broad-scale forces that act on human activities, such as regulations, policies, economic forces, and climate. It is important to recognize that stressors may have initial positive consequences for some species (e.g., habituation to human settlement by bears and geese) that then lead to undesirable secondary consequences (e.g., property damage or reduced diversity of native species).

The majority of uncertainties associated with terrestrial ecosystems pertain to the linkages between vegetation management and climate change (i.e., natural disturbances) and their effects on vegetation structure, composition, and associated fire hazards (fig. 6.1). A more limited set of questions pertain to the effects of forest fuels treatments on plant and animal communities, populations, and habitats. The

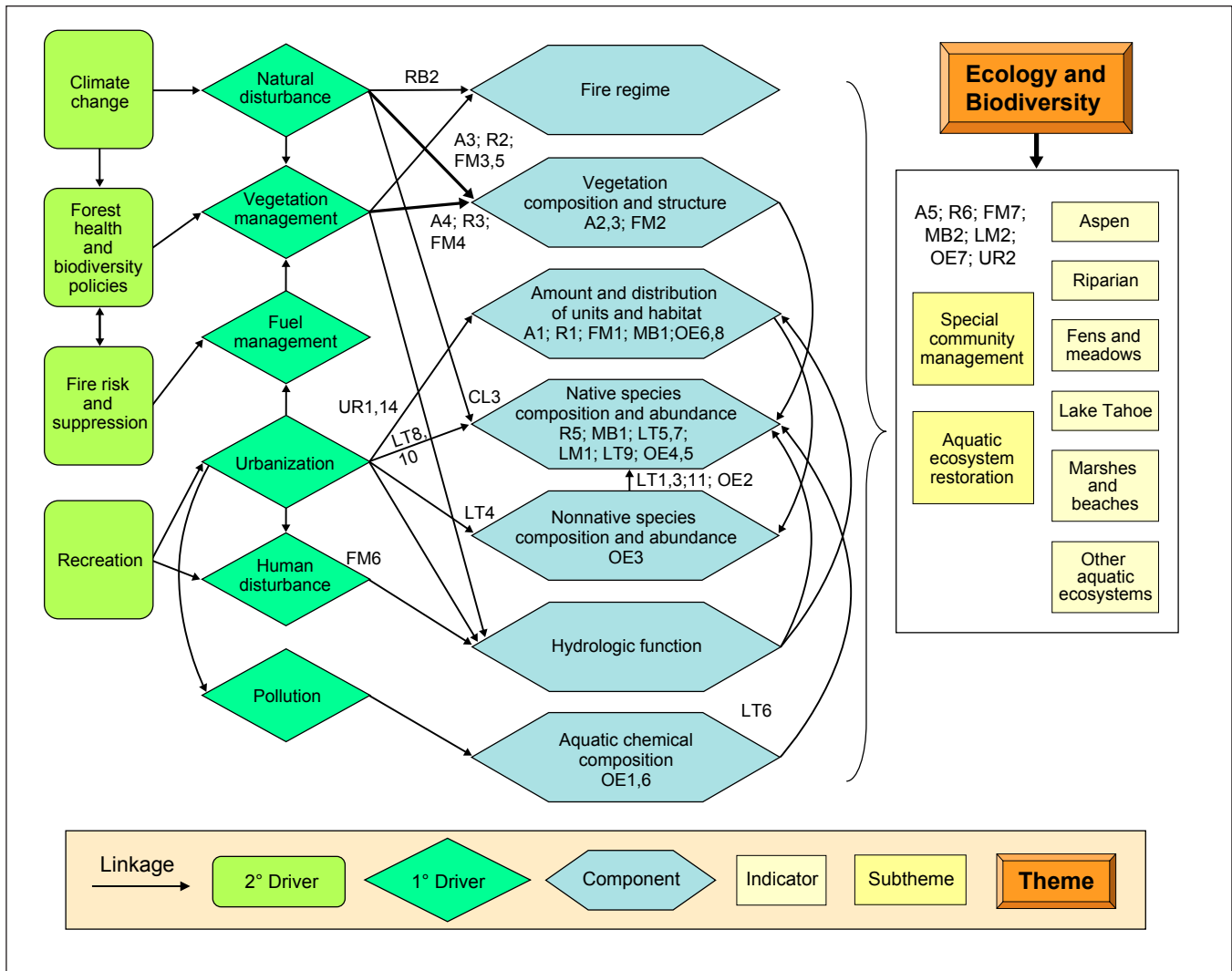


Figure 6.2—Conceptual model of the aquatic ecosystem subthemes in the Ecology and Biodiversity theme. Identified are the primary components of aquatic ecosystems in the Lake Tahoe basin, the natural and human-caused phenomena that affect their conditions, and the focus of research questions in the theme area, which are based on management concern and uncertainty. Thick arrows indicate especially important linkages between drivers and components. Research needs are indicated by alphanumeric symbols (e.g., R2, FM3) and correspond to the descriptions presented later in the chapter.

limited set of questions regarding biodiversity does not reflect lower uncertainty and risk, but rather it reflects the priorities of management, and the assumption that fuels treatments will not substantially alter the habitats of animals and herbaceous plants. Land and resource managers are interested in identifying key measures of conditions that can be used as indicators for progress toward desired conditions. These circumstances are not unique to the terrestrial ecosystems or the ecology and biodiversity theme; rather they recognize an area of substantial investment by management agencies at the present time.

The majority of uncertainties associated with the special communities and aquatic ecosystems are weighted toward basic information, as opposed to linkages between activities and the condition of components (fig. 6.2). This is a function of limited investment in research and monitoring in aquatic ecosystems other than Lake Tahoe itself; so it is generally thought that basic information on current conditions is the first step toward informing management. Not all special communities are identified, but the suite that is identified represents those of greatest management interest. In addition to the pursuit of basic information, greater understanding is needed about the linkages between natural disturbances, and the role of fire and fuels reduction on vegetation composition and structure, particularly in riparian and meadow habitats. As with terrestrial ecosystems, indicators would be selected for the purposes of assessing the condition of each of the special communities and aquatic ecosystems.

The research questions that are identified here constitute the highest priority information needs over the next 10 years, based on the combination of three considerations: (1) uncertainty based on lack of knowledge, (2) current risk based on the current condition of biophysical components, and (3) potential future risk based on current or future management activities or climate change. The questions represent those that, if addressed through research, would make a substantial contribution toward reducing uncertainty and risk in conservation and restoration efforts targeting biological diversity and ecological integrity in the Lake Tahoe basin. Some of the questions presented are more time sensitive than others, either as a function of their placement in a sequence of discovery or the ease of answering the question relative to the value of the contribution to reducing uncertainty and risk. The most time-sensitive questions within each subtheme are indicated in bold.

Old-Growth and Landscape Management

Past management activities, particularly historical logging, followed by fire suppression, substantively shaped the amount, distribution, and condition of old-growth forests in the Lake Tahoe basin today. Current management activities continue to affect the character and distribution of the basin's forest ecosystems. The combination of these anthropogenic and natural disturbances has determined the current distribution of seral conditions across the basin, including the distribution and abundance of the remaining old-growth forest patches (Manley et al. 2000). Forests in the Lake Tahoe basin now differ in a number of important aspects from their pre-Euro-American appearance. In the montane zone, the tree species composition and diameter distribution have changed greatly; there are far more small-diameter trees (e.g., < 30 cm diameter at breast height [DBH]) of shade-tolerant species

(particularly white fir, *Abies concolor* (Gordon & Glend) Lindl ex Hildebr.) in the understory than there were formerly, and far fewer larger-diameter (e.g., ≥ 75 cm DBH), older trees (Barbour et al. 2002). Moreover, the proportion of the landscape in montane chaparral has diminished, having been converted to forest (Nagel and Taylor 2005). Both of these changes indicate a reduced proportion of the landscape in both early and late-successional stages relative to the pre-Euro-American Tahoe basin landscape. The majority of the landscape is single-aged, fire-suppressed, second-growth fir and pine, a condition that would not exist historically.

Knowledge Gaps

The departure from historical landscape conditions in the Tahoe basin resulting from timber harvest and fire suppression has contributed to a reduction in terrestrial biodiversity, as well as apparent increases in fire risk (Weatherspoon and Skinner 1996). Debate exists regarding the extent of old-growth forests that historically occurred in the basin. A better understanding of historical old-growth reference conditions could help in assessing how the basin has changed over time, what those changes represent in terms of accompanying plant and animal diversity, and what targets might be set for future conditions in terms of the extent and condition of old-growth forests in the basin (Manley et al. 2000).



Seth Bigelow

Old-growth mixed-conifer stand in the Upper Truckee watershed, Lake Tahoe basin (2006).

Central questions for Lake Tahoe basin forest managers pertain to how much of various forest conditions is desired, and how those conditions should be distributed spatially to ensure the persistence of associated species, functions, and services. A well-defined vision for desired conditions can be used to design forest management and speed the transition to desired conditions; alternatively, forest management lacking such a vision can impair progress toward desired conditions. Agency managers in the basin have identified species of special concern and interest. For example, species of special concern identified in the Pathway planning process that have an association with old-growth forests include northern goshawk (*Accipiter gentilis*), American marten (*Martes americana*), pileated woodpecker (*Dryocopus pileatus*), and California spotted owl (*Strix occidentalis*). Other species of concern associated with old-growth components include osprey (*Pandion haliaetus*), bald eagle (*Haliaeetus leucocephalus*), and black bear (*Ursus americanus*). The population of brown-headed cowbird (*Molothrus ater*), another species of concern based on its potential ecological impact, is also affected by forest management practices. Coyote (*Canis latrans*) and black bear are species of high public interest in the basin (Manley et al. 2000); their populations are likely to change in response to forest management, and given their status as top carnivores in the basin, changes in their populations are likely to precipitate changes in wildlife community composition and structure (Crooks and Soule 1999).

There are many areas in the basin that cannot support certain forest structural conditions owing to physiographic constraints, such as slope, aspect, elevation, and soil depth, which affect vegetation growth rates and disturbance regimes (Taylor and Skinner 1998, Urban et al. 2000). Vegetation growth models can help define how those structural conditions will change over time across the basin, but a concrete understanding of how landscape configuration constrains the basin's vegetation communities is needed.

Disturbance fundamentally shapes forest structure and species composition in the Lake Tahoe basin. Current management activities with the greatest potential to affect old-growth forest vegetation conditions and landscape configuration are fuel treatments, fire suppression activities, and salvage logging. Wildfire, avalanches, and landslides are the most common natural disturbances shaping forest structure in the basin. Although we now understand the fundamentals about the role of fire in maintaining historical vegetation structure in the basin (Scholl and Taylor 2006, Taylor 2004, Taylor and Beaty 2005), relatively little is known about the role of avalanches and landslides, and their interactions with fire regime. Avalanches can break up landscape-level fuel continuity, and conversely, forested areas diminish

avalanche risk (Kattelman 1996). A better understanding of the basin's natural disturbance regimes and their interactive effects would aid forest restoration efforts. Recreation activities, both motorized and nonmotorized, can greatly affect the occurrence and abundance of wildlife species and thereby the structure of animal communities. Thus, recreation represents an added source of disturbance to wildlife, and its management is relevant to achieving desired forest conditions.

Research has begun to examine how forest restoration planning should consider a changing climate regime (Harris et al. 2006). Most research suggests that by the year 2070, a mean increase of two to five degrees centigrade in June–August temperatures will manifest in the Western States (Running 2006). This dramatic temperature change, and attendant changes in the hydrologic cycle, will predispose the basin to more extensive and intense wildfires (Taylor and Beaty 2005, Westerling et al. 2006) and change the distribution and interactions among plant and animal species. This means that desired-condition decisions and associated management strategies now informed and shaped by historical reference conditions also could be informed by current and projected future climatic conditions and disturbance regimes.

These issues and uncertainties translate into the following broad management questions:

- What stand conditions should management create to ensure that forest health and resilience is restored in the future?
- How much and where should various stand conditions be located throughout the basin to ensure that populations and communities of native plant and animal species are maintained?
- What key measures of stand conditions and landscape configurations will be most effective and efficient in monitoring forest ecosystem health and informing forest management?

Research Needs

In the subsequent research needs sections, and figures 6.1 and 6.2, research questions are identified by combined text and numeric codes. Text codes are defined as follows: OG for old-growth and landscape management; FR for fire and fuels management; FM for fens and meadows; A for aspen; R for riparian areas; LM for lakeside, beach, and marsh; LT for Lake Tahoe aquatic ecosystems; OE for other aquatic ecosystems; UR for urbanization; RE for recreation; and CL for climate change. Numbers refer to the sequence of questions presented in each subtheme. Bold codes indicate the most time-critical research needs.

Following are the old-growth and landscape management research questions:

(OG1) What more can we learn about pre-Euro-American settlement (prior to 1850) characteristics of forests in the Lake Tahoe basin with respect to plant species composition; diameter distribution of trees, snags and logs; and proportional representation of seral stages? How did these characteristics differ according to topographic position (slope, aspect, and elevation), longitude, and soil substrate? What is the relationship between historical stand structure and composition, and existing map products depicting “potential natural vegetation?”

(OG2) Does the condition of the pre-Euro-American settlement forests in the Tahoe basin represent a satisfactory model for forest restoration (i.e., desired future condition), and if not, how should it be modified to account for factors such as climate change and irreversible changes in land use? What are the projected changes in range and elevation of dominant tree species within the Tahoe basin owing to climate change?

(OG3) How did the historical disturbance regime (e.g., fires, landslides, avalanches, insect outbreaks) differ spatially, in intensity and extent, within the Tahoe basin? How did these disturbances shape the structure and composition of the forest? Did upper and lower elevation zones exhibit different spatial patterns of disturbance and resulting structure?

(OG4) What animal species are most closely associated with old-growth forests in the basin, and what are the relative effects of different stand conditions and landscape configurations on the persistence of these species and biodiversity, with particular emphasis on special-status species? How do closely associated species use old-growth stands, compared to other available areas, for foraging, shelter, dispersal, and reproduction, and what are the most favorable amount and configuration of forested conditions to support forest biological diversity and special-status species?

(OG5) What were and are the effects of historical logging and fire suppression on forest-associated wildlife species, including composition, abundance, co-occurrence, and diversity?

(OG6) What are the likely spatial changes in range and elevation of sentinel animal and plant species (i.e., species that are sensitive indicators of change) within the Tahoe basin in response to climate change?

(OG7) What elements of old-growth forests are key to maintaining their biological diversity (including density of large trees, basal area, stand contiguity, tree age structure, or standing or fallen large woody debris)? What is an effective set of indicators of the physical and biological conditions of old-growth forests?

(OG8) What performance measures—including presence and abundance of plants and animals, and other ecological community metrics—can be used to assess the effectiveness of efforts to restore historical (or achieve desired) old-growth forest structure, composition, and function?

(OG9) What landscape features and locations (e.g., dispersal/migration corridors) play key roles in maintaining populations within the basin, and what species or measures can serve as indicators of the function of these key features?

Fire and Fuels Management

Fire was undoubtedly the most pervasive agent of ecological disturbance in the Lake Tahoe basin prior to its settlement by Euro-Americans in the latter half of the 1800s. Reconstructions of the presettlement fire regime from cross-dated fire scars in old stumps and logs have shown that the historical fire-return interval ranged from an average of about 11 years in Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) and white fir forests (Taylor 2004), to 28 years in montane chaparral stands (Nagel and Taylor 2005), to 76 years in high-elevation red fir (*Abies magnifica* A. Murr.) and western white pine (*Pinus monticola* Douglas ex D. Don) forests. Fires then consumed surface fuels, thinned forest stands, and produced openings in the forest where shade-sensitive tree species could regenerate. Although historical fires were likely predominantly of low severity, the presence of extensive patches of montane shrubs in some areas indicates that stand-replacing fires of higher severity also occurred (Nagel and Taylor 2005).

Forests that developed under fire suppression after extensive logging in the Tahoe basin during the middle and later 1800s are now very different than those historical forests. Tree densities, particularly in smaller size classes, are now much higher, and species composition has shifted to favor firs over pines (Barbour et al. 2002, Taylor 2004). The abundance of trees and lack of fire return has led to unnaturally high amounts of surface fuels (Barbour et al. 2002), and greater fuel continuity, contributing to high fire hazard and greater probability of stand replacement upon burning (Manley et al. 2000, McKelvey et al. 1996, Skinner and Chang 1996).

