CLOSING CANOPIES AND CHANGING TROPHIC ENERGY PATHWAYS IN WESTERN CONIFER FORESTS: WHERE DO WE GO FROM HERE?

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ABSTRACT: The persuasive evidence of closing forest canopies across the western United States during the last century suggests that primary energy production in forest ecosystems is shifting from herbaceous and shrubby vegetation to trees. This conclusion is supported by established inverse relationships between tree crown density and forage in the form of shrubs and herbaceous plants. Shrub and herbaceous layers in forest ecosystems are essential habitat elements for many species providing critical trophic pathways to numerous primary consumers. Essential to understanding and conserving ecological function should be the maintenance of energy transfer through diverse food webs. The relationships between producer plants and consumer animals, between predator and prey, and kinds of organisms in a given environment, are all controlled by the basic concepts of energy, ultimately limited by light. Yet in spite of this fundamental principle, much of the focus in contemporary forest management has been on a few secondary consumers thought to have reproductive habitat requirements associated with dense, late seral forest conditions, with relatively little attention given to the habitat requirements of prey for these species. Shifts in vegetation composition and the decline of critical ecological elements, argues for an approach to forest management that focuses more on fundamental processes and the promotion of vegetative diversity rather than featured species, especially secondary consumers.

Key words: canopy, closing, conifers, consumers, ecosystem, energy, herbaceous, producers, seral, shrubs, trophic, western

EVIDENCE OF INCREASING CONIFER CANOPY AND DECLINING SHRUBBY AND HERBACEOUS HABITAT ELEMENTS

Several authors report that lengthening fire intervals resulting from suppression has been the primary cause of loss of openings in western forests (Weaver 1943, Morrison and Swanson 1990, Skinner 1995, Agee 1998). It has also been reported that historical climatic patterns were drier than recent decades, contributing to a less frequent contemporary fire pattern (Laudenslayer and Skinner 1995). Much of the early documentation of changes in western vegetative patterns was in the Intermountain region and focused on historical photographs with matched retakes (Phillips 1963, Rogers 1982, Gruell 1983, Gruell 1986.) More recent work in the Sierra Nevada region (Gruell 2001) provides a visual assessment of successional shifts to more woody vegetation. While these works may not be representative of conditions throughout all western forest habitats, they provide compelling evidence of increasing tree canopy in the areas studied. Other change detection studies based on temporal data comparisons support the conclusions of closing forest canopies demonstrated by photographic retake work. Peek et al. (2000) examined aerial photographs and satellite imagery to compare changes from 1953 to 1988 in an 85,268 ha area in south central Oregon and reported a significant shift from 63.1% open-canopied forests in 1953 to 25.3% open in 1988. The major change has been towards a moderate canopy that occupied 64.3% of the study area in 1988. Above 1600 m elevation, a shift from open-canopy forest occupying 86.3% of the study area to 85.9% moderate canopy occurred between 1953 and 1988. Minnich et al. (1995) compared forest vegetation plot data in mixed conifer stands gathered between 1929 and 1935 in the San Bernardino Mountains of southern California with data obtained at the same plots in 1992. The comparison indicated an increase in total stem density of trees having dbh larger than 12 cm from 116 per ha to 207 per ha, a 79 % increase. Skinner (1995) investigated changes in forest openings in a 24,600 ha area of northwestern California from aerial photographs in 1944 and 1985 and reported a 39% reduction in the area occupied by openings in 1944. Distances from random points to the nearest opening doubled from 1944 to 1985. Schaefer, et al. (2002) summarized data gathered in northeastern California on range transects installed prior to 1957 and measured 4 times between 1957 and 1998 at 10 year intervals. Tree overstory increased for all years as live shrubs declined and dead shrubs increased between 1967 and 1998. Juniper (*Juniperus occidentalis*) and Ponderosa pine (*Pinus ponderosa*) were recorded as canopy on 4.2 % of transect plots in 1957 increasing to 17.6 % in 1998.

A satellite imagery accuracy assessment study over 14 million acres provides a landscape evaluation of conifer density throughout northern California. Crown canopy was measured from 1,271 low elevation stereo-paired photographs taken at random intervals along 130 random, 10 mile long flight transects (Fox 2000). Tree cover information was placed in 4 canopy closure classes: sparse (10 - 24%), open (25 - 39%), moderate (40 - 59%) and dense (>60%). Mixed conifer and mixed conifer-hardwood habitat types sampled by canopy class were: sparse, 10.4%, open, 15.2%, moderate, 24.3% and dense, 50.1%. The weighted-mean of the class midpoints was 58.7% indicat-

ing that coniferous habitats throughout millions of acres of northern California are relatively dense. While no comparable early data exists to allow a quantitative assessment of change in crown density, Fox's work provides evidence that coniferous habitats in Northern California are considerably more dense today than suggested by pre-settlement descriptions.

