Present and past old-growth forests of the Lake Tahoe Basin, Sierra Nevada, US

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Abstract. We described 38 relictual old-growth stands – with data on the mortality, regeneration, floristic richness, fuel load and disease incidence in our study area in the Tahoe Basin of California and Nevada. The stands are within the lower and upper montane zones (1900-2400 m a.s.l.) and they are rare, occupying < 2% of the land in the Basin's watershed. Correlation matrices and ANOVAs of forest types and conifer species with environmental gradients revealed significant relationships with elevation, distance east of the Sierran crest, slope aspect, annual precipitation, date of complete snow melt, litter depth and degree of soil profile development. Pathogens, parasites and wood-boring insects were present on 23% of living trees; 16% of all trees were dead. We compared these stands to a reconstruction of pre-contact Basin forests and to ecologically analogous old-growth forests of Baja California that have never experienced fire suppression management. Currently, overstorey trees (> 180 yr old) in the Basin stands have ca. 33% cover, 54 $m^2.ha^{-1}$ basal area and 107 $individuals.ha^{-1}$, values very similar to reconstructions of pre-contact Basin forests and to modern Baja California forests. Understorey trees (60-180 yr old), however, are several times more dense than historic levels and species composition is strongly dominated by *A. concolor*, regardless of the overstorey composition. The ratio of *Pinus* : *Abies* has increased – and the age structure of extant stands predicts that it will continue to increase – from approximately 1:1 in pre-contact time to 1:7 within the next century. Disease incidence and mortality in Baja forests were lower. Although we quantitatively defined current Basin old-growth forests – in terms of stand structure – we realize that our definition will differ from that of both past and future old-growth forests unless management protocols are changed.

Keywords: *Abies concolor; Abies magnifica*; California; Coarse woody debris; Fire ecology; Forest pathology; Mortality; *Pinus jeffreyi*; Stand dynamics; Succession.

Nomenclature: Hickman (1993) for vascular plants; Furniss & Carolin (1977) for bark beetles; Hansen & Lewis (1997) for pathogens.

Introduction

Old-growth forest stands are of interest because of their rarity, what they can tell us about human-induced change and their use as management goals for restoration. Restoration targets require quantitative description but existing old-growth definitions are typically qualitative. The most quantitative definitions for selected Sierra Nevada forests were prepared by Forest Service zone ecologists (Potter 1998; Potter et al. 1992a, b; Fites et al. 1991, 1992) in formats for limited distribution; they focus on overstorey tree age and height, density and basal area of large-diameter trees and on density of large-diameter snags and logs. These attributes do not include data for total tree density, relationships between overstorey and understorey tree density and species composition, cover by trees/shrubs/herbs, species richness or biomass of coarse woody debris.

Montane forests of California have been impacted by Euroamericans for ca. 150 yr. Major activities which caused change in old-growth forests included logging, grazing by domesticated livestock, road building, soil compaction by human and animal traffic, the production of airborne pollutants and a policy of fire suppression management implemented ca. 1920. Estimates of how much forest area in lower and upper montane zones of the Sierra Nevada still retain a significant number of old-growth traits vary from less than one-sixth to as much as one-third of the area occupied 150 yr ago, depending on the forest type and the location (Franklin & Fites-Kaufman 1996). Such forests are called old-growth even if they have been entered and partially harvested in the recent past. Estimates of the area of unentered, pristine old-growth forest are not available for the entire Sierra Nevada, but local studies indicate it is much less, perhaps < 5% of the forested area (e.g. Barbour et al. 2000). Furthermore, the remaining old-growth forests are highly fragmented, the largest continuous areas being limited to national parks.

Before the 20th century, late-summer and fall sur-

face wildfires were a natural part of the montane mediterranean ecosystem, with a mean fire return period of 15-25 yr. One consequence of fire suppression seems to be an increase in tree density and fuel loads by several-fold (Bouldin 1999; Minnich et al. 1995). The high tree densities have increased mortality and competition for soil moisture and the high fuel loads have changed fire behaviour, decreased the range of fire intensities and increased the probability of high-intensity crown fires (Martin & Sapsis 1992).