Knowledge Gaps

Reducing surface and ladder fuels using prescribed fire or mechanical treatments has been shown to substantially improve the resilience of forest stands to wildfire (Agee and Skinner 2005, Pollet and Omi 2002); however, because of the importance of tourism, forest proximity to populated areas, and concerns about protection of natural resources, fuel management in the Lake Tahoe basin presents unique challenges. Smoke and liability issues may limit the use of prescribed burning in many areas. As a result, fuels in these areas are often treated mechanically or by hand, rather than through burning. Unfortunately, the extent to which mechanical forest treatments can mimic the ecological role of fire is poorly understood for many forest attributes (Weatherspoon and Skinner 2002). Because much of the excess forest biomass in the basin is in the form of small trees of low value, mechanical removal may not be cost-effective. As a result, new implementation strategies for reducing fire hazard, such as mechanical mastication or chipping, have been initiated. These methods leave the fuels on site, but alter their vertical profile, and have been shown not to result in soil compaction or erosion—yet concerns about fire effects such as soil heating, if the material should burn, remain (Busse et al. 2005, Hatchet et al. 2006; also see chapter 5, “Soil Conservation”).

Even in areas where prescribed burning is a viable management option, smoke management and the narrow window available for prescribed burns in many years severely limit the number of acres that can be treated. Most fires in the Lake Tahoe basin historically occurred in the late summer or fall (Taylor 2004), and managers have often opted to conduct prescribed burns at that time of year; however, recent research has found that early-season prescribed burns, which typically consume less fuel, may have some benefits for at least the first burn in areas with heavy fuel loading (Knapp et al. 2005). Not only was the recovery of understory plant species more robust following early-season burns, but tree mortality was lower in early-season burns than late-season burns (Thies et al. 2005), although not significantly (Schwilk et al. 2006). Fire disturbance may also promote the invasion of exotic species (Keeley et al. 2003), and Merriam et al. (2006) and Kerns et al. (2006) reported a greater abundance of exotic plant species after late-season burns.

Forest fuels treatments can change forest habitat attributes required by many wildlife species, including vertical layering of vegetation, age structure of trees, tree composition, spatial distribution of remaining trees, snag and log densities and characteristics, and understory cover and species composition. The intensity and extent of fuels treatments and their objectives (i.e., only fuels reduction or some balance of ecological outcomes) can greatly differ among agencies and projects; thus, the magnitude of effects of treatments on plants and animals is directly related



Prescribed pile burning as a means to reduce excess forest fuel loads. Tahoe Pines, Lake Tahoe basin.

to the intensity and extent of treatments. Treatments designed with fuel reduction as the primary objective tend to simplify and homogenize forest structure and composition. Further, they may extend impacts associated with urbanization farther into the forest by functionally extending edge effects. Simplified forest structure as observed in urban forest remnants (Heckmann et al. 2008) exhibited reduced biological diversity and ecosystem resilience (Manley et al. 2006; Sanford et al., in press; Schlesinger et al. 2008). Long-term environmental changes associated with fuel treatments are less certain, and will differ based on the combination of over-story treatments and postharvest treatments (chipping, pile and burn, prescribed burns) applied.

The impact of fuel treatments on plant and animal populations in the Tahoe basin is not known because of the general lack of information on the distribution and status of wildlife and plant populations in the basin, and the unique combinations of understory treatment (including chipping), large extent of actions, and rapid implementation of treatments being employed in the basin. Populations of many forest-associated species, particularly those associated with the montane zone, could be at risk of habitat fragmentation and isolation as a result of forest alterations.

These issues and uncertainties suggest the following broad management questions:

- What vegetation management approaches will be most effective and efficient in meeting a variety of management objectives, including reducing fire hazard, restoring forest health, increasing the amount and integrity of old-growth forests, maintaining and conserving biological diversity, and restoring a more natural fire regime?
- What locations are the highest priority for management and what balance of objectives are most appropriate in each location and throughout the basin?
- What measures are most informative and efficient in determining the effectiveness of vegetation management approaches in meeting fire and fuels management objectives?

Research Needs

Following are fire and fuels management research questions:

(FR1) How do current fuel treatments and future treatment scenarios simultaneously affect fire hazard and other values such as scenic and recreational amenity, water yield and quality, soil erosion, old-growth characteristics, and plant and animal diversity (including less-abundant species, narrowly distributed species, and forest and aquatic associates)? What are the effects of spatial distributions of fuel treatments on primary ecological management objectives in the basin, including (a) connectivity of populations of species expected to be most sensitive to changes in forest structure and understory conditions; and (b) maintaining quality habitat for aquatic species?

(FR2) Are there fuel treatment solutions that are optimal with respect to the multiple forest management objectives that exist in the basin (see question FR1), including considerations of cost? (This question could be addressed within a multiobjective modeling framework; the quality of the answers would depend at least in part on data from the kinds of field studies outlined below and elsewhere in this plan.)

(FR3) How do sensitive and vulnerable animal species associated with montane forests and aquatic inclusions (e.g., ponds and streams) use treated (masticated versus prescription-burned) and untreated areas to meet various needs (e.g., reproduction, foraging, movement, and shelter)?

(FR4) What are the projected consequences of current and projected fuel treatments for landscape connectivity for sensitive and vulnerable animal species?

(FR5) How does intensity of tree canopy thinning affect a range of ecosystem attributes? Is there a relationship between residual canopy cover after fuel treatments, and subsequent rates of surface and ladder fuel development? Do canopy openings and soil disturbance from fuel treatments favor establishment of shade-intolerant pine species? Is there a relationship between residual canopy cover and wildlife habitat value?

(FR6) How do alternative understory fuel treatments (e.g., canopy thinning followed by biomass removal, mastication and mulching, or prescribed burning) affect the trajectory of forest succession, including understory plant and animal species composition, relative abundances, and ecological community states and transitions? Do these treatments differ in resultant opportunities for invasive plant establishment? (It is recommended that the definition of forest succession include tree, shrub, herb, and grass plant forms, and that measurements include rate of fuel reaccumulation so that fire hazard can be calculated.)

(FR7) Mastication followed by mulching is a dominant mode of treatment of understory fuels currently used in the Lake Tahoe basin. Is the longevity of fire hazard reduction produced by mastication treatments related to vegetation type, resprouting potential, microenvironment, or chip depth? What are the ecological consequences of mulching compared to other treatment options? Will multiple cycles of treatment with mastication result in the buildup of unacceptably high amounts of surface fuels?

(FR8) How do alternative techniques for prescribed burning that are currently in use in the Lake Tahoe basin (jackpot, piling, understory, and piling with understory burns) compare in terms of fuel consumption and fire hazard, soil heterogeneity, wildlife responses, and wildlife habitat?

(FR9) What are the ecological consequences of season of treatment (early or late) when applying fuel treatments, such as mastication, mulching and prescribed burning? Important response variables might include mortality of remnant trees, resprouting of shrubs, and germination of species that have seed banks, and effects on small mammals and birds.

(FR10) What is the relative importance of ozone damage, soil depth, periodic drought, insect attack, and stand density in determining spatial patterns and temporal dynamics of tree mortality and subsequent surface fuel accumulation? What is the optimal range of temporal and spatial dynamics of tree mortality based on current and future climate conditions?

(FR11) What fuel treatments, if any, are most appropriate for the higher elevation forests in the Tahoe basin? What are the considerations for protecting against the spread or reducing the prevalence of root rot in red fir through fuel treatments?

(FR12) How effective are current fuel treatments in altering fire behavior, improving fire suppression effectiveness, and reducing fire severity, under the range of fire-weather conditions likely in the Lake Tahoe basin?

(FR13) What performance measures—including presence and abundance of plants and animals, forest structure and composition, and other biotic metrics—can be used to assess the effects and effectiveness of fuel treatment success at various times after treatment?

Special Communities Management

Biological diversity in the Lake Tahoe basin is a composite of species and the ecological communities of which they are members. Ecological communities that proportionally dominate the landscape typically are the primary focus of management. The Lake Tahoe basin, however, supports a number of classes or types of ecological communities that are limited in geographic extent but have great functional importance: among these are meadows, fens, aspen stands, riparian areas, and lakeshore marsh and beach communities.

These communities support disproportionately large numbers and a high diversity of animal and plant species, and some serve as nodes linking upland ecosystems and Lake Tahoe. Each community has particular threats to its integrity. Ecological communities and species with high conservation value are addressed individually, including their status and the composite of potential effects of management activities.

Aspen

Quaking aspen (*Populus tremuloides* Michx.) occurs in the Lake Tahoe basin in riparian areas, bordering meadows, as stand-alone groves in snow pockets or avalanche paths, or as disjunct patches interspersed with conifer forest (Shepperd et al. 2006). Aspen stands support high plant diversity relative to surrounding vegetation (Potter 1998), and use less water than conifer forests of equivalent area (Gifford et al. 1984). Many authors contend that in the semiarid West, aspen is second only to riparian habitats themselves in terms of the biodiversity they support and in importance as wildlife habitat. Aspen stands typically support a greater diversity and abundance of birds, mammals, and invertebrates than adjacent vegetation types (DeByle 1985, Flack 1976, Salt 1957, Schimpf and MacMahon

1985). For example, several bird species have a strong affinity with aspen, including northern goshawk, red-naped and red-breasted sapsuckers (*Sphyrapicus nuchalis/ruber*), dusky flycatcher (*Empidonax oberholseri*), warbling vireo (*Vireo gilvus*), Swainson's thrush (*Catharus ustulatus*), and MacGillivray's warbler (*Oporornis tolmiei*) (Finch and Reynolds 1988, Flack 1976, Heath and Ballard 2003, Richardson and Heath 2004, Salt 1957). Several mammal species also show affinities for aspen, including ungulates such as mule deer (*Odocoileus hemionus*), rodents such as pocket gophers (*Thomomys*), voles (*Microtus*), shrews (*Sorex*), and mountain beaver (*Aplodontia rufa*) (Beier 1989, Coggins and Conover 2005, Loft et al. 1991). The invertebrate communities associated with aspen in the Sierra Nevada are not well studied, but in Rocky Mountain National Park, 33 of 49 resident butterfly species were found in aspen, and 7 of those were unique to aspen forests (Chong et al. 2001).

Knowledge Gaps

In the absence of disturbance by fire, conifers have heavily encroached upon most aspen stands in the Lake Tahoe basin. Encroachment of conifers into aspen stands can have negative impacts on herbaceous cover, stand moisture, and invertebrate, mammal, and bird species richness and abundance. Many species of plants, birds, mammals, and invertebrates benefit from the thick herbaceous layer and deep leaf litter typical of aspen stands that experience periodic disturbance. In a recent inventory and assessment effort by the U.S. Forest Service, approximately 68 percent of aspen stands were designated as being at moderate to extremely high risk of extirpation (Shepperd et al. 2006). Restoration of decadent aspen stands elsewhere in the northern Sierra Nevada has met with considerable success (Jones et al. 2005). Information on the value of aspen in supporting animal populations in the Tahoe basin is still limited, but the few local studies that have been conducted suggest healthy herbaceous communities and limited conifer intrusion may be the optimal habitat condition for at least aspen-associated breeding birds (Richardson 2007, Richardson and Heath 2004). Clearly, approaches to managing aspen in the basin will directly affect many plant and animal species.

These issues and uncertainties suggest the following broad management questions:

- Where and to what ecological condition should aspen stands be restored in the Lake Tahoe basin?
- What is the desirable extent, configuration, and distribution of aspen stands (patches) that will assure ecological benefits to wildlife and co-occurring vegetation?

- What management actions can contribute to restoring and sustaining aspen stands in the Lake Tahoe basin?

Research Needs

Following are aspen research questions:

(A1) How well can we map and predict aspen existence from currently available methods (e.g., satellite imagery)? How well can stand condition be assessed with these methods, compared with ground surveys? What variables best predict the occurrence of plants of concern (e.g., physiographic, woody debris, indicator species, soil types, hydrologic regimes)?

(A2) What was the historical versus the current ecological status of aspen communities and associated plant and animal populations? How have these communities changed in the absence of periodic disturbance from fire? What stand attributes (e.g., stand area, species composition) are critical to maintaining populations of the most closely associated species?

(A3) What management tools and actions can be identified that will best facilitate conversion of conifer forest to desired aspen conditions?

(A4) How does aspen restoration affect associated plant and animal populations, and ecological communities? Are species and communities responding to restoration efforts as expected?

(A5) What performance measures—including presence and abundance of plants and animals and other ecological metrics—can be used to assess treatment effects and effectiveness in restoring aspen biological diversity and ecological function and monitoring conditions over time?

Riparian Areas

Riparian areas support high diversities of plant and animal species owing to the presence of water, diverse vegetation composition and structure, and abundant food resources. Many riparian areas in the Lake Tahoe basin were degraded from overuse in the late 1800s, but current problems stem largely from lack of fire combined with the legacy of historical channel alterations.

Knowledge Gaps

Riparian areas have been mostly excluded from forest fuel treatments because of concerns about soil disturbance resulting in nutrient and sediment deposition into streams and ultimately into Lake Tahoe. The limited management activity in proximity to stream riparian areas (also known as Stream Environment Zones or



Riparian habitat along the Upper Truckee River, Lake Tahoe basin.

SEZs) has resulted in the invasion of shade-tolerant conifers into many riparian areas. Conifers are thought to compete strongly with riparian vegetation (Haugo and Halpern 2007, Jones et al. 2005, Lang and Halpern 2007, Stam et al. 2008). Consequences of the lack of fire in riparian habitats include a greater density of small-diameter trees and an overabundance of small woody debris in some areas. There are concerns that altered conditions in riparian areas translate into higher risk of high-intensity fire in these areas, substantially increasing sedimentation and nutrient inputs to Lake Tahoe. There also is potential for fire from lower elevations to expand into higher elevations via riparian corridors despite aggressive upland fuel treatment efforts. In addition, one special status species—the mountain beaver—is most closely associated with riparian areas, so riparian management is likely to directly affect the mountain beaver. The lack of information on the historical and current status of riparian ecosystems, including the status of associated plant and animal species, impedes determination of the ecological characteristics of natural community recovery, desired conditions, and opportunities for habitat and stream restoration. Management in these zones could be carried out with greater confidence if more information existed regarding historical vegetation structure and composition, and riparian area disturbance regimes.

These issues and uncertainties suggest the following management questions:

- What is the extent and condition of riparian ecosystems in the Lake Tahoe basin, and what conditions should management attempt to create through available techniques, including the use of fire?
- What measures are most informative and efficient in determining the condition of riparian ecosystems and their potential responses to management and environmental factors?

Research Needs

Following are riparian research questions:

(R1) How well can we map riparian vegetation using currently available methods (e.g., satellite imagery), and what is the current location, extent, and condition of riparian vegetation in the basin based on these methods? How effectively can riparian condition be assessed using these methods, compared with ground surveys? What variables best predict the occurrence of plants of concern (e.g., physiographic variables, woody debris, indicator species, soil types, or hydrologic regimes)?

(R2) What was the historical versus the current ecological status of riparian plant and animal communities in the basin? What was the historical role of fire frequency and intensity in shaping riparian-area composition and structure in the basin? What was the historical composition and structure of vegetation in riparian areas, including the density of standing and downed woody debris?

(R3) Are riparian systems recovering naturally from historical anthropogenic disturbances? The need exists for a system to objectively classify riparian vegetation and its condition, compile and assess stream and wetland restoration efforts in the basin, review the efficacy of stream and wetland restoration techniques that are in use, and develop a system for assessing success of riparian restoration projects.

(R4) Does stream restoration have desired effects on riparian habitat and associated plant and animal species? How does restoration involving fire or fuel treatments differentially affect species richness or abundance?

(R5) What is the distribution and abundance of the mountain beaver population in the Tahoe basin, with what habitat features are they most closely associated, and how can their populations be most efficiently monitored?

(R6) What performance measures—including presence and abundance of plants and animals and other ecological metrics—can be used to assess treatment effects and effectiveness in maintaining, restoring, and rehabilitating riparian biological diversity and ecological function, and to monitor conditions over time?

