

Introduction to the Special Issue on Sierran Mixed-Conifer Research

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LIKE MUCH OF THE WESTERN UNITED STATES, California's forest has been severely altered by a century of fire suppression. The Sierra Nevada's largest forest type, mixed conifer, which is primary habitat for more vertebrate species than any other Californian forest community, historically burned every 12–17 years. In 1894, John Muir wrote "The inviting openness of the Sierra woods is one of their most distinguishing characteristics. The trees of all the species stand more or less apart in groves, or in small, irregular groups, enabling one to find a way nearly everywhere, along sunny colonnades and through openings that have a smooth, parklike surface . . ."; (Muir 1894). Now most mixed-conifer forest is characterized by dense thickets of small shade-tolerant fir and cedar, which could quickly transfer a ground fire into the overstory crowns. Estimates based on the area burned each year project the current fire return interval at >600 years. Regional and national plans such as the Sierra Nevada Forest Framework and the Healthy Forest Initiative have made restoration a priority, yet these plans are highly controversial, in part because there is so little ecological information for guiding management prescriptions. Any effort to restore these forests to "health" or an active fire regime will only be improved with an understanding of how the ecosystem functions. This collection of articles investigates the connections between forest structure and composition, and the ecological processes that define Sierran mixed conifer.

A common theme in this collection of articles is the importance of patch structure and water availability in influencing mixed-conifer's ecological processes. All of these studies were conducted in an old-growth forest at the Teakettle Experimental Forest, which even after 140 years without a fire has a distinct patch pattern. Fire suppression has increased the stem density in tree clusters, but the forest is still characterized by three distinct patch types: tree groups, gaps, and shrubs. Several articles in this collection stratified their sampling by these patch types and found significant differences among patches in tree regeneration (Gray et al.), soil nitrogen pools and dynamics (Erickson et al.), invertebrates (Marra and Edmonds), and respiration (Ma et al.). These patches, all dynamically linked through forest seral development, appear to provide important functional and habitat heterogeneity in mixed conifer.

Another important influence on forest processes was the duration and availability of soil moisture. Mixed conifer receives 90% of its annual precipitation as snow, with soils at field capacity in May, drying down to an average of 4% soil moisture by early July, and rarely receiving any precipitation until Oct. Because of this strong seasonal drought, regional climatic events such as El Niño can have a signif-

icant pulse effect on flora and fauna, influencing tree establishment (North et al.), nutrient cycling (Erickson et al.), canopy invertebrates (Schowalter and Zhang), and pest mortality (Smith et al.). Mediating the climate's top-down effects on ecosystem function are within-stand differences in site conditions that have a bottom-up influence on ecosystem structure, composition, and function. These conditions include litter depth, soil depth, canopy-moderated surface temperatures, and stem density, all of which can significantly increase the duration and abundance of soil moisture. The important role of vegetation patch type, climate, and soil moisture may help future research understand the dynamic ecological processes of mixed-conifer forest and managers more effectively tailor restoration practices to ecosystem functions.

Marra and Edmonds found a highly diverse soil invertebrate community that differed between vegetation patch types. The community, dominated by mites, was significantly influenced by annual differences in soil moisture and spatial differences in bulk density due to litter from vegetation patches. They suggest invertebrate community response to restoration treatments will likely hinge on recovery of understory vegetation, which moderates soil temperatures and provides organic inputs.

Izzo et al. examined the diversity of mixed-conifer ectomycorrhizae and which species were regularly consumed by small mammals that are known fungivores. Ectomycorrhizal fungi are essential for conifer nutrient and water uptake, and their above- ("mushrooms") and below- ("truffles") ground fruiting bodies are an important food source for many forest mammals such as the flying squirrel, the main prey of the California spotted owl. Izzo and colleagues found that the ectomycorrhizal community has a high percentage of hypogeous ("truffle") fungi, and they suggest this prevalence may be due to the Sierra's extended seasonal drought and deep litter layers due to fire suppression. Fungi producing truffle fruiting bodies can only inoculate new areas when they're consumed and their spores are excreted. With a greater dominance of truffle-producing fungi, the connection between trees, truffles, and small mammals may be particularly tight in these drier forests where below-ground fungal fruiting produces a longer lasting food source.

Canopy invertebrates, which can influence tree growth, vigor, and litter inputs into the soil, were examined by Schowalter and Zhang. They found invertebrates differed by tree species host and that there were significant differences between the communities in overstory conifers and understory angiosperms. They also suggest that significant annual variations in invertebrate abundance and diversity

may be due to year-to-year climate differences driven by El Niño effects on California precipitation patterns.