Our objectives were: (1) to locate all conifer stands in the Lake Tahoe Basin that met qualitative criteria for old-growth – that is, to determine how much old-growth forest area remains; (2) to quantitatively describe them in terms of tree density, tree age structure, basal area, species composition, floristic richness, disease incidence, mortality, coarse woody debris and site physical factors; (3) to assess their stability in terms of population size/age structure; (4) to determine what abiotic traits best correlate with the presence of old-growth stands; (5) to compare existing stands with quantitative reconstructions of the pre-contact landscape to quantify changes in tree species balance, density, age structure, mortality and changes in fuel load and fire regime.

Study area

The Lake Tahoe Basin has a small watershed land area (82 000 ha) for Lake Tahoe's large surface area of 49 000 ha. The modern lake surface elevation (39° N, 120° W) varies from year to year but is normally ca. 1920 m a.s.l. The surrounding watershed crest reaches 3400 m a.s.l.

Because the Basin is situated east of the Sierra Nevada crest it has a colder and drier environment than similar elevations west of the crest. There is a west-to-east gradient of declining precipitation within the Basin, such that mean annual precipitation on the west shore is ca. 50% greater than that of the east shore (James 1971; Kittel 1998; Rogers 1974). Annual precipitation is 500-1500 mm, depending on shore and elevation; two-thirds falls from December to March and > 80% falls in the form of snow. Mean snowpack depth and duration increase with elevation such that April 1 snow depth in subalpine forests > 2300 m a.s.l. is ca. 5.0 m and snowpack duration is > 200 d (Nachlinger & Berg 1988), whereas snowpack depth near the lake shore is only ca. 0.5 m and lasts < 130 d (Rogers 1974).

Mean daily minimum winter temperature at lake elevation is – 6 °C, mean daily maximum summer temperature is 24 °C and length of the frost-free growing season is 75 d. Potential evapotranspiration, as calculated by the Thornthwaite method, is 480 mm but actual evapotranspiration is only 270 mm because soil moisture available for plant uptake is depleted by mid-July (Rogers 1974). Therefore the P:E ratio is between 1 and 2.

The geologic substrate along the eastern, southern and western shores is typically granite. Bedrock along the north shore is volcanic material ca. 10 million years old. Most soils are shallow Entisols or Inceptisols and the most developed soils are Alfisols (Rogers 1974).

Ca. 67% of Basin forests were clear-cut during the last third of the 19th century (Elliott-Fisk et al. 1996), generating 1 678 500 m^3 of lumber and 500 000 cords of wood. Less intensive harvesting continued into the 20th century for residential and recreational purposes (Lindstrom 1999). The Forest Service's current management objective is to return > 80% of the forested landscape to old-growth status.

Methods

Locating old-growth stands

We first examined 1978 vegetation maps of the Basin that had been prepared by United States Forest Service staff from aerial photographs, combined with on-the-ground verification. The maps consisted of polygons of homogeneous vegetation at a scale of 1:24 000. Forest vegetation polygons on the maps carry 3 attributes: the name of the leading 1-to-3 dominant tree species, the mean canopy size of overstorey trees (5 categories), and the density of trees (4 categories; Johnson 1995). Minimum polygon size is 5 ha and the largest polygons approach 65 ha.

We selected ca. 400 potential old-growth polygons in which: (1) the leading dominants were characteristic of lower and upper montane forests on zonal habitats (thus excluding subalpine woodland, lodgepole/aspen forest and riparian forest); (2) overstorey trees had large canopies (categories 4 and 5 of Johnson 1995) and (3) there were at least 5 overstorey trees.ha^{-1} (> 76 cm DBH), large enough to function as nest sites for animals (Verner 1992). We then visited the polygons by road and trail over a period of 2 summers and verified that only 38 satisfied old-growth criteria. Most polygons were rejected because: (1) they had been entered and thinned since 1978 (stumps and skid trails were present); (2) they had been mistyped as to leading dominants, size or density or (3) the homogeneous portion of stand area was < 3 ha.