Fens and Meadows

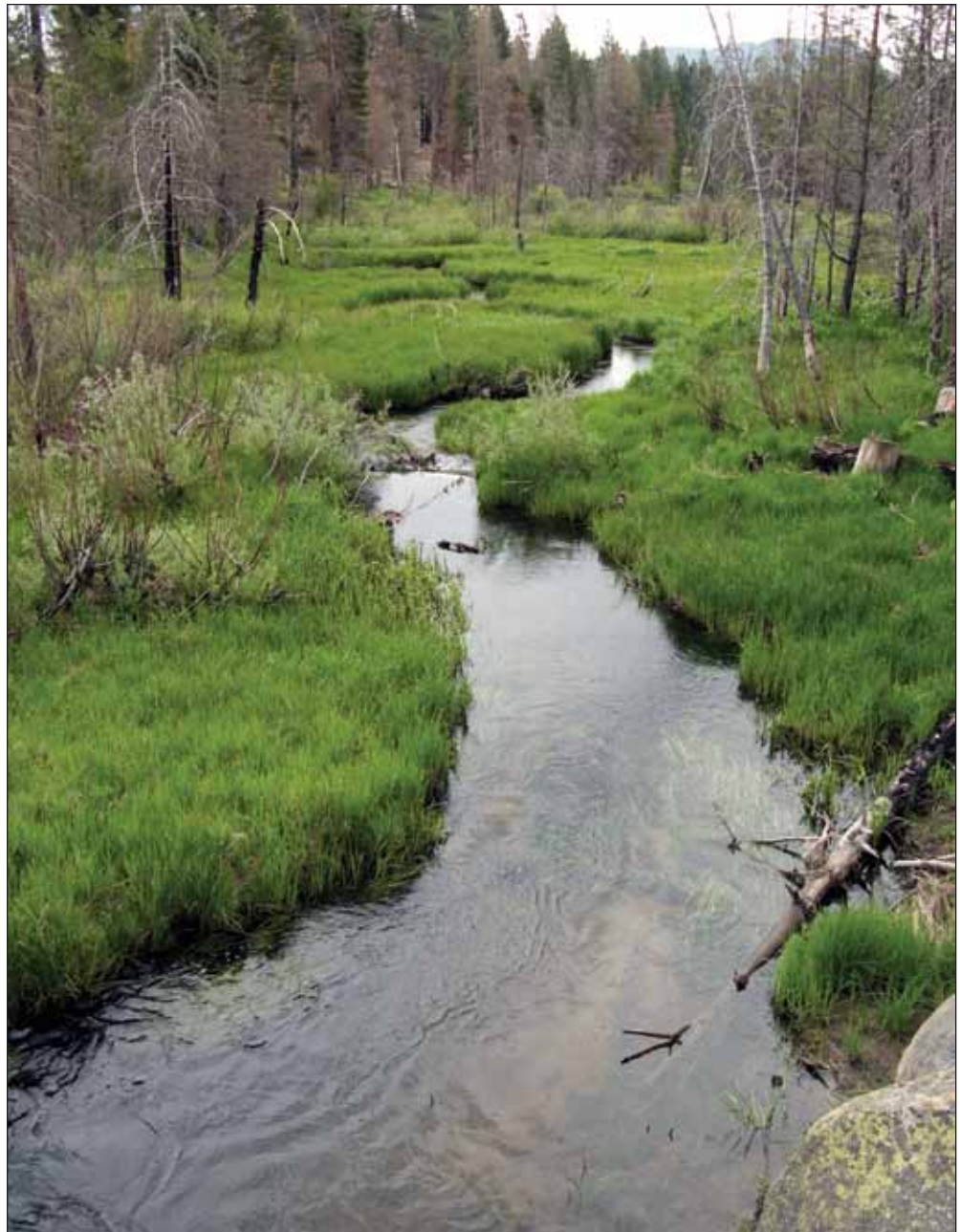
Fen and wet meadow communities are tightly linked to water-table attributes (Allen-Diaz 1991, Castelli et al. 2000, Kluse and Allen-Diaz 2005) and soil water chemistry (Atekwana and Richardson 2004, Bartholome et al. 1990). Many species of plants and some animal species, such as butterflies, fossorial mammals (e.g., gophers, moles, and marmots), meadow nesting bird species (e.g., willow flycatcher [*Empidonax traillii*] and mountain bluebird [*Sialia currucoides*]), and soil macro-invertebrates, are restricted to fens or meadows, which themselves are susceptible to impacts from human activities in the Lake Tahoe basin.

Knowledge Gaps

Past land uses, including grazing and water diversions, have resulted in degraded resource conditions. Approximately half of the basin's meadows have been permanently lost, fragmented, or altered in critical physical and biotic characteristics owing to these disturbances (Cobourn 2006, Elliot-Fisk et al. 1997). Grazing is no longer prevalent in meadows in the Lake Tahoe basin, but there may be substantial legacies of this former major land use (particularly altered plant and animal species composition), similar to circumstances elsewhere in the Sierra Nevada (Dull 1999).

Meadows and fens also suffer current impacts primarily from recreation activities, which can result in soil compaction, desiccation owing to incision of streambeds, and conifer encroachment (Martin and Chambers 2004). Recreational activities in meadows primarily consist of hiking, biking, cross-country skiing, and snowmobiling, with some motorcycle and all-terrain vehicle (ATV) activity. These activities can have both direct and indirect negative impacts on plants and animals. Hiking, mountain biking, and off highway vehicle (OHV) use leads to proliferation of trails in heavily used areas, causing fragmentation and soil compaction and erosion. Trail use also disturbs many wildlife species, leading to increased stress or decreased foraging time, which may have negative consequences for survival and reproduction. Snowmobile use is prevalent in meadows during the winter (and on established routes through the forest). Snowmobile use compacts the layer of snow close to the ground where small mammals, particularly voles, move during winter, and commonly damages vegetation. Mammalian carnivores and raptors (including bobcat [*Lynx rufus*], northern goshawk, and bald eagle) tend to be sensitive to vehicle use, but also may use compacted snow for travel, changing the spatial pattern of their movements and predation. Preliminary results from recent research suggest summer and winter OHV use does not affect the probability of use of an area by marten, a species of concern in the Tahoe basin (Zielinski and Slauson 2008).

Scott Hinton



Meadow-stream complex, Angora Creek, Tahoe Paradise, Lake Tahoe basin.

Although we have a basic understanding of general cause-effect relationships between recreation and plant and animal responses, the information is not specific enough to inform the development of management thresholds. It is not clear which species are most impacted by recreation, the ecological and social consequences of those impacts in the basin, and how growing numbers of visitors may exacerbate those effects. Two special-status species are closely associated with fens and

meadows: mountain yellow-legged frog (*Rana muscosa*) and willow flycatcher. The only robust population of mountain yellow-legged frogs in the basin is located in a fen (see “Special Communities” for more details).

Stream restoration may reverse some losses of meadow habitat, and reconfigurations of channels may allow streams to meander more, and carry water to a greater area. Similarly, where some streams meet roads, they have historically been forced through a single culvert; planned additional culverts will increase the area “watered” by a stream (e.g., at Blackwood Creek). These restoration efforts may expand meadow habitat; influences on these populations could be detected by monitoring before and after restoration.

These issues and uncertainties suggest the following management questions:

- Where are the Tahoe basin’s fens and meadows located, and what are their current conditions?
- What management actions can contribute to restoring and sustaining fens and meadows in the basin?
- What measures are appropriate to assess the condition of fens and meadows and efficacy of management actions?

Research Needs

Following are fens and meadows research questions:

(FM1) Where are fens and meadows located in the Tahoe basin, and what are their current ecological characteristics and conditions? How important is water chemistry and ground-water hydrology in establishing and maintaining fen conditions?

(FM2) What are appropriate reference conditions and historical conditions for fens and meadows in the Lake Tahoe basin?

(FM3) How do current and potential future management and restoration practices in fens and wet meadows, including application of fire or fire surrogates, affect their susceptibility to invasion by unwanted plant species?

(FM4) How well do predictive models of meadow recovery, with and without restoration, apply to the Lake Tahoe basin circumstances? Which meadows should be used to validate these models, and what data need to be collected? How should meadows be assigned in a priority scheme for restoration?

(FM5) How are fens and meadows impacted by current disturbances, including water use, fire suppression, recreation, and beaver activities? Which meadows are most critical to maintaining populations of meadow-dependent species in the basin?

(FM6) To what extent do recreation-associated impacts (both direct and indirect) in meadows change composition, abundance, and behavior of wildlife species? Do some species seasonally avoid meadow and riparian habitat because of snowmobiles, bike or foot traffic, or dogs?

(FM7) What performance measures—including presence and abundance of plants and animals and other ecological metrics—can be used to assess conditions, assess the effects and effectiveness of efforts to restore or rehabilitate meadow biological diversity and ecological function, and monitor conditions over time?

Lakeside Marsh and Beach Habitats

Marsh and beach habitats in the Lake Tahoe basin are limited in number and extent. The largest marshes occur in the southern part of the basin in association with the mouth of Upper Truckee River, Trout Creek, and Tallac Creek. Marshes provide the only suitable habitat for a large number of species in the basin, including many species of waterbirds (Manley et al. 2000). Beaches are numerous around Lake Tahoe, but they are limited in extent, particularly in years of high lake levels.

Knowledge Gaps

Lakeside marsh and beach habitats have had their historical hydroperiods altered by the damming of the lake's outlet. This has had adverse effects on Tahoe yellow cress (*Rorippa subumbellata* Rollins) (Pavlik and Murphy 2002), caused changes in marsh plant communities (Kim and Rejmankova 2001), hindered recent attempts to restore marsh habitat destroyed by lakeside housing developments,⁷ reduced populations of waterbirds, and may have fostered encroachment by lodgepole pine (*Pinus contorta* Douglas ex Loudon) into lakeside areas.

Tahoe yellow cress is a low-growing, perennial species endemic to the shores of Lake Tahoe. The species is listed as endangered by both states, is considered endangered or threatened by the California and Nevada Native Plant Societies, and is a candidate species for listing under the Endangered Species Act. The species has been the focus of a conservation strategy for the past 4 years, with the goal of restoring a self-sustaining metapopulation. Lack of access to certain privately held lakeshore areas has made it difficult to know whether this goal is being achieved. Additional uncertainty comes from lack of knowledge of seed bank dynamics, seed and rootstock longevity and dispersal, and genetic relationships among core and satellite populations.

⁷ Hunter, J. 2008. Personal communication. Senior ecologist, EDAW, Inc., 870 Emerald Bay Rd., South Lake Tahoe, CA 96150.



Dairy Meadows in autumn, Taylor Creek watershed, South Lake Tahoe, California.

Waterbirds (including ducks, shorebirds, and rails) are special-status species that find their primary habitat in lakeside marshes. Their populations have fallen in response to the loss of much of Pope Marsh to development in the 1960s (Manley et al. 2000). The TRPA has conducted surveys of key marshes around the lake for the past 7 years, and their findings are summarized in the Pathway planning documents.⁸

These issues and uncertainties suggest the following management questions:

- What management actions will contribute to restoring and sustaining desired ecological values and biodiversity in Lake Tahoe's lakeside marsh and beach habitats?
- What ecosystem attributes should be subjected to monitoring to assess the effectiveness of management actions directed at lakeside marsh and beach habitats?

Research Needs

Following are lakeside, beach, and marsh research questions:

(LM1) For shoreline plants of concern, does the spatial extent of existing populations support life-history requirements (including access to pollinators, disturbance regimes, seed dispersal)? What environmental factors most affect the persistence,

⁸ Kelchlin, E. 2007. Personal communication. Wildlife biologist, Tahoe Regional Planning Agency, 128 Market Street, Stateline, NV 89449.

extent, and reproductive success of populations at a given site? Are there genetic strains of shoreline plants that are more robust to environmental stressors, thus conferring enhanced survival?

(LM2) What is the ecological status of marsh habitats in the basin, and what measures can be taken to retain and restore their ecological integrity?

(LM3) What performance measures—including presence and abundance of plants and animals and other ecological metrics—can be used to assess treatment effects and effectiveness in maintaining, restoring, and rehabilitating the biological diversity and ecological function, and to monitor conditions in marsh and beach habitats?

Aquatic Ecosystem Restoration

The ecology of the aquatic ecosystems within the Lake Tahoe watershed has been altered dramatically over the last two centuries. Most of our knowledge of historical change has focused on alterations to Lake Tahoe itself; however, lakes, streams, and meadows within the upper watershed also have been altered resulting in the increased need to manage these ecosystems. In this section, we differentiate Lake Tahoe and other aquatic ecosystems to assist in interpreting the change and research needs for these distinctive ecosystems. We focus specifically on alterations from eutrophication, potential changes owing to atmospheric loading of nitrogen, and the influence of nonnative species (plant and animal) on the restoration or management of native biota.

Lake Tahoe

Prior to large changes in community structure and conditions of nutrient loading brought about by human activities, Lake Tahoe's community assemblage was relatively simple with 12 orders of zoobenthic taxa, 6 zooplankton species, and 8 fish taxa (Chandra 2003, Frantz and Cordone 1996, Juday 1906, Miller 1951, and Vander Zanden et al. 2003). The benthic invertebrate community supported one endemic, wingless form of stonefly. Beginning in the mid to late 1800s, species introductions combined with landscape disturbances started to alter the lake's biology.

The preinvasion food web (circa 1872) was dominated by a single predator, Lahontan cutthroat trout (*Oncorhynchus clarki*, subspecies *henshawi*), which fed primarily on pelagic tui chub (*Siphateles bicolor pectinifer*) and zooplankton (Chandra 2003, Juday 1906, Vander Zanden et al. 2003). Forage fishes obtained energy from a mix of benthic and pelagic primary production sources. By 1939, cutthroat trout were extirpated from Lake Tahoe, and a lake trout (*Salvelinus namaycush*) population replaced them as the top predator (Cordone and Frantz

1966). Three primary reasons for the demise of cutthroat trout were predation from introduced lake trout, the degradation of spawning stream habitat from increased siltation owing to watershed deforestation (Moyle 2002), and the hybridization of cutthroat trout with rainbow trout owing to hatchery propagation.⁹ There have been several attempts to reestablish both fluvial (stream form) and lacustrine (lake form) cutthroat populations in the Tahoe basin, all of which failed. As part of the U.S. Fish and Wildlife Service recovery plan for cutthroat trout (Coffin and Cowan 1995) in its native range, efforts have begun to restore cutthroat in Fallen Leaf Lake, located in the southern end of the basin.

Crayfish (*Pacifastacus leniusculus*) were introduced multiple times into Lake Tahoe and were established by 1936; they are now found in large numbers (55 million in the late 1960s and 230 million by early 2000 (Abrahamsson and Goldman 1970, Chandra and Allen 2001). Studies suggest that, under low densities (0.16 adult/m²), the crayfish stimulate periphyton productivity by removing old senescent cells (Flint 1975). Today, crayfish do not contribute to the energetics of nonnative lake trout except for the largest size classes (>50 cm).

Chandra et al. (2005) investigated the effects of cultural eutrophication on the coupling between pelagic primary producers and benthic consumers in Lake Tahoe. At depths where ambient light levels equal 1 percent (which have shifted with time from 50 to 85 m), pelagic primary producer and zoobenthic consumer coupling was positive. Historically, the zoobenthos from this depth zone obtained 32 percent of their energy from phytoplankton sources; after 43 years of eutrophication, they obtained 62 percent of their energy from those sources. A simple model indicated increased pelagic production and resultant export of matter, combined with the loss of benthic primary production, has contributed to the change in zoobenthos energetics. Recent samplings of zoobenthos during 2008–09 suggest there may be a 50 to 80 percent loss in benthic invertebrate density and biomass in Lake Tahoe. Furthermore, there has been a substantial decrease in the density of native, endemic invertebrates such as the blind amphipod and more cosmopolitan invertebrates such as oligochaete worms (Chandra and Caires 2001). Whether this loss is due to a shift in pelagic to benthic coupling or from alterations to Mysid shrimp is unclear (see below).