Landscape patterns of mixed conifer forests prior to 1900 have not been well described and descriptions are based primarily on anecdotal accounts (Skinner and Chang 1996). Photographic retake studies indicate declines in shrubs, grasses and forbs (Phillips 1963, Rogers 1982, Gruell 1983, Gruell 1986, Gruell, 2001,) but do not provide quantitative analysis of the changes. The evidence of increasing forest canopy and the established inverse relationship between shrub and herbage production and tree crown density (Pase 1958, Jameson 1967, McConnell and Smith 1965, Miller et al. 2000) strongly suggests that shrubs, grasses and forbs have declined during recent decades throughout the coniferous biomes of the western United States.

THE ECOLOGICAL IMPLICATIONS OF INCREASING TREE CANOPY IN CONIFEROUS FORESTS

The intensity of light impinging on a given surface area controls an entire ecosystem through its influence on gross primary production (GPP) (Odum 1960). GPP is the sum of the photosynthesis by all leaves and is measured at the ecosystem scale. In most closed-canopy ecosystems, photosynthetic capacity decreases exponentially through the canopy in parallel with the exponential decline in irradiance (Hirose and Werger 1987). As forest canopies close, leaves at the top of the canopy develop more cell layers than shaded leaves and therefore contain more nitrogen than leaves at lower levels. New leaves produced at higher rates at the top of dense canopies cause nitrogen to be transported to the top of the canopy as forest canopies close (Hirose and Werger 1987, Field 1991). Leaves at lower canopy levels senesce when they become shaded below the light compensation point and the potential energy lost from areas in the lower portions of the canopy is transported to the top of the canopy to support new leaf production (Field 1991). Leaf area index (LAI) is the total surface area of leaves and is a critical determinant of GPP on most of Earth's terrestrial surface (Schulze et al. 1994). Soil resources and light extinction through forest canopies determine the upper limit of the leaf area that an ecosystem can support. Following major disturbances, such as wildfire, LAI shifts from densely forested canopies to rapidly developing herbaceous and shrubby plants, and over time increases and then (at least in forests) often declines in late succession (Chapin et al. 2002).

Net primary production (NPP) is the carbon gain by vegetation and equals the difference between GPP and plant respiration. It is this NPP that constitutes a basic, fundamental ecological constraint to the animal production that any plant-based ecosystem can support. The proportion of net primary productivity available to herbivores varies greatly as a function of plant allocation to structure and the large proportion of structural (woody) tissue in trees minimizes the proportion of plant production that can be converted to secondary production. The decrease in biomass with successive trophic links is most pronounced in forests, where the dominant plants are long lived and produce a large proportion of inedible biomass available to vertebrates. The proportion of available primary production consumed by herbivores is maximal in early to middle succession because the rapidly growing herbaceous and shrub species that dominate this stage have high concentrations of nitrogen with little allocated to plant defense (Chapin et al. 2002).

These fundamental principles of ecology, indicate that increasing tree canopy across expansive landscapes of the western United States, has led to a shifting of trophic energy, once available in a diverse assemblage of plants adapted to variable fire regimes, from forest floor environments to trees. Loss of primary producers in the form of herbaceous and shrubby plants has resulted in a redirection of energy flow from the predator chain through parasitic and saprophytic pathways leading to increases in decomposers and dead organic matter with fewer herbivores and carnivores (Odum 1960).

Elements most often associated with treeless or open forest conditions (shrub and herbaceous layers and tree/non-tree interfaces) are essential components of habitats for many more species of vertebrates than are dependent on dense or late seral forests (Zeiner et al, 1988, 1990(a,b). However, some species are restricted to one or the other condition. Furthermore, it is the transition area (ecotone) as forest cover changes either abruptly or gradually along a gradient that commonly contains many of the organisms of both cover conditions. More importantly, some species are not found in either of the more monotypic areas flanking the ecotone (Odum 1960). Johnston and Odum 1956, reported that 13 of 50 (26 %) of breeding bird species were not recorded on "uniform" tree or grass/shrub portions of the study area but were restricted to variable mixes of shrub or grass interfaces with tree stands. An additional 7 (14%) species were found only in low numbers in homogeneous areas. The authors concluded that about 40 percent of the breeding birds were primarily or entirely associated with ecotones. Beecher 1942, reported nesting bird densities measured in quarter-acre quadrats were 5 times higher at sites containing 4 distinct plant assemblages compared to nest sites in a single type.