North et al. found that the five major species in mixed conifer had different recruitment responses to fire and wet El Niño years. They suggest that differences in species drought tolerance and within-stand slope location interact with fire and climate events to influence when different species became established. Although mixed conifer had distinct groups of trees, these groups were not age cohorts, because different species became established at different times depending on fire and climate events. They suggest managers do not need to use group selection thinning to restore forest structure and that successful regeneration will depend on understanding which species should be managed for, where, and how climate and fire may affect their establishment.

Smith et al. examine patterns of dead trees in current forest conditions, now that the primary historical mortality agent, fire, has been suppressed. They examined a theory of whether chronic pest mortality is higher on small, shade-tolerant trees in dense clusters, thus operating as a corrective force for the effects of fire suppression. They did find that trees in dense clusters had higher mortality. However, individual species mortality was proportional to overall stand composition, and mortality of large trees was higher than expected. This suggests that current mortality is not acting to correct the effects of fire suppression and that many of the large trees that managers wish to retain in the forest may have high mortality when surrounded by dense clusters of young trees. This finding emphasizes that active management to reduce stem densities may be needed to restore historic mortality patterns.

Ma et al. report on factors that influence soil respiration, an important potential source or sink for terrestrial carbon. They find that respiration rates increase with increasing temperature when soil moisture is not limiting, but unlike many other temperate forests, respiration starts to decrease with increasing temperature once soils dry out. This means that models of carbon sequestration for forests may need to account for climate regimes where limited soil moisture can override the expected increase in respiration with temperature. They also find that soil respiration rates significantly differ by understory patch type because vegetation strongly influences litter inputs that affect microbial activity and their contribution to respiration and local root respiration. They suggest that calculations of respiration rates for mixed conifer need to scale and extrapolate their measures based on patch condition and extent.

Erickson et al. also find understory patch condition to be an important influence on ecosystem function, in this case soil nutrient pools and fluxes. Soil total nitrogen pools are substantially higher under ceanothus shrubs probably because of their association with the nitrogen fixing bacteria *Frankia*. They also show that these shrubs are islands of highly available forms of nitrogen, which may enrich soils

that otherwise are nutrient poor. Managers sometimes consider ceanothus an undesirable shrub because it can suppress tree regeneration and reduce tree seedling growth. Erickson et al., however, suggest that it is also an important source of available nitrogen in these otherwise nutrient-poor systems. Furthermore, because more nitrogen is stored in the mineral rather than organic layers in ceanothus and gap areas compared to closed canopy forest, fire restoration treatments that consume most of the organic layer may leave closed canopy patches with lower nitrogen pools than gaps and old ceanothus patches.

Gray et al. examined conditions associated with tree seedling establishment and growth, finding all conifers except Jeffrey pine associated with areas of high soil moisture and low levels of direct solar radiation. Seedlings were disproportionately found on mineral soil in comparison to other substrates, but soil cover was only 5%, and many species were positively associated with greater litter depth, possibly reflecting greater early-season moisture retention. Unlike other forests where canopy gaps may provide favorable sites for tree regeneration, larger gaps in mixed conifer may persist because of high temperatures and dry soils lethal to regeneration. Shading by shrubs may have aided initial seedling survival, but few tree saplings besides bitter cherry were found in shrub patches, probably related to lower early-summer soil moisture levels found under shrubs than elsewhere in stands. Gray and colleagues suggest that fire restoration treatments may benefit conifer tree regeneration most by providing moderate amounts of shade, reducing shrub competition, and increasing the abundance of mineral seedbed.

This collection of articles on Sierran mixed-conifer forest emphasizes the need to understand the complex connections between structure, composition, and function to effectively restore these forests. Restoring these forests to Muir's condition of "inviting openness" should involve more than creating the appearance of an open stand. If we're truly interested in forest "health," we need to understand the functions that support the ecological web of mixed-conifer processes. We hope the articles in this special issue can begin to shed some light on these processes. This issue would not have been possible without the help of *Forest Science* editors Greg Amacher and Ed Green, manuscript editors Janet Michaels, Fran Pflieger, and Matt Walls, financial support from USDA Forest Service Sierra Nevada Research Center, logistical help from the Sierra National Forest, and constructive reviews from over two dozen dedicated reviewers. I also want to thank all the authors for their hard work and for many enjoyable evening discussions at Teakettle about the mystery of how these forests "work."

Literature Cited

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