The establishment of the invertebrate *Mysis relicta*, corresponded with shifts in the trophic niches of forage fishes (chubs) and the top predator lake trout, and a feeding shift of lake trout to pelagic energy sources. The resultant increase in lake trout may have increased predation rates on native forage fishes and decreased

⁹ Cordone, A.J. 2007. Personal communication. Fisheries biologist, retired. California Department of Fish and Game, 1416 Ninth Street, Sacramento, CA 95814.

their abundance (Vander Zanden et al. 2003). Growth rates of lake trout before and after mysid introduction do not appear to have changed, except in the smaller size classes. Post *Mysis* invasion studies in Lake Tahoe showed impacts on other biological components of the lake. A strong restructuring of the zooplankton community as a result of *Mysis* predation on native cladocerans occurred, shifting the lake's pelagic environment to a *Mysis* and copepod-dominated system. Furthermore, modeling and empirical measurements suggest mysids may be influencing the carbon dynamics at the sediment-water interface as they feed in the deep part of the lake during the daytime and resuspend sediment particles through excretion during the nighttime as they migrate to the pelagic zone (Chandra 2003). Thus the insertion of *Mysis* into the middle of the food web played a strong determining role in restructuring upper trophic level energetics, and in disrupting community dynamics in the middle and lower parts of the food web. Their role and impact at lower depths is unclear; however they may be playing a role in disrupting carbon dynamics in the deepwater and pumping particles back into the water column.

In the mid to late 1970s, and again in the late 1980s, a variety of nonnative species were discovered in the near-shore environment, primarily driven by the establishment and expansion of nonnative aquatic plants, which provided habitat and refugia for nonnative fishes. The warm-water fish introductions were illegal and thought to be the result of anglers eager to catch these fish. During that period, in the Tahoe Keys, a major rearing area of native fishes, warm-water fish species were rarely found, whereas native minnows remained abundant as evidenced by a snapshot sample obtained in 1999; however, by 2003, largemouth bass (*Micropterus salmoides*) were common, whereas redbreasted sunfish (*Richardsonius balteatus*) and speckled dace (*Rhinichthys osculus*) populations declined or were virtually eliminated from the Tahoe Keys (Chandra 2009, Kamerath 2009). The change in fish structure was substantiated by fishing guides operating out of the Tahoe Keys: within a decade they could no longer collect the minnows that were commonly used as bait by fishing charters on the lake.

Until 1994, no lakewide surveys for rooted aquatic macrophytes had been conducted in efforts to document the presence of nonnative species. Early reports (1975) of water milfoil species near Taylor Creek did not identify the species of *Myriophyllum*, nor were vouchers or photographic records made. However, severe impacts from aquatic plants were observed in the Tahoe Keys by the end of the 1970s and early 1980s, during which time mechanical harvesting was begun. Recent studies have documented the role of some of the invasion pathways and vectors (boats and boat trailers) for aquatic plants that are transported both to and away from Lake Tahoe (Wittmann 2008). These vectors contribute to issues of

continued reinfestation and potential new infestations of nonnative aquatic plant species.

In 2008, established populations of the nonnative bivalve species, the Asian clam (*Corbicula fluminea*), were discovered in the southeastern portion of Lake Tahoe by University of California, Davis researchers during regular near-shore periphyton surveys. Asian clams were first detected in Lake Tahoe in very low numbers at Timber Cove in 2002 (3 to 20 clams/m²—Hackley et al. 2008), and at Nevada Beach in 2003.¹⁰ Extensive field surveys during summer 2008 revealed much higher densities of Asian clams (50 to 3,000 clams/m²), suggesting evidence for local population growth and possible reintroduction from external populations. Asian clams in Lake Tahoe compete with other local native molluscan species, such as the montane pea clam (*Pisidium* spp.) and the ramshorn snail (Planorbidae). Its current known distribution (area ~1 million m²) is patchy along the southeast shore of the lake from Zephyr Cove to El Dorado Beach, and is rapidly expanding and colonizing a variety of physical circumstances.

Knowledge Gaps

Lake Tahoe's ecological community has changed through the elimination of native trout, restructuring of food web energy flow, and introduction of species that occur in both the limnetic and littoral zones. It is unclear, however, how some of these introduced species are impacting near-shore and offshore water quality as well as native fish biomass and production. In addition, three special status species are primary participants in the Lake Tahoe food web—Lahonton cutthroat trout, osprey (*Pandion haliaetus*) and bald eagle. Populations of osprey and bald eagle are likely to be affected by changes in the relative and absolute abundance of fishes in Lake Tahoe.

Mysis shrimp are the lake's dominant macrozooplankton, exhibiting a large (up to 400 m) diel vertical migration to the lake bottom (Rybock 1978). While on the bottom, mysids feed on sediment detritus and may actively pump detritus and nutrients into the lake's limnetic zone (Chandra 2003). Research from other ecosystems suggesting mysids are supported by benthic detrital energy sources is supported by a number of studies (Lasenby and Lanford 1973, Lasenby and Vanduyne 1992, Lester and McIntosh 1994, Song and Breslin 1999, Viherluoto et al. 2000). Many ecotoxicological studies have determined that *Mysis* ingest heavy metals and organochlorines directly from sediment (Lasenby and Vanduyne 1992, Lester

¹⁰ Herbst, D. 2003. Personal communication. Aquatic invertebrate ecologist, University of California Sierra Nevada Aquatic Research Laboratory, HCR 79, P.O. Box 198, Mammoth Lakes, CA 93546.

and McIntosh 1994, Song and Breslin 1999), and serve as a vector for contaminant transport to the pelagic zone. Gut content information also suggests mysids may derive a substantial amount of their energy from benthic resources, including zoobenthos and organic-rich sediment particles (Lasenby and Lanford 1973).

The effect of warm-water invasive species on the native fish community and the potential for recycling nutrients in the near-shore habitat are important uncertainties. Recent surveys suggest warm-water fish such as bass (*Micropterus salmoides*), bluegill (*Lepomis macrochirus*), and catfish (*Ameiurus nebulosus*) are found around the lake. Recent assessment of their distribution indicated the densities are still very low compared to other ecosystems and can be variable over time. Overall the densities were low around most of the lake with higher densities in some locations such as Meek's Marina and intermediate densities in the Tahoe Keys. Anecdotal observations indicated that bass may be in open water areas of the lake; however, it is unclear the extent to which bass have established in these areas or if they were moving through migration zones before they reach more enclosed sites such as marinas and embayments (Chandra et al. 2009). Although preliminary research suggests these fish are competing and/or preying upon native fishes in the near shore (Kamerath 2009), the role that nonnative crayfish and other physical factors may play in controlling warmwater fish establishment as well as recruitment around the lake remains unclear. Crayfish are a preferred food source for bass in their native habitats. Currently, the invasive crayfish in Lake Tahoe seem to have expanded in population since estimates were first made in the 1970s, with over 230 million individuals in the lake estimated in 2001 (Chandra and Allen 2001). Current models that predict warmwater fish distribution (Chandra et al. 2009, Kamerath 2009) do not account for crayfish as a food resource in the lake and how they may contribute to bass growth and maintenance. Furthermore, using Lake Tahoe fishes researchers have found that ultraviolet light penetration may control recruitment of nonnative fishes and allow the persistence of native fishes.¹¹ Thus, there may be direct ties between the lake's clarity and the distribution of warmwater fishes. These two resource controls of food availability and physical light constraints should be incorporated into existing models predicting warmwater fish establishment in the lake to refine areas for monitoring as well as management.

The recent invasion of the near-shore area by warm-water species such as bass species could lead to the remobilization of nutrients in this habitat. Examination of seasonal nutrient availability is recommended, particularly during low flow periods, to determine the biological contribution of nutrients to near-shore

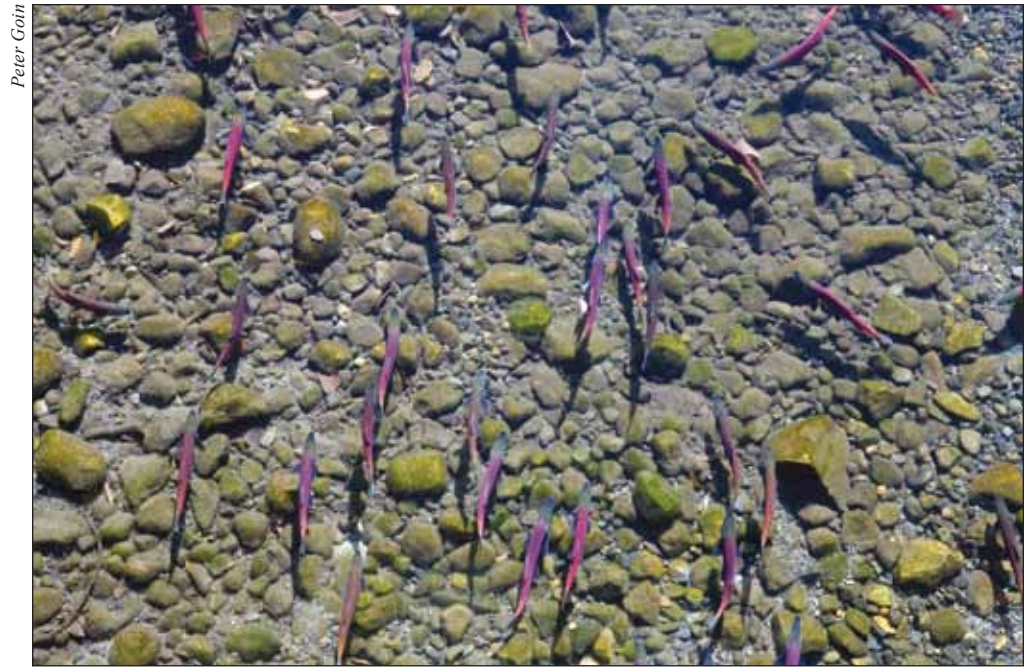
¹¹ Williamson, C. 2009. Personal communication. Professor in ecology, Miami University, Department of Zoology, Pearson Hall 158, Oxford, OH 45056.

production and lake clarity. The interactions between native and nonnative plants also are poorly understood. With the continued expansion of Eurasian water milfoil (*Myriophyllum spicatum*), and the newly expanded populations of curly leaf pondweed (*Potamogeton crispus*), the uncertainties of fish/plant interactions are even more complex.

Eutrophication of Lake Tahoe has led to a shift in energy flowing to the bottom of the lake (Chandra et al. 2005). It is unclear, however, if increased coupling between pelagic to benthic energy flows along with carbon alteration due to *mysid* shrimp are altering benthic invertebrate community structure and production—an issue of particular importance when trying to manage native, benthic biodiversity such as the endemic, wingless stonefly (*Capnia lacustra*) or blind amphipod (*Stygobromus* sp.) and in evaluating the potential for the reintroduction of native species.

Environmental impacts resulting from Asian clam establishment in Lake Tahoe related to water quality, benthic community structure and production, and the potential for the facilitation of invasion of other near-shore invasive species through habitat disturbance and localized increases in nutrient concentrations are uncertain. In particular, the Asian clam (1) excretes elevated levels of nitrogen and phosphorus into the water column and sediment substrate (Wittmann et al. 2008)—which can promote increased algal growth; (2) is able to filter extremely high volumes of water (Vaughn and Hakenkamp 2001)—potentially impacting both water quality and pelagic communities including Lake Tahoe sports fisheries; and (3) can increase levels of calcium through the concentration of dead shell matter—providing potential substrate and appropriate biochemical conditions for the establishment of other nonnative bivalve species such as the quagga (*Dreissena rostriformis bugensis*) and zebra mussel (*Dreissena polymorpha*). Current knowledge about the Asian clam in Lake Tahoe is limited because of the short time since its discovery. Continued efforts to assess the life history, environmental impact, and distribution, and to identify possible control and management actions in Lake Tahoe are underway.

Finally, little is known about the ecology and nutrient dynamics of Emerald Bay. This bay is an important destination for recreational boaters from various parts of the lake and particularly the Tahoe Keys, where most of Lake Tahoe's nonnative species issues currently reside. At least 8 nonnative species have been observed in Emerald Bay including but not limited to Eurasian watermilfoil, largemouth bass, catfish, Mysid shrimp, lake trout, crayfish, Asian clam, and kokanee salmon. Efforts to integrate and assess the limnology and food web ecology of this bay are recommended as it is likely that future invaders will establish in this location owing to the amount of propagule pressure occurring through boat traffic,



Kokanee spawning, Taylor Creek, South Lake Tahoe.

warmer temperatures, and increased productivity. Furthermore, due to its isolated nature and increased productivity compared with Lake Tahoe, this may be an important area for restoring the native Lahontan cutthroat trout.

These issues and uncertainties suggest the following key management questions:

- What management actions are necessary to restore and sustain a desired food web in Lake Tahoe, and will those actions be consistent with efforts to reverse declines in the lake's clarity?
- What are the appropriate measures of management and restoration program actions to assess their effectiveness in meeting ecosystem objectives?

Research Needs

Following are Lake Tahoe aquatic ecosystem research questions:

(LT1) What is the interaction between nonnative and native species in the basin, and how does this affect our ability to manage native biodiversity?

(LT2) What is the linkage between habitats (i.e., profundal-pelagic, littoral-pelagic) for carbon, phosphorus, and sediment transport particularly with the introduction of nonnative species? How does this affect Lake Tahoe water quality and clarity and native benthic invertebrate biodiversity?

(LT3) What is the seasonal role of mysid shrimp in controlling native plankton and benthic invertebrate populations and reducing water clarity through the transport of benthic nutrients and sediment particles into the water column? Ideally, research would focus on understanding the life cycle, contemporary feeding behavior, and the role mysid shrimp may play in reducing water clarity in Lake Tahoe.

(LT4) Can we predict future invaders (plant or animal) and the potential impacts to the lake's water clarity or biodiversity?

(LT5) Will current limnological characteristics support the establishment of non-native species or the potential recovery of native fish populations in Emerald Bay?

(LT6) What is the variability of benthic algal production and does this affect near-shore production and clarity? Will nonnative species alter this production? Future research is recommended to examine the production of benthic algae and invertebrates such as invasive crayfish to determine if eutrophication is affecting ecological community structure.

(LT7) What is the status of osprey and bald eagle populations in the basin, and how do their distribution, abundance, and productivity track changes in fish populations in Lake Tahoe?

(LT8) How can we best ensure the survival of native fish and other desired aquatic vertebrates? What stressors are affecting native species, and what can be done to lessen negative impacts?

(LT9) How can we restore native fishes and other aquatic vertebrates to the lake? What portions of Lake Tahoe are best suited to reintroduction efforts for native species? How will established nonnative species likely affect the success of restoration efforts?

(LT10) How can water quality and water clarity be protected from the effects of introduced species and human activities? What aspects of water quality and clarity are at most risk? What management actions might contribute to minimizing negative impacts from those sources?

(LT11) What is the current distribution of the Asian clam in Lake Tahoe, and what are its ecosystem-level impacts? How does it impact near-shore quality and the potential facilitation of the invasion of other nonnative aquatic species?

Other Aquatic Ecosystems in the Lake Tahoe Basin

Much of the research carried out in the Lake Tahoe basin has focused on understanding the impacts of watershed development, nutrient loading, water quality, and aquatic ecology in Lake Tahoe itself. Very little effort has been placed on evaluating the response of other lakes, streams, and other aquatic habitat types to the array of human disturbances affecting them, including ground disturbance, increased inputs from atmospheric pollution, and the impacts of nonnative species (fish, amphibians, plants) introductions.

The aquatic ecosystems research that has been conducted has been short term (seasonal or one-time assessments), primarily owing to funding constraints. For example, Marlette, Cascade, Fallen Leaf, Echo, and Spooner Lakes all have been evaluated for one or all of the following constituents: nutrient status (e.g., phosphorus, and nitrogen), basic physical and chemical measurements (e.g., dissolved oxygen, temperature, and pH), pelagic primary production, and zooplankton composition and biomass (e.g., Lico 2004, Reuter et al. 1996; University of California, Davis and University of Nevada, Reno 2003, 2006). In 2006, an effort was made to assess the nutrient concentrations via depth profiles and limitation (nitrogen, phosphorus, or co-limitation) for Upper and Lower Echo, Upper and Lower Angora, Fallen Leaf, Tahoe, Eagle, Spooner, and Marlette Lakes. Results showed the pelagic primary production in five lakes (Tahoe, Marlette, Fallen Leaf, Lower Echo, Lower Angora) was co-limited; Spooner Lake exhibited possible nitrogen limitation, and data from Eagle Lake were inconclusive (Chandra and Rost 2008).