Habitat suitability models suggest that habitat quality for most forest wildlife declines as forest canopy closes. I reviewed suitability indices for 266 species of birds, mammals, reptiles and amphibians occurring in 12 coniferous forest types in the Sierra Nevada Ecological Province (Zeiner et al, 1988, 1990(a,b). One hundred and fifty five species (58%) were predicted to have declining suitability as tree crown canopy increased. Fifty-four species (20%) had increasing habitat suitability with increasing canopy and 57 species (22%) had no change in habitat quality with changes in crown density.

DISCUSSION

Spatial heterogeneity within and among ecosystems is critical to system function throughout entire regions. Patch dynamics literature describes landscapes subject to frequent disturbances as mosaics of patches of different ages, generated by cycles of disturbance and post-disturbance succession (Pickett and White 1985). In ecosystems characterized by these patterns of disturbance and response, the vegetation is always changing but averaged over a relatively large area, the proportion of the landscape in each successional stage is relatively constant. Over time, this "gap-phase" pattern of disturbance contributes to the maintenance of the productivity and nutrient dynamics of entire forests (Chapin et al, 2002). As natural disturbance cycles such as fire are interrupted and become less frequent, larger patches of a single stage occur on the landscape and spatial heterogeneity is reduced leading to reduced vegetative and wildlife diversity and ecological function.

Early phases of ecological thought emphasized the transfer of energy among organisms. Elton (1927) described the role that each animal in a community plays, based on what it eats and what it is eaten by, and his work provided the foundation of ecological theory. Tansley (1935) suggested that focus on individual organisms would result in the failure to recognize the importance of the exchange of materials between organisms and their abiotic environments. Lindeman (1942) recognized that energy flow from green plants through primary and secondary consumer pathways would ultimately constrain the abundance of consumers. The publication of Lindeman's work, led Odum (1960) to develop a "systems approach" to ecology that emphasized the general properties of energy flow and metabolism, leading to the term "ecosystem."

In spite of the progressive direction established by early ecologists, the application of ecological theory to resource management appears to have regressed from traditional teachings of systems approaches to more simplified strategies that focus on selected "indicator" or "endangered" species. Landres et al. (1988) provide a historical account of the use of selected species to document environmental conditions and the impacts of development and land management activities. The authors noted that much of the current use of indicator species was initiated by the U. S. Department of Interior, Fish and Wildlife Service and the USDA Forest Service to "document the quality and quantity of available habitat for selected species of wildlife." Habitat evaluation procedures (HEP) were developed to assess conditions for selected species of wildlife and the capacity of habitats to support the evaluation species was approximated by a Habitat Suitability Index (HSI) derived from conceptual or mathematical models (USDI 1980). This process led to a requirement that each National Forest identify "Management Indicator Species" (MIS) with management goals and objectives for these species described in National Forest Plans. Included in the MIS were (1) recovery species— those identified by state or federal governments as threatened, endangered or rare, (2) featured species— those thought to have social or economic value and (3) sensitive species—those felt to have habitat requirements sensitive to management activities. Standards and guidelines for MIS were described in each National Forest Plan to be used to guide forest management activities.

Assumptions used to develop this simplified approach to forest management fail on both conceptual and empirical grounds (Landres et al 1988). Each of the species selected as MIS have breeding characteristics, foraging behavior and diet, and habitat characteristics that are unique (Block et al. 1986). The trustee responsibilities of both state and federal resource agencies is unlikely to be fulfilled by focusing on a relatively few species of wildlife, habitats or habitat conditions that are suspected of being in decline. Managing an area for a "sensitive' or 'indicator" species may provide only the environmental conditions thought to be needed by those species, ignoring the ecological processes and resources needed by other species (Kushlan 1979). Community based approaches are needed when the quality or integrity of a habitat or community is of concern. Focus should be on attributes of community structure, including plants other than trees, a variety of vegetative habitat elements and on processes such as nutrient cycling, primary and secondary production and the factors regulating these processes (Landres et al. 1988). Land management decisions based on information gathered for a limited number of species may not provide suitable conditions for numerous other species. For example, some species require a combination of habitat types in certain proportions and spatial arrays (Forman and Godron 1986, Picket and White 1985). This is an especially critical issue when secondary consumers utilize seral habitats for part of their life history requirements that are considerably different from that of their preferred prey species. Recent work by Franklin et al. (2000) demonstrates that the spotted owl (*strix occidentalis*) a supposed "indicator" for late seral for-