Other research has focused on the ecology of some of the small lakes in the Tahoe basin. For example, Cascade Lake has a biological assemblage that closely resembles that of Lake Tahoe prior to the introduction of the two nonnative species (*Mysis relicta* and lake trout, *Salvelinus namaycush*). Vander Zanden et al. (2003) presented a food web structure for this lake in 2001, finding that hybridized cutthroat trout are a dominant predator feeding on pelagic energy sources (e.g., zooplankton). Since 2001, researchers from the Universities of California-Davis, Nevada-Reno, Wisconsin-Madison have been monitoring the biology and general limnology (nutrients, chlorophyll a) during spring, summer, and fall in Fallen Leaf Lake. This lake experienced the reintroduction of native Lahontan cutthroat trout (information on the bioenergetics, historical changes to the lake's fishery, and limnology can be found in Allen et al. 2006). The California Fish and Game and U.S. Forest Service have also attempted to control nonnative brook trout populations on an annual basis to promote the persistence of cutthroat trout in the Upper Truckee River and Meiss Meadows watershed. This effort of more than 10 years has promoted the recovery of native trout; however, the effect of removal of brook trout

on life history characteristics of cutthroat trout (including growth, survival, and condition) has not been evaluated on a regular basis. Limited food web and genetic information has been obtained for Stony Ridge and Gilmore Lakes.

Most amphibian species in the basin are primarily associated with standing water bodies. Pacific treefrog (*Hyla regilla*), long-toed salamander (*Ambystoma macrodactyla*), and western toad (*Bufo boreas*) are all primarily associated with standing water, although the two frogs are also found in streams. Stocking non-native fish creates large populations of predators that prey on larval amphibians. The U.S. Forest Service has conducted surveys of lakes throughout the watershed to determine the presence of fishes, amphibians, snakes, and waterbirds over the last decade. The limited distribution of most amphibian species has led to an analysis of genetic diversity by University of California, Davis, University of Nevada, Reno and U.S. Forest Service researchers¹² of three species: long-toed salamander, western toad, and mountain yellow-legged frog. These data are being analyzed to better inform restoration efforts and promote amphibian populations that have been shown to be in decline in the Sierra Nevada.

Based on research to date in and near the Lake Tahoe basin, nonnative trout are likely to be a primary factor limiting the distribution and population size of native amphibians there (Knapp and Matthews 2000, Manley and Lind 2005). Although fish stocking has been discontinued on the California side of the basin, it continues on the Nevada side. Some streams in the California side of the basin have been designated “Wild Trout Areas” and are not (officially) stocked with nonnative fishes. It is not clear to what degree this management response benefits amphibians and stream-associated reptiles. Studies in the Sierra Nevada have shown that, without intervention, decades are required for trout populations to decline once stocking has ceased (see Knapp et al. 2001). Fish stocking could potentially benefit garter snake populations, as they can prey on fry. Bullfrogs (*Lithobates catesbeianus*) are also a potential threat to amphibian populations in the basin; however, they currently have a limited distribution, primarily in the mouths of streams in the southern basin. The number of sites occupied is fairly low, but where they exist, their populations are large and affect the native fauna (Manley and Lind 2005).

Stream channel restoration is an active pursuit in the Lake Tahoe basin. Stream restoration and surveys are commonly conducted by the U.S. Forest Service as part of managing the national forest. Surveys have been conducted for most streams

¹² Manley, P., and Lind, A., research wildlife biologists, USDA Forest Service, Pacific Southwest Research Station, Sierra Nevada Research Center, Davis, CA; Shaffer, H.B., professor, University of California-Davis, Davis, CA; Peacock, M., assistant professor, University of Nevada-Reno, Reno, NV; and Vredenburg, V., research associate, University of California-Berkeley, Berkeley, CA.

in the basin over the past 10 years by the U.S. Forest Service; stream habitat types are mapped as are occurrences of fish and amphibian species. Stream restoration has been actively pursued by the U.S. Forest Service and the California Tahoe Conservancy for the past 5 years; in many cases, that work includes before and after measurements of responses of plant and animal species, including aquatic, riparian, and upland associates.¹³ The geomorphologic and water quality elements of these efforts are addressed in chapter 4, “Water Quality.”

In addition to biological threats, lakes and streams face physical degradation as well. Firefighting often involves the collection of water from lakes to deposit on the fire; associated siphoning activities can potentially directly affect amphibian populations. An evaluation of the ecological value and sensitivity of various water bodies in the basin has not been conducted; thus activities such as siphoning may occur in areas where impacts could be high (e.g., Watson Lake).

Development has been responsible for the loss and fragmentation of marshes in the southern portion of the basin, specifically the Tahoe Keys development in the Upper Truckee Marsh. Surveys are being conducted to assess how development of this marsh has affected water birds and to evaluate the potential to restore affected species. Impacts to the physical condition of lakes, ponds, and marshes also are occurring in the basin, such as shoreline compaction and pollution from human uses. Anglers and hikers appear to have the greatest impact on the shoreline and nearby upland areas around existing lakes and ponds. The most common impacts include compaction of soil and removal of vegetation around the shoreline; however, some paved and dirt roads exist extremely close to shorelines creating the potential for erosion and conveyance of polluted runoff. Research has shown that degraded shoreline conditions can have a negative effect on the presence or abundance of aquatic species that occupy a site (Manley and Lind 2006).

Knowledge Gaps

In the last decade a watershed management approach to restoration activities in the Lake Tahoe basin has dominated. Although nutrient limitations and their shifts have been studied in Lake Tahoe (Jassby et al. 1994), it is unknown how atmospheric nitrogen loading has shifted nutrient limitation in the other lakes in the basin watershed (see chapter 3, “Air Quality”). Understanding the nutrient limitation is critical if we are going to promote the persistence of native fish or amphibian species in these ecosystems. It also is important for us to understand the degree to which nonnative fish are limiting amphibian populations in small lakes, and what

¹³ Romos, S. 2008. Personal communication. Science and evaluation program manager, Tahoe Regional Planning Agency, 128 Market Street, Stateline, NV 89449.

options exist for effective reductions in these negative interactions. Understanding the movement patterns of nonnative trout, including barriers and distribution mechanisms, would greatly inform effective options for conservation and restoration of native species. We still lack information on the habitat associations and population dynamics of Pacific treefrog and the two aquatic-system-associated garter snakes. Population models and spatially explicit landscape evaluations of habitat conditions and values have not been developed for any amphibian or aquatic snake species. Management agencies are considering attempting to reintroduce the mountain yellow-legged frog into multiple locations in the basin; additional assessment and evaluation are recommended to establish an information-rich foundation for a reintroduction plan.

Uncertainties and concerns exist for native fish populations, as well. Restoration of native trout has been initiated at Fallen Leaf Lake. It is important to follow the effect of this restoration effort on all aspects of the lake's ecology and limnology. In particular, measurements are recommended to determine the lake's responses—nutrient, primary and secondary production—to the reintroduction. Overstocking of native trout in the lake, for example, could lead to trophic cascades and either increase or decrease the lake's clarity. Most appropriately, this study effort would occur throughout the life cycle of the trout or until they are extirpated from the lake. Beyond the Lahonton cutthroat trout, little information exists about the status of native fishes (e.g., sculpin or redbreast-sucker).

These issues and uncertainties suggest the following key management questions:

- Which lakes and other aquatic systems should receive priority management attention, and what actions should be undertaken to restore desired ecosystem values to each?
- What spatial and temporal strategy of restoration and management actions can be employed to maximize learning to inform future management decisions in aquatic systems with like conservation needs?
- What monitoring targets and sample techniques will best support adaptive management of Lake Tahoe's aquatic systems and their biota?

Research Needs

Following are other aquatic ecosystem research questions:

(OE1) What are the limiting factors of production for other lakes in the Tahoe basin? Do variations in limitation affect secondary production and the ability to support fish and amphibians?

(OE2) What are the ecological and limnological impacts of native fish reintroduction into Fallen Leaf Lake? What are the long-term changes to the lake owing to introductions and alterations to the lake's biota? What impediments (e.g., stream habitat, or secondary production) need to be overcome to produce a self-sustaining population of native trout in the lake?

(OE3) What was the historical progression of occupancy of lakes and streams by nonnative fishes, and how does it correspond to changes in the distribution and abundance of native aquatic fauna?

(OE4) What is the status of populations of amphibians and aquatic snakes in the basin, including habitat needs, population dynamics (e.g., metapopulation structure), prevalence of disease (particularly chytrid fungus) and distributions that are important to maintaining or restoring populations?

(OE5) What is the distribution and abundance of native fishes in lakes and streams, and what factors regulate their populations?

(OE6) What is the chemical and physical status of lentic ecosystems in the Tahoe basin (other than Lake Tahoe), including measures of nutrients and pH?

(OE7) What performance measures—including macroinvertebrates, presence and abundance of plants and animals, and other ecological metrics—can be used to assess the condition and restoration effectiveness in maintaining, restoring, and rehabilitating the biological diversity and ecological function, and in monitoring conditions of lake and stream ecosystems?

(OE8) What is the limnological and ecological status of Star Lake and how has it changed in response to human stressors?

Urbanization

The urbanization of natural landscapes is a substantial factor in the erosion of biological diversity in the United States (Hansen et al. 2005, Theobald 2005). Urbanization imposes a suite of stressors for ecological communities, including habitat loss, alteration and fragmentation, reduced soil quality, increased soil erosion, water and air pollution, introduction of nonnative species, and human disturbance, all of which have negative consequences for native species (Baxter et al. 1999, Donnelly and Marzluff 2006, Fernández-Juricic 2000, McDonnell and Pickett 1990, McKinney 2002, Miller et al. 2003, Miller and Hobbs 2000, Pouyat et al. 1994, Steinberg et al. 1997). Urbanization can lead to lower diversity (structure and composition) of native plants and animals, losses of vulnerable species, and increases in exotic and generalist species. After the resource extraction era in the Lake Tahoe basin ended

in the early 1900s, many wildland areas in the lower elevation montane zone began undergoing conversion to urban uses, with subsequent changes in the amount and quality of habitat for wildlife. However, if well managed, it is thought the basin's urbanized areas could maintain much of their native plant and animal diversity.

Knowledge Gaps

Numerous impacts of urban development on plant and animal communities have been documented in the Tahoe basin (e.g., Heckmann et al. 2008, Manley et al. 2006, Schlesinger et al. 2008). Nonetheless, many important uncertainties remain regarding the relative role of various urban-related stressors, such as habitat loss, fragmentation, or alteration, in affecting negative changes in population viability of species of concern or community integrity. The dynamic nature of native forest communities makes balancing social, ecological, and economic objectives a challenge (Folke et al. 2005). Stressors associated with urbanization act at both local and landscape scales; understanding the individual and interacting effects at multiple scales is key to managing future urban and recreational growth in a manner that conserves and maintains biological diversity and ecological integrity of native ecosystems.

Wildlife—

Land development for housing, commercial enterprises, and infrastructure decreases the amount and changes the distribution and quality of habitat for wildlife. Habitat quality for wildlife species also may be affected by forest and fire management practices in and near urban areas, which can in turn lead to structural and compositional changes in those forests (see “Fire and Fuel Management” and “Old-Growth and Landscape Management” sections in this chapter). Wildlife species most likely to be negatively affected by these changes are those that are primarily associated with lower elevation montane forests, and those that have large area requirements and small populations in the Tahoe basin, such as northern goshawk, California spotted owl, spotted skunk (*Spilogale putorius*), and bobcat (*Lynx rufus*). Passerine bird species that are associated with old-growth forests or the understory habitats of older forests also may suffer population declines.

Recent research conducted by Manley et al. (2006) has identified a number of species, species groups, and community metrics that respond to various aspects of urbanization, including development and human activity. They studied birds, small mammals, large mammals, ants, and plants. In general, birds and large mammals were most negatively affected by development, followed by individual species of small mammals and ants. Understory bird species were most sensitive

to surrounding development, as were mustelids and black bears. Coyotes showed no difference in frequency of occurrence with development, and domestic dogs were prevalent throughout all development areas. In contrast, few domestic cats were detected. Forest structure and composition did not change within undeveloped parcels in response to surrounding development, with the exception of lower snag and log densities and an increase in the richness of exotic plants with higher development. Not all relationships were linear; rather, in some cases sudden shifts in species abundance and composition were observed. But it is not known at what stage of development—earlier or later—that such responses may manifest. The study primarily identified patterns of richness and abundance, which suggest cause-effect relationships that can be confirmed and clarified through research focused on individual questions.

In general, concentration of humans in urban environments leads to increased disturbance of wildlife habitats and mortality (from traffic and recreation), increased densities of exotics and domestic species (especially pets), and, in certain circumstances, habitat enrichment (including increases in food, cover, or water resources that can confer an advantage for certain species such as black bears and coyotes). Determining the site-specific impacts from high-intensity recreation and increased numbers of exotic species in the Tahoe basin's urban forests is an outstanding information need. Pets and humans can contribute to the spread of exotic plants and diseases, with areas subjected to higher rates of human visitation at greater risk. Exotic plants pose a problem for wildlife species if they outcompete native plants that provide food or other essential resources, or if they lead to changes in habitat structure. Currently, the basin has few invasive exotic plants, so they do not pose a particularly high ecological risk to wildlife; however, effective measures to reduce the potential for future establishment of exotic plants are needed.

Habitat enrichment in the form of supplemental food and cover is varied but common in developed areas of the Lake Tahoe basin. It is likely that habitat enrichment has increased the prevalence of some bird species, coyotes, and black bears, and increased conflicts with humans (Manley et al. 2006). The effects of habitat enrichment on distributions and population sizes of these and other species are not clear. Habitat enrichment may lead to population growth in select species only in developed areas, or in the whole basin more widely, or it may simply cause shifts in animal species distributions, especially if animals abandon formerly suitable sites and move to urban areas. For example, Beckmann and Berger (2003a, 2003b) found in a study of black bears in Lake Tahoe that urban bears had smaller home ranges and spent significantly less time foraging compared to wildland bears. Urban environments offer enriched and novel sources of food (e.g., garbage bins

and coolers) and cover (e.g., cabins and decks), making urban areas desirable for foraging and denning. Enriched environments typically have a greater carrying capacity than native ecosystems, with unknown long-term consequences.

Plants—

Forest structure and composition is affected by urbanization in the Lake Tahoe basin. Manley et al. (2006) found that on undeveloped forest fragments (most of which were >1 ha), snag and downed wood densities declined and exotic plant species increased with increases in the amount of surrounding development. McBride and Jacobs (1986) found even greater changes in the urban matrix, characterized by decreased tree density and cover and increased tree species richness and age-class diversity.

Exotic plant species are an immediate problem locally in certain areas of the Lake Tahoe basin. Elsewhere most exotic plants originally were introduced for horticultural uses by nurseries, botanical gardens, and individuals (Reichard and White 2001), but it is unclear whether plants used in horticulture are an important source of invasive species in the Lake Tahoe basin. Many of the established invasive plants in the basin (Donaldson 2004) appear to be plants that have spread into disturbed areas, particularly along roadsides, and that have no obvious horticultural application.

The nutrient applications and water uses on residential and commercial landscapes can have adverse effects on local nutrient cycles, allowing nutrients in runoff and drainage to reach local water bodies (e.g., Bormann et al. 2001). Surprisingly, conventional turfgrass landscapes may retain applied nutrients better than multi-species landscapes that may have been designed for low nutrient and water inputs (Erickson et al. 2001, 2005). Regardless of landscape type, having more knowledge about the nutrient status of landscape plants allows more efficient application of fertilizer (e.g., Scharenbroch and Lloyd 2004).

Revegetation efforts on roadside edges are common projects within the Lake Tahoe basin, particularly because they are believed to decrease runoff and soil leaching. Not all revegetation projects have been successful; however, the use of locally adapted plant ecotypes may best support the steep elevation and dramatic precipitation gradients in the basin. In cases where native plant revegetation projects have been successful, there can be concerns about alteration of genetic structure of native plant communities (e.g., Gehring and Linhart 1992).

Construction projects in the basin often occur close to large trees, and precautions are always taken to retain these trees as visual and ecological amenities. Regrettably, these trees often die prematurely, possibly from damage sustained by



Urban forest lot, South Lake Tahoe, California.

roots during construction. Current practice is to protect the root zone that occurs inside the edge of the tree crown (the “critical root zone”), yet evidence from ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) excavations indicates that the maximum horizontal extent of conifer roots can be much greater than the crown edge (Berndt and Gibbons 1958, Curtis 1964, Greb and Black 1961, Hermann and Peterson 1969).

These issues and uncertainties suggest the following broad management questions:

- What aspects of urban development are most detrimental to conserving and restoring biological diversity and ecosystem integrity, and what facets of biodiversity are most vulnerable to urban stressors?
- What locations in the basin are most valuable for maintaining biological diversity, and what management approaches are most effective in minimizing the impact of urbanization?
- What risks do traditional landscaping and revegetation approaches pose to the introduction of nonnative native species to the basin, and what effective alternatives exist?

Research Needs

Following are urbanization research questions:

(UR1) What mechanisms determine observed declines in biotic diversity in the urban environments of the basin (e.g., habitat loss, habitat fragmentation, habitat alteration, disturbance, mortality from vehicles and pets)?

(UR2) Are there threshold levels of development at which sweeping changes in wildlife species abundances and ecological community composition occur?

(UR3) How does the current spatial pattern and extent of development affect connectivity of animal populations? Are there important areas (corridors, connectors) determined by the combination of fixed environmental characteristics (e.g., slope, elevation, or rock outcrops) and human development?

(UR4) Which urban forest types and sites are most impacted by recreation and exotic species (including pets)? Impacts include creating functional barriers, ecological constraints, and limitations to habitat availability. Studies are needed to determine how these impacts can be mitigated.

(UR5) Does habitat enrichment cause basinwide or local increases in geese (*Branta* spp.), coyote, and bear populations, or shifts in their distributions? Is enrichment leading to changes in the survival, reproductive success or behavior (e.g., habitat use or response to humans) in these species? Are those changes likely to put those species or humans at demonstrably greater risk or otherwise affect area- and disturbance-sensitive species?

(UR6) Are roads serving as conduits for invasive species into the Lake Tahoe basin? Are plants used in residential and commercial landscaping contributing to invasive species problems in Lake Tahoe basin wildlands?

(UR7) Which plant species, plant ecotypes, and planting techniques are best for enabling successful establishment of native species in disturbed roadside areas? What plants and planting techniques should be employed at the greater basin scale (e.g., by elevation and longitude), and at local scales (e.g., road shoulder versus exposed steep slope)?

(UR8) Would increased use of water-efficient plants for residential and commercial landscaping result in lower demands on water supplies within the basin, and less runoff? Would use of nutrient-efficient plant genotypes for home and commercial landscaping result in lower fertilizer application rates?

(UR9) What is the effectiveness of various conservation measures to maintain large trees in developed areas? What is the relationship between stem DBH and maximum horizontal extent of rooting for large trees (e.g., Jeffrey pine, sugar pine [*Pinus lambertiana* Douglas], incense cedar [*Calocedrus decurrens* Torr. Florin], red fir, and white fir) retained in developed areas of the Lake Tahoe basin? How should the critical root zone be designated for each species to preserve most surface roots, while acknowledging the realities of construction operations?

(UR10) What is an effective set of indicators—including plant, animal, and other ecological community metrics—that can be used to assess the effects and effectiveness of forest management efforts, and to monitor biological diversity in and adjacent to urbanized areas? How should urban parcels be prioritized for interventions to improve ecological function?

(UR11) What is the relative importance of potentially competing uses (e.g., reducing fire risks, or maintaining biological diversity) of urban lots in the urban-wildland interface? What are the tradeoffs among competing uses, both short and long term, including maintaining and restoring biological diversity?

Recreation

Outdoor recreation is a primary activity for residents and visitors of the Lake Tahoe basin. Many forms of recreation are available in the basin. In the summer, backcountry hiking, biking, mountain climbing, horseback riding, and fishing are popular. Activities on Lake Tahoe are numerous, including swimming, kayaking, sailing, speed boating, fishing, and jet skiing. Outdoor recreation is just as popular during the winter, including downhill and backcountry skiing, snowshoeing, and snowmobiling.

Knowledge Gaps

Residents and visitors who hike or bike can disturb the activities of many vertebrate species, particularly species at higher trophic levels, such as northern goshawk, California spotted owl, American marten, and bobcat. Hiking and biking pose slightly different challenges and stresses to wildlife species—hikers have a longer residence time, thus having a greater impact on species sensitive to human presence, whereas bikes move quickly, posing a risk of physical impact, and some trails have a steady stream of users potentially posing barriers to wildlife movement. Dogs are common hiking companions in the Tahoe basin; they chase and sometimes kill wildlife species, particularly lower trophic-level species, such as mice, chipmunks, squirrels, and ground-dwelling birds.



Peter Goin

Ski slope in autumn, Mount Rose ski resort, Nevada.

Off-highway vehicle use in the Lake Tahoe basin during the summer and winter is restricted to relatively circumscribed areas; however, in the winter, snowmobile use can be widely dispersed in undesignated areas (e.g., the McKinney-Rubicon trail). Snowmobile use can affect resident wildlife species at times of their highest physical stress. The U.S. Forest Service recently completed route mapping for OHVs, and it is still evaluating designations. A study of the effects of summer and winter OHV use on American marten was conducted in the McKinney-Rubicon area, as well as at a southern study area on the Sequoia National Forest (Zielinski and Slauson 2008). Another study still underway is looking at community-wide responses of wildlife to summer OHV use, including study sites throughout the basin.¹⁴

Downhill ski areas have several potential adverse effects on wildlife: (1) forest losses and fragmentation (only shrub and grass layers remain on ski slopes), which affect late-seral associated species, such as American marten, northern goshawk, California spotted owl, and spotted skunk; (2) high human disturbance during daytime on ski slopes may create barriers to habitat use and between-habitat patch movement for diurnal species; (3) changes in forest cover and human disturbance may create “sink” habitat for American marten; (4) night lighting and grooming on

¹⁴ Manley, P.; Campbell, L. 2008. Personal communication. Research wildlife biologists. USDA Forest Service, Pacific Southwest Research Station, 1731 Research Park Dr., Davis, CA 95618.

ski slopes may interfere with the behavior of nocturnal species; and (5) losses of snags in forested areas between ski runs owing to hazard tree removal can locally reduce wildlife habitat quality. In the Lake Tahoe basin, it is important to know the extent to which existing or potential ski resort expansions may affect the persistence of basin wildlife populations.

The spatial extent of intensive cross-country skiing is limited, thus it does not appear to pose a major risk to wildlife. It is likely that although usage can be substantial locally, sufficient management structures are in place (including snow grooming, and bridges across streams), and monitoring to determine wildlife use in cross-country ski areas is probably the appropriate data-gathering investment at this time.

These issues and uncertainties suggest the following management questions:

- What recreational activities are the most detrimental to wildlife resources, and are there land management actions that can reduce impacts while accommodating those activities?
- What are appropriate measures of recreational impacts on wildlife, and how might those measures be integrated into monitoring programs?

Research Needs

Following are recreation research questions:

(RE1) What are the characteristics of key locations inhabited by animal species of concern that are sensitive to summer or winter recreation activities? Where do these key locations occur, for purposes of recreation planning and study design?

(RE2) What combination of summer recreation activities (motorized and nonmotorized; amount, timing, and location) and environmental factors present a risk of site abandonment by sensitive wildlife species?

(RE3) What are the combined effects of snowmobile use (amount, timing, and location) in association with particular environmental factors that present a risk of site abandonment by resident wildlife species?

(RE4) To what degree are dogs impacting wildlife populations and communities?

(RE5) Are the locations of OHV routes (summer and winter) likely to pose biologically significant barriers to one or more species with large area requirements?

(RE6) Are existing ski areas predominantly occupied by male martens, and if so, does the extent of this population response pose a threat to the persistence of this species in the Tahoe basin?

(RE7) To what degree may existing and potential expansions of ski areas fragment the landscape mosaic for species that have large home ranges and are dependent on closed-canopy forest conditions for nesting, foraging, and movement?

(RE8) What tools can be developed to assess how best to manage recreation and habitats to reduce people-wildlife conflicts?

(RE9) What tools are most effective and efficient in measuring recreation use of various types in a manner that informs interpretations of effects on biological diversity and ecosystem function?

Climate Change

Conservation planners and managers have acknowledged the reality of climate change and incorporate expected changes into their land and resource planning efforts (McCarty 2001). Despite uncertainty in many aspects of climate predictions, there is widespread agreement that in California and Nevada, mean summer temperatures will increase, there will be more extreme heat events, residual summer snowpacks will decrease, and consequently the ranges of organisms that are restricted to higher elevations will shrink (Hayhoe et al. 2004, Kim et al. 2002). Disturbance regimes that are climate dependent also will be subject to changes. Fires in the Lake Tahoe basin are expected to be more frequent and intense under higher average temperature regimes (Taylor and Beaty 2005, Westerling et al. 2006). Organisms will respond to these changes in species-specific ways, creating communities that may have no modern analogue (Ibáñez et al. 2006, Millar et al. 2006).

Knowledge Gaps

The span of elevations in a relatively small geographic area makes the Lake Tahoe basin particularly vulnerable to change in species distribution and abundance because of the limited amount of suitable habitat for many species. It also makes the basin a valuable test case for how plants and animals may respond to climate change. The first challenge is to obtain precise and accurate measurements of climatic conditions through meteorological monitoring stations. Currently, three weather-monitoring stations are located in the basin, and a Global Observation Research Initiatives in Alpine Environments (GLORIA) monitoring site was established on Freel Peak in 2006 (see <http://www.gloria.ac.at/> for more information).

The proper targets or desired conditions for ecosystem management are not obvious given the complex realities of organism responses to climate change (Harris et al. 2006). Research for such a contextual stressor as climate change

can be approached in multiple ways. One approach to answering questions regarding species responses to climate change is to build statistical models of species occurrences (as climate and soil envelopes) by relating present-day distributional ranges to climate and soil variables. The models are then applied to climate scenarios that have been generated by global circulation models or regional climate models (e.g., Ibáñez et al. 2006, Kueppers et al. 2005, Sala et al. 2001). An alternative approach, most suitable for intensive work on individual species, is to build process-based, mechanistic models of species responses to the environment, and to apply these models to climate scenarios. That approach may be particularly advantageous when multiple environmental values are being considered (e.g., carbon sequestration by trees) or there are strong feedback effects.

These issues and uncertainties suggest the following broad management questions:

1. What are the anticipated responses of wildlife, fish, and vegetation communities in the Lake Tahoe basin owing to climate change? What are the appropriate responses of land and resource managers to changes in these natural communities?
2. How can ongoing monitoring programs and research efforts be adjusted to provide the information necessary to allow managers and decisionmakers to integrate climate change into management planning and implementation?

Research Needs

Following are other climate change research questions:

(CL1) How is climate changing in and around the Lake Tahoe basin? (Note: this basic information, coupled with question 2 above, can also be used to support research projects proposed in the “Water Quality” and “Soil Conservation” chapters)

(CL2) How is climate change predicted to change the elevational boundaries between ecosystem types (e.g., montane and subalpine forest, and subalpine and alpine zones) in the Lake Tahoe basin over the next 10 to 100 years?

(CL3) How is climate change predicted to change the ranges and populations of plant and animal species of concern over the next 10 to 100 years?

(CL4) What are an effective set of indicators of the physical and biological changes that may occur as a result of climate change?

(CL5) How might management practices be altered in response to the projected environmental effects of climate change?

Summary of Near-Term Research Priorities

The research needs identified under the ecology and biodiversity theme represent a coherent set of information that is needed to reduce uncertainties and improve the probability of achieving desired conditions for living resources and their habitats in the next 5 to 10 years. The near-term value of some information is greater in some cases than in others. In many cases, steps toward building a knowledge base are most efficient when pursued in a particular sequence. In other cases, individual pieces of information are highly valuable in their own standing in that they can positively contribute to meeting management objectives as soon as they become available. Research needs that match one or both of these situations are considered near-term research priorities, and given equivalent opportunities for funding, they are recommended for funding and implementation first. Near-term research needs and priorities are synthesized below.

Subtheme 1: Old-growth and landscape management—

The ultimate objective of forest management is to restore and maintain forest health and resilience such that forests maintain and restore their full range of functions and native biological diversity, and thereby retain their resilience and associated ecosystem services upon which human communities in the basin depend. The primary uncertainty limiting management's ability to meet this objective is a clear understanding of desired environmental conditions, and when and where to create them. Specific questions pertain to the historical amount and distribution of forest structural conditions, associated plant and animal species composition, and how to translate historical conditions into target conditions for the future that will enable forested ecosystems to adapt to future environmental stressors without the loss of function or biological diversity. Old forests are of particular concern and interest, because, despite the maturity of existing forests, it is apparent that extant forests have lost some ecological complexity associated with old forests, and therefore species and functions restricted to old forests are rare and most at risk from uninformed management. Finally, development of robust measures of forest biological diversity and resilience are recommended to enable simple and effective tracking of management progress and success.

Subtheme 2: Fire and fuels management—

One of the greatest ecological risks associated with fire is the uncertainty associated with the effects of fuel reduction treatments—both their effectiveness in changing fire behavior, and the unintended consequences of treatment effects on other ecological conditions, such as biological diversity and forest ecosystem resilience. The near-term research needs pertain to addressing risks and uncertainties

posed by current management activities, which target fuel reduction treatments on tens of thousands of acres without a specific understanding of the ecological consequences. Therefore, near-term research needs include improving the understanding of the effects of various types and intensities of treatments on the spectrum of ecosystem management objectives, including but not restricted to fire behavior. Of primary concern is the fate of terrestrial species and processes, because they are directly affected by forest conditions. It would be most efficient to develop and test silvicultural prescriptions in the course of addressing near-term research priorities, as opposed to after ecological risks are more clearly understood. Once the primary ecological objectives at risk related to actions of reducing the threat of catastrophic wildfire are understood, it is important to develop simple and informative measures of their status for long-term monitoring.

Subtheme 3: Special communities management—

The conservation and restoration of special communities in the basin are best served by similar sets of information: (1) maps of current location and condition throughout the basin, (2) reference conditions based on historical data and other relevant data sources, (3) evaluation of the effectiveness of restoration approaches, and (4) the development of performance measures to assess status and restoration effects. A few unique information needs are associated with individual special communities. In aspen communities, techniques for converting conifer-encroached stands back to aspen-dominated habitats is a primary information need. Fens and meadows are under an unknown level of threat from various human activities. Information on the current status of marshes is lacking. Finally, detailed information on genetic and environmental sensitivities of Tahoe yellow cress are needed to aid population restoration efforts of this endemic species.

Subtheme 4: Aquatic ecosystem restoration—

The emphasis of aquatic ecosystem research is on conservation and restoration of vertebrate biota in Lake Tahoe and the conservation of species in the rich array of other aquatic ecosystems around the basin. In Lake Tahoe, the uncertainties with the greatest potential impact on management are those associated with the interactions between nonnative and native plant and animal species. These interactions have potential consequences for biodiversity, lake clarity, and near-shore aesthetics. Research on measures to control established nonnative species is urgently needed, and is best pursued through an adaptive management approach using information from careful assessment of pilot projects to guide longer term management strategies. Restoration of native fishes in Lake Tahoe presents a steep challenge, and

information on the ecological interactions is key to making progress. The other aquatic ecosystems are in need of more basic information: (1) the status of vertebrate populations and communities, and (2) factors limiting the ability of sites to support native species. Once these kinds of information are developed and better understood, it would then be appropriate to develop efficient measures that can be used to track conditions over time.

Subtheme 5: Urbanization—

Research recently conducted in the Lake Tahoe basin identified substantial and unexpected effects of urban development and human activities on various elements of biological diversity (Manley et al. 2006). The patterns observed differed by taxonomic group (i.e., birds, small mammals, mammalian carnivores, ants, and plants), among species (some were sensitive, whereas others were not), and by type of human disturbance (e.g., habitat loss, habitat alteration, habitat enrichment, or different types of human activities). The results of that work suggest the need to understand mechanisms of key responses such that development and management can be conducted in a manner that minimizes and mitigates negative effects on biological diversity. Questions of particular priority pertain to better understanding thresholds of change in habitat loss, habitat alteration, or habitat use indicated by past research, specifically changes observed at 30 to 40 percent development. Above this threshold, it is unclear what happens, but sites likely become sinks, traps, or abandoned by a wide array of species. In addition to site-scale mechanisms, landscape-wide modeling is needed to understand the implications of existing results and facilitate the rapid evaluation of the implications of new information on landscape design and management priorities. Finally, as in other subthemes, the development and testing of effective measures for use in monitoring and assessment are recommended, as vulnerable species and target ecological objectives in more urban areas are clarified.