est habitats, had higher levels of fitness when nesting and foraging areas consisted of a mix of closed canopy, large tree core nesting areas and "other" habitats as measured by the amount of linear edge between seral stages. Presumably these were more open, disturbed areas, and when combined with suitable areas of large, dense trees, provide reproductive habitat components conducive to a diverse prey base. Core areas consisting primarily of closed canopy conifers or "other" habitats had relatively low levels of fitness as measured by the production and survival of young owls suggesting that the "indicator species" for old growth forest conditions may, in fact be an "edge" species.

Ironically, the ecologically myopic focus on spotted owls and other secondary consumers such as Northern goshawk (*Accipiter gentilis*) fisher (*Martes pennanti*), and American marten (*Martes americana*) may perpetuate the reduction, and possibly extirpation of these and other species. Because of legitimate concern for the loss of late seral forest elements, focus on these species has been primarily on describing nesting and denning habitats. Yet even a cursory review of life history requirements of potential prey species, suggests that most are dependant on recently disturbed or open forests associated with herbaceous and shrubby components (Zeiner et al, 1988, 1990(a,b). These are the vegetative habitat elements (shrub and herbaceous layers in forests, and tree/non-tree interfaces) that decline as tree canopy increases.

Documented changes in forest structure and composition presents a challenge to the managers of ecological systems. Much of the effort to understand life history requirements for species selected as "indicators" of some forest condition such as "old growth" that intensified in the 1970's, may have simply described adaptive strategies as these and other species attempt to adjust to rapidly declining heterogeneity and ecological function. Failure of researchers and managers to recognize that decisions to manage for conditions described in contemporary habitat "preference" studies for selected "indicator" species, may serve only to accelerate the trend towards the homogenization of forest ecosystems by advocating the "conservation" of sub-optimal conditions.

RELEVANCE TO CONSERVATION AND MANAGEMENT IMPLICATIONS

In his landmark book contributing to the evolution of the science of ecology, Eugene Odum (1960: 421) wrote: "Conservation in the broadest sense is probably the most important application of ecology. Unfortunately, the term "conservation" suggests "hoarding," as if the idea were simply to ration static supplies so that there would be some left for the future. The aim of good conservation is to insure a continuous yield of useful plants, animals, and materials, by establishing a balanced cycle of harvest and renewal. Thus, a "no fishing" sign on a pond may not be as good conservation as a management plan which allows for removal of several hundred pounds of fish per acre year after year. The principle of the ecosystem, therefore, is the basic and most important principle underlying conservation."

Approaches to forest management on public lands must quickly abandon the astigmatic focus on the "conservation" of trees. Failure to remove trees in both temporal and spatial patterns that mimic the results of natural disturbance is likely to result in the failure to conserve other resources essential to ecological function. The complexities of coniferous forest ecosystems evolved around disturbance resulting in variable patterns of forest succession, ultimately leading to similarly variable old-growth forest conditions. (Pacific Northwest Research Station 2003). These processes provided heterogeneity that consisted of critical habitat elements including herbaceous and shrub layering and interface elements that provide diverse energy pathways to many primary and secondary consumers in forest ecosystems. Biodiversity in forested habitats is most likely to be restored and maintained by modifying the "survey and manage" process that searches for species on a restricted list and then prescribes "protective conservation" prescriptions. Strategies that involve adaptive, variable density thinning prescriptions (Carey and Wilson 2001) can be designed to produce and maintain not only decadence features associated with large, old trees, but the essential habitat elements necessary for diverse energy pathways. Restoring and maintaining the patterns of natural variability created by disturbance processes is likely to be successful if strategies are directed at the biotic community level where the emphasis on conservation is based on providing for a "functional unit" held together by the interdependence of its members. This requires managers to recognize that interdependent species often require habitat conditions and elements that are spatially incompatible. Manipulative strategies can be implemented that are designed to provide diversity by insuring the presence of essential habitat elements that occur within forests consisting of mixes of crown canopy closure classes, tree sizes and species. This approach redistributes attention down the ecological pyramid from consumers to primary producer elements that provide both energy and structural reproductive habitat components for most forest wildlife.

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