Subtheme 6: Recreation—

Recreational uses have been identified to have substantial effects on the occupancy and abundance of many and diverse species, based on multiple research projects. Alternatively, species thought to be impacted by certain recreational activities (e.g., effects of OHV use on occurrence of American marten) did not exhibit negative responses. Specific uncertainties in the Tahoe basin pertain to the effects of dogs on retaining biological diversity in more urban environments, and the effects of ski areas on montane obligates, namely American marten. Although population sizes of northern goshawk and bald eagle are limited, their sensitivity to the presence

of people has important implications for the management of events and ongoing recreational uses in the vicinity of known use sites. Effective measures of use and effects are lacking and their development will be important for monitoring.

Subtheme 7: Climate change—

Climate change is perhaps the ultimate source of uncertainty, and arguably poses a high environmental and economic risk. Under such circumstances, information needs start at the basics. In the case of ecological elements and processes, this translates to applying existing and new information to modeling potential responses—plant and animal ranges and associated effects on population sizes, species interactions, and ecological services—to predicted or potential climate change and associated broad-scale environmental responses. It is important for modeling to be conducted in the basin, as opposed to relying on modeling outside the basin or at larger scales because detailed information will be needed to inform management agencies about how they can respond to potential threats. As with all other subtheme areas, as information is accrued, the development of effective and reliable measures of key population and community metrics for monitoring is recommended.

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References

- Abrahamsson, S.; Goldman, C.R. 1970.** Distribution, density, and production of the crayfish *Pacifastacus dana* in Lake Tahoe (California-Nevada). *Oikos*. 21: 83–91.
- Agee, J.K.; Skinner, C.N. 2005.** Basic principles of forest fuel reduction treatments. *Forest Ecology and Management*. 211: 83–96.
- Allen, B.C.; Chandra, S.; Vander Zanden, M.J.; Reuter, J.E. 2006.** Evaluation of the re-introduction of native Lahontan cutthroat trout, *Onchorhynchus clarki henshawi*. In: Fallen Leaf Lake, California, and development of management strategies for recovery. 57 p. Unpublished report. On file with: U.S. Fish and Wildlife Service, 1340 Financial Blvd, Reno, NV 89502.
- Allen-Diaz, B.H. 1991.** Water table and plant species relationships in Sierra Nevada meadows. *American Midland Naturalist*. 126: 30–43.
- Atekwana, E.A.; Richardson, D.S. 2004.** Geochemical and isotopic evidence of a groundwater source in the Corral Canyon meadow complex, central Nevada, USA. *Hydrological Processes*. 18: 2801–2815.
- Barbour, M.; Kelley, E.; Maloney, P.; Rizzo, D.; Royce, E.; Fites-Kaufmann, J. 2002.** Present and past old-growth forests of the Lake Tahoe basin, Sierra Nevada. *U.S. Journal of Vegetation Science*. 13: 461–472.
- Bartolome, J.B.; Erman, D.C.; Schwarz, C.F. 1990.** Stability and change in Sierran minerotrophic peatlands. Res. Pap. PSW-198. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Station. 11 p.
- Baxter, J.; Pickett, S.; Carreiro, M.; Dighton, J. 1999.** Ectomycorrhizal diversity and community structure in oak forest stands exposed to contrasting anthropogenic impacts. *Canadian Journal of Botany*. 77: 771–782.
- Beckmann, J.P.; Berger, J. 2003a.** Rapid ecological and behavioural changes in carnivores: the responses of black bears (*Ursus americanus*) to altered food. *Journal of the Zoological Society of London*. 261: 207–212.
- Beckmann, J.P.; Berger, J. 2003b.** Using black bears to test ideal-free distribution models experimentally. *Journal of Mammalogy*. 84: 594–603.
- Beier, P. 1989.** Use of habitat by mountain beaver in the Sierra Nevada, California. *Journal of Wildlife Management*. 53: 649–654.

- Berndt, H.W.; Gibbons, R.D. 1958.** Root distribution of some native trees and understory plants growing on three sites within ponderosa pine watersheds in Colorado. Res. Pap. RM-37. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.
- Bormann, F.H.; Balmori, D.; Geballe, G.T. 2001.** Redesigning the American lawn: a search for environmental harmony. 2nd ed. New Haven, CT: Yale University Press. 192 p.
- Busse, M.D.; Hubbert, K.R.; Fiddler, G.O.; Shestak, C.J.; Powers, R.F. 2005.** Lethal temperatures during burning of masticated forest residues. *International Journal of Wildland Fire*. 14: 267–276.
- Castelli, R.M.; Chambers, J.C.; Tausch, R.J. 2000.** Soil-plant relations along a soil-water gradient in Great Basin riparian meadows. *Wetlands*. 20(2): 251–266.
- Chandra, S.; Allen, B.C. 2001.** Crayfish density data collected from around Lake Tahoe and scaled to provide population estimates. Unpublished data. On file with: S. Chandra, Department of Natural Resources and Environmental Science, University of Nevada, Reno, NV 89512.
- Chandra, S. 2003.** The impact of nonnative species and cultural eutrophication on the Lake Tahoe food web over time. Davis, CA: University of California, Davis. 91 p. Ph.D. dissertation.
- Chandra, S.; Rost, A. 2008.** Nutrients and clarity of subalpine lakes in the upper Lake Tahoe watershed during early summer. Presented at: 4th biennial Tahoe basin science conference: Science as a tool in Lake Tahoe basin management: making sense of complexity. Lake Incline, NV. <http://www.nvwra.org/docs/2008/Tahoe%20Presentations/Chandra%20Nutrient%20limitation%20in%20other%20lakes.pdf>. (November 9, 2009).
- Chandra, S.; Ngai, K.L.C.; Kamerath, M.; Allen, B.C. 2009.** The warmwater fishes of Lake Tahoe. 107 p. Unpublished report. On file with: Nevada State Lands, 901 S Stewart Street, Suite 5003, Carson City, NV 89701.
- Chandra, S.; Vander Zanden, M.J.; Heyvaert, A.C.; Richards, B.C.; Allen, B.C.; Goldman, C.R. 2005.** The effects of cultural eutrophication on pelagic-benthic coupling in Lake Tahoe. *Limnology and Oceanography*. 50: 1388–1376.
- Chandra, S.; Caires, A. 2001.** Benthic invertebrate density and biomass data collected from around Lake Tahoe during the 1960s and 2008–09. Unpublished data. On file with: S. Chandra, Department of Natural Resources and Environmental Science, University of Nevada, Reno, NV 89512.

- Chong, G.W.; Simonson, S.E.; Stohlgren, T.J.; Kalkhan, M.A. 2001.** Biodiversity: aspen stands have the lead, but will nonnative species take over? In: Shepperd, W.D.; Binkley, D.; Bartos, D.L.; Stohlgren, T.J.; Eskew, L.G., eds. Sustaining aspen in western landscapes, symposium proceedings. RMRS-P-18. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 261–271.
- Cobourn, J. 2006.** How riparian ecosystems are protected at Lake Tahoe. *Journal of the American Water Resources Association*. 42: 35–43.
- Coffin, P.D.; Cowan, W.F. 1995.** Recovery plan for Lahontan cutthroat trout, Portland, OR: U.S. Department of the Interior, Fish and Wildlife Service, Region 1. 157 p.
- Coggins, S.T.; Conover, M.R. 2005.** Effect of pocket gophers on aspen regeneration. *Journal of Wildlife Management*. 69: 752–759.
- Cordone, A.J.; Frantz, T.C. 1966.** The Lake Tahoe sport fishery. *California Fish and Game*. 52: 240–274.
- Crooks, K.R.; Soulé, M.E. 1999.** Mesopredator release and avifaunal extinctions in a fragmented system. *Nature*. 400: 563–566.
- Curtis, J.D. 1964.** Roots of a ponderosa pine. Res. Pap. INT-9. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 10 p.
- DeByle, N.V. 1985.** Wildlife. In: DeByle, N.V.; Winkour, R.P., eds. Aspen: ecology and management in the Western United States. Gen. Tech. Rep. RM-GTR-19. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Experiment Station: 135–152
- Donaldson, S. 2004.** Invasive weeds of the Lake Tahoe basin. Reno, NV: University of Nevada Cooperative Extension, University of Nevada. 55 p.
- Donnelly, R.E.; Marzluff, J.M. 2006.** Relative importance of habitat quantity, structure, and spatial pattern to birds in urbanizing environments. *Urban Ecosystems*. 9: 99–117.
- Dull, R.A. 1999.** Palynological evidence for 19th century grazing-induced vegetation change in the southern Sierra Nevada, California, U.S.A. *Journal of Biogeography*. 26(4): 899–912.

- Elliot-Fisk, D.L.; Cahill, T.C.; Davis, O.K.; Duan, L.; Goldman, C.R.; Gruell, G.E.; Harris, R.; Kattleman, R.; Lacey, R.; Leisz, D.; Lindstrom, S.; Machida, D.; Rowntree, R.A.; Rucks, P.; Sharkey, D.A.; Stephens, S.L.; Ziegler, D.S. 1997.** Lake Tahoe case study. In: Erman, D.C., ed. Sierra Nevada Ecosystem Project; final report to Congress. Addendum. Wildland Resources Center Report No. 40, Davis, CA: University of California: 217–276. Vol. 13.
- Erickson, J.E.; Cisar, J.L.; Snyder, G.H.; Volin, J.C. 2005.** Phosphorus and potassium leaching under contrasting residential landscape models established on a sandy soil. *Crop Science*. 45: 546–552.
- Erickson, J.E.; Cisar, J.L.; Volin, J.C.; Snyder, G.H. 2001.** Comparing nitrogen runoff and leaching between newly established St. Augustine grass turf and an alternative residential landscape. *Crop Science*. 41: 1889–1895.
- Fernández-Juricic, E. 2000.** Local and regional effects of pedestrians on forest birds in a fragmented landscape. *Condor*. 102: 247–255.
- Finch, D.M.; Reynolds, R.T. 1988.** Bird response to understory variation and conifer succession in aspen forests. In: Emerick, J.; Foster, S.Q.; Hayden-Wing, L.; Hodgson, J.; Monarch, J.W.; Smith, A.; Thorne, O.; Todd, J., eds. *Proceedings III: issues and technology in the management of impacted wildlife*. Boulder, CO: Thorne Ecological Institute: 87–95.
- Flack, J.A.D. 1976.** Bird populations of aspen forest in western North America. *Ornithological Monographs*. 19: 1–97.
- Flint, R.W. 1975.** The natural history, ecology, and production of the crayfish *Pacifastacus* in a subalpine lacustrine environment. Davis, CA: University of California, Davis. 150 p. Ph.D. dissertation.
- Folke, C.; Hahn, T.; Olsson, P.; Norberg, J. 2005.** Adaptive governance of social-ecological systems. *Annual Review of Environment and Resources*. 30: 441–473.
- Frantz, T.C.; Cordone, A.J. 1996.** Observations on the macrobenthos of Lake Tahoe, California-Nevada. *California Fish and Game*. 82(1): 1–41.
- Gehring, J.L.; Linhart, Y.B. 1992.** Population structure and genetic differentiation in native and introduced populations of *Deschampsia caespitosa*. *American Journal of Botany*. 79: 1337–1343.
- Gifford, F.G.; Humphries, W.; Jaynes, R.A. 1984.** A preliminary quantification of the impacts of aspen to conifer succession on water yield-II. Modeling results. *Water Resources Bulletin*. 20: 181–186.

- Greb, B.W.; Black, A.W. 1961.** Effects of windbreak plantings of adjacent crops. *Journal of Soil and Water Conservation*. 16: 223–227.
- Hackley, S.; Allen, B.C.; Schladow, G.; Reuter, J.E.; Chandra, S.; Wittmann, M. 2008.** Notes on visual observations of clams in Lake Tahoe and on the beaches along the southeast shore—Zephyr Cove to Timber Cove Marina: April 25, 2008. Davis, CA: Tahoe Environmental Research Center, University of California, Davis.
- Hansen, A.J.; Knight, R.L.; Marzluff, J.M.; Powell, S.; Brown, K.; Gude, P.H.; Jones, K. 2005.** Effects of exurban development on biodiversity: patterns, mechanisms, and research needs. *Ecological Applications*. 15: 1893–1905.
- Haugo, R.D.; Halpern, C.B. 2007.** Vegetation responses to conifer encroachment in a western Cascade meadow: a chronosequence approach. *Canadian Journal of Botany*. 3: 285–298.
- Harris, J.A.; Hobbs, R.J.; Higgs, E.; Aronson, J. 2006.** Ecological restoration and global climate change. *Restoration Ecology*. 14(2): 70.
- Hatchet, B.; Hogan, M.P.; Grismer, M.E. 2006.** Mechanical mastication thins Lake Tahoe forest with few adverse impacts. *California Agriculture*. 60: 77–82.
- Hayhoe, K.; Cayan, D.; Field, C.B.; Frumhoff, P.C.; Maurer, E.P.; Miller, N.L.; Moser, S.C.; Schneider, S.H.; Cahill, K.N.; Cleland, E.E.; Dale, L.; Drapek, R.; Hanemann, R.M.; Kalkstein, L.S.; Lenihan, J.; Lunch, C.K.; Neilson, R.P.; Sheridan, S.C.; Verville, J.H. 2004.** Emissions pathways, climate change, and impacts on California. *Proceedings of the National Academy of Sciences*. 101: 12422–12427.
- Heath, S.K.; Ballard, G. 2003.** Bird species composition, phenology, nesting substrate, and productivity for the Owens Valley alluvial fan, eastern Sierra Nevada, California, 1998–2002. *Great Basin Birds*. 6: 18–35.
- Heckmann, K.E.; Manley, P.N.; Schlesinger, M.D. 2008.** Ecological integrity of remnant montane forests along an urban gradient in the Sierra Nevada. *Forest Ecology and Management*. 255: 2453–2466.
- Hermann, R.K.; Peterson, R.G. 1969.** Root development and height increment of ponderosa pines in pumice soils of central Oregon. *Forest Science*. 15: 226–237.
- Ibáñez, I.; Clark, J.S.; Dietze, M.C.; Feeley, K.; Hersh, M.; LaDeal, S.; McBride, A.; Welch, N.E.; Wolosin, M.S. 2006.** Predicting biodiversity change: outside the climate envelope, beyond the species-area curve. *Ecology*. 87: 1896–1906.

- Jassby, S.D.; Reuter, J.E.; Axler, R.P.; Goldman, C.R.; Hackley, S.H. 1994.** Atmospheric deposition of nitrogen and phosphorus in the annual nutrient load of Lake Tahoe (California-Nevada). *Water Resources Research*. 30: 2207–2216.
- Jones, B.E.; Rickman, T.H.; Vazquez, A.; Sado, Y.; Tate, K.W. 2005.** Removal of encroaching conifers to regenerate degraded aspen stands in the Sierra Nevada. *Restoration Ecology*. 13(2): 373–379.
- Juday, C. 1906.** Notes on Lake Tahoe, its trout and trout fishing. *Bulletin of the United States Bureau of Fishes*. 26: 133–146.
- Kamerath, M.; Chandra, S.; Allen, B.C. 2008.** Distribution and impact of warmwater fishes in Lake Tahoe. *Aquatic Invasions*. (3)1: 35–41.
- Kamerath, M. 2009.** Predicting establishment and impact of warmwater non-native fishes in a large, sub-alpine, oligotrophic lake. Reno, NV: University of Nevada, Reno. 90 p. M.S. thesis.
- Kattelman, R. 1996.** Impacts of floods and avalanches. In: Erman, D., ed. *Sierra Nevada Ecosystem Project: final report to congress, Status of the Sierra Nevada, Vol. II. Assessments and scientific basis for management options*. Davis, CA: Center for Water and Wildlands Resources, University of California, Davis: 1263–1269.
- Keeley, J.E.; Lubin, D.; Fotheringham, C.J. 2003.** Fire and grazing impacts on plant diversity and alien plant invasions in the southern Sierra Nevada. *Ecological Applications*. 13: 1355–1374.
- Kerns, B.K.; Thies, W.G.; Niwa, C.G. 2006.** Season and severity of prescribed burn in ponderosa pine forests: implications for understory native and exotic plants. *Ecoscience*. 13: 44–55.
- Kim, J.; Kim, T.K.; Arrit, R.W.; Miller, N.L. 2002.** Impacts of increased atmospheric CO₂ on the hydroclimate of the Western United States. *Journal of Climate*. 15: 1926–1942.
- Kim, J.; Rejmankova, E. 2001.** The paleoecological record of human disturbance in wetlands of the Lake Tahoe basin. *Journal of Paleolimnology*. 25: 437–454.
- Kluse, J.S.; Allen-Diaz, B.H. 2005.** Importance of soil moisture and its interaction with competition and clipping for two montane meadow grasses. *Plant Ecology*. 1: 87–99.

- Knapp, E.E.; Keeley, J.E.; Ballenger, E.A.; Brennan, T.J. 2005.** Fuel reduction and coarse woody debris dynamics with early season and late season prescribed fires in a Sierra Nevada mixed conifer forest. *Forest Ecology and Management*. 208: 383–397.
- Knapp, R.A.; Matthews, K.R. 2000.** Effects of nonnative fishes on wilderness lake ecosystems in the Sierra Nevada and recommendations for reducing impacts. In: *Proceedings RMRS-P-15-Vol. 5: Wilderness science in a time of change*. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 312–317.
- Knapp, R.A.; Matthews, K.R.; Sarnelle, O. 2001.** Resistance and resilience of alpine lake fauna to fish introductions. *Ecological Monographs*. 71: 401–421.
- Kueppers, L.M.; Snyder, M.A.; Sloan, L.C.; Zavaleta, E.S.; Fulfrost, B. 2005.** Modeled regional climate change and California endemic oak ranges. *Proceedings of the National Academy of Sciences*. 102: 16281–16286.
- Lang, N.L.; Halpern, C.B. 2007.** The soil seed bank of a montane meadow: consequences of conifer encroachment and implications for restoration. *Canadian Journal of Botany*. 85: 557–569.
- Lasenby, D.C.; Lanford, R. 1973.** Feeding and assimilation of *Mysis relicta*. *Limnology and Oceanography*. 18: 280–285.
- Lasenby, D.C.; Vanduyn, J. 1992.** Zinc and cadmium accumulation by the opossum shrimp *Mysis relicta*. *Archives of Environmental Contamination and Toxicology*. 23: 179–183.
- Lester, D.C.; McIntosh, L. 1994.** Accumulation of polychlorinated biphenyl congeners from Lake Champlain sediments by *Mysis relicta*. *Environmental Toxicology and Chemistry*. 13: 1825–1841.
- Lico, M.S. 2004.** Gasoline-related organics in Lake Tahoe before and after prohibition of carbureted two-stroke engines. *Lake and Reservoir Management*. 20: 164–174.
- Loft, E.R.; Menke, J.W.; Kie, J.G. 1991.** Habitat shifts by mule deer: the influence of cattle grazing. *Journal of Wildlife Management*. 55: 16–26.
- Manley, P.N. 2005.** The future of biodiversity in the Sierra Nevada through the Lake Tahoe basin looking glass. In: Murphy, D.D.; Stine, P.A., eds. *Proceedings of the Sierra Nevada science symposium: science for management and conservation*. Gen. Tech. Rep. PSW-GTR-193. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 207–217.

- Manley, P.N.; Fites-Kaufman, J.A.; Barbour, M.G.; Schlesinger, M.D.; Rizzo, D.M. 2000.** Chapter 5: Biological integrity. In: Murphy, D.D.; Knopp, C.M., eds. Lake Tahoe basin watershed assessment: Vol. I. Gen. Tech. Rep. PSW-GTR-175. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 403–600.
- Manley, P.N.; Lind, A.J. 2005.** Status and trends of amphibian and reptile populations and associated lentic habitat conditions in the Lake Tahoe basin. 42 p. Unpublished report. On file with: U.S. Department of Agriculture, Forest Service, Lake Tahoe Basin Management Unit, South Lake Tahoe, CA 96150.
- Manley, P.N.; Lind, A.J. 2006.** Multi-scale environmental relationships of the long-toed salamander (*Ambystoma macrodactylum*) in the Lake Tahoe basin. 30 p. Unpublished report. On file with: U.S. Department of Agriculture, Forest Service, Lake Tahoe Basin Management Unit, South Lake Tahoe, CA 96150.
- Manley, P.N.; Murphy, D.D.; Campbell, L.A.; Heckmann, K.E.; Merideth, S.; Parks, S.A.; Sanford, M.P.; Schlesinger, M.D. 2006.** Biotic diversity interfaces with urbanization in the Lake Tahoe basin. *California Agriculture*. 60(2): 59–64.
- Martin, D.; Chambers, J. 2004.** Restoration of riparian meadows degraded by livestock grazing above- and belowground responses. *Plant Ecology*. 163: 77–91.
- McBride, J.R.; Jacobs, D.F. 1986.** Presettlement forest structure as a factor in urban forest development. *Urban Ecology*. 9: 245–266.
- McCarty, J.P. 2001.** Ecological consequences of recent climate change. *Conservation Biology*. 15(2): 320–331.
- McDonnell, M.; Pickett, S. 1990.** Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology. *Ecology*. 71: 1232–1237.
- McKelvey, K.S.; Skinner, C.N.; Chang, C.R.; Erman, D.C.; Husari, S.J.; Parsons, D.J.; van Wagtenonk, J.W.; Weatherspoon, C.P. 1996.** An overview of fire in the Sierra Nevada. In: Erman, D., ed. *Sierra Nevada Ecosystem Project: final report to Congress, Status of the Sierra Nevada, Vol. II. Assessments and scientific basis for management options*. Davis, CA: Center for Water and Wildland Resources, University of California: 1033–1040.
- McKinney, M.L. 2002.** Urbanization, biodiversity, and conservation. *BioScience*. 52: 883–890.
- Merriam, K.E.; Keeley, J.E.; Beyers, J.L. 2006.** The role of pre-fire fuel manipulations in the invasion of nonnative plants. *Ecological Applications*. 16: 515–527.

- Millar, C.I.; King, J.C.; Westfall, R.D.; Alden, H.A.; Delany, D.L. 2006.** Late Holocene forest dynamics, volcanism, and climate change at Whitewing Mountain and San Joaquin Ridge, Mono County, Sierra Nevada, CA, USA. *Quaternary Research*. 66: 273–287.
- Miller, R.G. 1951.** The natural history of Lake Tahoe fishes. Palo Alto, CA: Stanford University. 160 p. Ph.D. dissertation.
- Miller, J.R.; Hobbs, N.T. 2000.** Recreational trails, human activity, and nest predation in lowland riparian areas. *Landscape and Urban Planning*. 50: 227–236.
- Miller, J.R.; Wiens, J.A.; Hobbs, N.T.; Theobald, D.M. 2003.** Effects of human settlement on bird communities in lowland riparian areas of Colorado (USA). *Ecological Applications*. 13: 1041–1059.
- Moyle, P.B. 2002.** Inland fishes of California. 2nd ed. Berkeley, CA: University of California Press. 502 p.
- Nagel, T.A.; Taylor, A.H. 2005.** Fire and persistence of montane chaparral in mixed conifer forest landscapes in the northern Sierra Nevada, Lake Tahoe basin, California, USA. *Journal of the Torrey Botanical Society*. 132: 442–457.
- Pavlik, B.; Murphy, D.D. 2002.** Tahoe Yellow Cress Technical Advisory Group. 2002. Conservation strategy for Tahoe yellow cress (*Rorippa subumbellata*). http://heritage.nv.gov/reports/rosu_CS.pdf. (May 9, 2005).
- Pollet, J.; Omi, P.N. 2002.** Effect of thinning and prescribed burning on crown fire severity in ponderosa pine forests. *International Journal of Wildland Fire*. 11: 1–10.
- Potter, D.A. 1998.** Forested communities of the upper Montane in the central and southern Sierra Nevada. Gen. Tech. Rep. PSW-GTR-169. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. 319 p.
- Pouyat, R.; Parmelee, R.; Carreiro, M. 1994.** Environmental effects on forest soil invertebrates and fungal densities in oak stands along an urban-rural land use gradient. *Pedobiologia*. 38: 385–399.
- Reichard, S.H.; White, P. 2001.** Horticulture as a pathway of invasive plant introductions in the United States. *BioScience*. 2: 103–113.

- Reuter, J.E.; Palmer, M.D.; Goldman, C.R. 1996.** Limnology and trophic status of Lower Echo Lake, Upper Echo Lake, and Fallen Leaf Lake. Report to the Tahoe Regional Planning Agency. On file with: Tahoe Regional Planning Agency, 128 Market Street, Stateline, NV 89449.
- Richardson, T.W. 2007.** Avian use, nest-site selection, and nesting success in Sierra Nevada aspen. Reno, NV: University of Nevada. 162 p. Ph.D. dissertation.
- Richardson, T.W.; Heath, S.K. 2004.** Effects of conifers on aspen-breeding bird communities in the Sierra Nevada. Transactions of the Western Section of the Wildlife Society. 39: 68–81.
- Running, S.W. 2006.** Is global warming causing more, larger wildfires? Science. 313: 927–928.
- Rybock, J. 1978.** *Mysis relicta* Loven in Lake Tahoe: vertical distribution and nocturnal predation. Davis, CA: University of California, Davis. 178 p. Ph.D. dissertation.
- Sala, O.E.; Chapin, F.S.; Armesto, J.J.; Berlow, E.; Bloomfield, J.; Dirzo, R.; Huber-Sanwald, E.; Huenneke, L.F.; Jackson, R.B.; Kinzig, A.; Leemans, R.; Lodge, D.M.; Mooney, H.A.; Oesterheld, M.; Poff, N.L.; Sykes, M.T.; Walker, B.H.; Walker, M.; Wall, D.H. 2001.** Global biodiversity scenarios of the year 2100. Science. 287: 1770–1774.
- Salt, G.W. 1957.** Analysis of avifaunas in the Teton Mountains and Jackson Hole, Wyoming. Condor. 82: 373–393.
- Sanford, M.P.; Manley, P.N.; Murphy, D.D. [In press].** Urban development impacts ant communities: implications for ecosystem services and management. Conservation Biology.
- Scharenbroch, B.C.; Lloyd, J.E. 2004.** A literature review of nitrogen availability indexes for use in urban landscapes. Journal of Arboriculture. 30: 214–230.
- Schimpf, D.J.; MacMahon, J.A. 1985.** Insect communities and faunas of a Rocky Mountain subalpine sere. Great Basin Naturalist. 45: 37–60.
- Schlesinger, M.D.; Manley, P.N.; Holyoak, M. 2008.** Distinguishing stressors acting on land bird communities in an urbanizing environment. Ecology. 89(8): 2302–2314.
- Scholl, A.E.; Taylor, A.H. 2006.** Regeneration patterns in old-growth red fir-western white pine forest in the northern Sierra Nevada, Lake Tahoe, USA. Forest Ecology and Management. 235(1–3): 143–154.

- Schwilk, D.W.; Knapp, E.E.; Ferrenberg, S.M.; Keeley, J.E.; Caprio, A.C. 2006.** Tree mortality from fire and bark beetles following early and late season prescribed fires in a Sierra Nevada mixed-conifer forest. *Forest Ecology and Management*. 232: 36–45.
- Shepperd, W.D.; Rogers, P.C.; Burton, D.; Bartos, D.L. 2006.** Ecology, management, and restoration of aspen in the Sierra Nevada. Gen. Tech. Rep. RMRS-178. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 122 p.
- Skinner, C.N.; Chang, C.R. 1996.** Fire regimes, past and present. In: Erman, D., ed. *Sierra Nevada Ecosystem Project: final report to Congress, Status of the Sierra Nevada: Vol. II: Assessments and scientific basis for management options*. Davis, CA: Center for Water and Wildland Resources, University of California, Davis: 1041–1069
- Song, K.H.; Breslin, V.T. 1999.** Accumulation and transport of sediment metals by the vertically migrating opossum shrimp, *Mysis relicta*. *Journal of Great Lakes Research*. 25: 429–442.
- Stam, B.R.; Malechek, J.C.; Bartos, D.L.; Bowns, J.E.; Godfrey, E.B. 2008.** Effect of conifer encroachment into aspen stands on understory biomass. *Rangeland Ecology and Management*. 61: 93–97.
- Steinberg, D.; Pouyat, R.; Parmelee, R.; Groffman, P. 1997.** Earthworm abundance and nitrogen mineralization rates along an urban-rural land use gradient. *Soil Biology and Biochemistry*. 29: 427–430.
- Taylor, A.H. 2004.** Identifying forest reference conditions on cut-over lands, Lake Tahoe Basin, USA. *Ecological Applications*. 14: 1903–1920.
- Taylor, A.H.; Beaty, R.M. 2005.** Climatic influences on fire regimes in the northern Sierra Nevada mountains, Lake Tahoe Basin, Nevada, USA. *Journal of Biogeography*. 32: 425–438.
- Taylor, A.H.; Skinner, C.N. 1998.** Fire history and landscape dynamics in a late-successional reseve, Klamath Mountains, California. *Forest Ecology and Management*. 111: 285–301.
- Theobald, D.M. 2005.** Landscape patterns of exurban growth in the USA from 1980 to 2020. *Ecology and Society*. 10(1): 32. <http://www.ecologyandsociety.org/vol10/iss1/art32/>. (October 15, 2008).

- Thies, W.G.; Westlind, D.J.; Loewen, M. 2005.** Season of prescribed burn in ponderosa pine forest in eastern Oregon: impact on pine mortality. *International Journal of Wildland Fire*. 14: 223–231.
- University of California, Davis and University of Nevada, Reno 2003, 2006.** Nutrient data collected from various lakes in the Tahoe basin. Unpublished data. On file with: S. Chandra, Department of Natural Resources and Environmental Science, University of Nevada, Reno, NV 89512.
- Urban, D.L.; Miller, C.; Halpin, P.N.; Stephenson, N.L. 2000.** Forest gradient response in Sierran landscapes: the physical template. *Landscape Ecology*. 15: 603–620.
- Vander Zanden, M.J.; Chandra, S.; Allen, B.C.; Reuter, J.E.; Goldman, C.R. 2003.** Historical food web structure and restoration of native fish communities in Lake Tahoe (CA-NV) basin. *Ecosystems*. 3: 274–288.
- Vaughn, C.C.; Hakenkamp, C.C. 2001.** The functional role of burrowing bivalves in freshwater ecosystems. *Freshwater Biology*. 46(11): 1431–1446.
- Viherluoto, M.; Kuosa, H.; Flinkman, J.; Viitasalo, M. 2000.** Food utilization of pelagic mysids, *Mysis mixta* and *M. relicta*, during their growing season in the northern Baltic Sea. *Marine Biology*. 136: 553–559.
- Weatherspoon, C.P.; Skinner, C.N. 1996.** Landscape-level strategies for forest fuel management. In: Erman, D., ed. *Sierra Nevada Ecosystem Project: final report to Congress, Status of the Sierra Nevada Vol. II: Assessments and scientific basis for management options*. Davis, CA: Center for Water and Wildland Resources, University of California, Davis: 1471–1492.
- Weatherspoon, C.P.; Skinner, C.N. 2002.** An ecological comparison of fire and fire surrogates for reducing wildlife hazard and improving forest health. Leavenworth, WA: Association for Fire Ecology: 239–245.
- Westerling, A.L.; Hidalgo, H.G.; Cayan, D.R.; Swetnam, T.W. 2006.** Warming and earlier spring increase in Western U.S. forest fire activity. *Science*. 313: 940–942.
- Wittmann, M. 2008.** Recreational boating and the spread of aquatic invasive species in and around Lake Tahoe, California-Nevada. Santa Barbara, CA: University of California. 199 p. Ph.D. dissertation.

- Wittmann, M.; Chandra, S.; Reuter, J.; Schladow, G. 2009.** Asian clam and Lake Tahoe: preliminary findings in support of a management plan. 47 p. Unpublished report. On file with: University of California, Tahoe Environmental Research Center, 291 Country Club Drive, Incline Village, NV 89451.
- Zielinski, W.J.; Slauson, K.M. 2008.** Effects of off-highway vehicle use on the American marten. *Journal of Wildlife Management*. 72: 1558–1571.