The polygons we accepted, in other words, were not a random subsample of available polygons but were a complete census of acceptable polygons.

Vegetation sampling procedures

Within each of the 38 acceptable polygons, we chose a random starting point and a random compass bearing for a 270 m long transect. Elevation, aspect and slope were measured at 10 evenly spaced points along the transect. Estimates of snowpack depth, Julian date of complete snow melt and the date of soil moisture exhaustion during the growing season were obtained from micro-environmental models developed by Royce (1997; also Royce & Barbour 2001a, b) specifically for the Sierra Nevada.

Trees along the transect were sampled by the point-centered quarter method (Mueller-Dombois & Ellenberg 1974; Engeman et al. 1994; Feldman 2000). We visited 10 points along the transect, located every 30 m. We chose a 30-m interval because shorter intervals could result in overlap of trees between adjacent points. Distances from each point and DBH were measured for 8 closest trees, they were also identified to species. Four of the trees were overstorey trees, defined as DBH > 40 cm and another 4 were understorey trees, defined as DBH 1-40 cm.

Along each transect, cores were taken at breast height from 3 overstorey trees of each species present ($n = 201$). The rings were later counted to determine tree age. One-third as many saplings ($n = 72$) that just reached breast height were harvested and rings counted at the base, to determine how many additional years were required to reach breast height. Tree age was determined as the sum of rings at breast height plus rings at sapling base.

Each point formed the center of a 25-m^2 circular quadrat. Within that quadrat all shrubs and herbs were identified to species and their live canopy cover separately estimated. Saplings (trees taller than 15 cm but shorter than breast height) were also counted by species. Branch whorl counts and ring counts at the base of 15 cm saplings indicated a mean age of 20 yr, regardless of species.

Tree data were summarized in terms of absolute and relative basal area, density and frequency. The 3 relative values were then averaged added and divided by 3 to obtain an importance percentage (Mueller-Dombois & Ellenberg 1974). Shrub and herb data were summarized in terms of absolute and relative cover and frequency. The 2 relative values were then added and divided by 2 to obtain an importance percentage.

We also estimated ground cover of litter, rocks and coarse woody debris (material > 25 cm diameter) by taking 4 samples at the cardinal points along the circumference of the quadrat. When litter was present its depth was measured.

At the 5th point of the transect we counted and quantified standing snags and coarse woody debris according to US Forest Service and National Park Service protocols. Log dimensions were transformed into volume, then volume into biomass using Smalian's formula, specific density values, and decay factors (Johnson 1995). Snag density was summarized by diameter class for all species combined.

Finally, at 3 random points along the transect we took 3 pairs of distance measures for overstorey trees and 3 for understorey trees to test our presumption of random tree distribution. The point-centered quarter method will generate biased estimates of density if trees are not randomly distributed. We used the T-squared method of pattern analysis (Ludwig & Reynolds 1988) and we randomly chose which 3 of the 10 points from which to take these additional distance measures. After all 38 polygons had been sampled and grouped by community type we combined the distance measures to generate a single T-squared value for each tree class (overstorey and understorey) of each community type.

Vegetation data of taxa × sites were subjected to traditional phytosociological analysis, using chord distance as a measure of similarity or dissimilarity (Ludwig & Reynolds 1988). We then subjected the provisional community types to ANOVAs against environmental variables (elevation, aspect, slope, maximum snowpack depth, date of complete snowpack melt, date of soil moisture exhaustion, litter-rock-coarse debris-bare ground cover, litter depth, biomass of coarse woody debris and degree of soil profile development on a scale of 1-4, 1 being an Inseptisol, 2 an Entisol, 3 and 4 Alfisols or Spodosols with increasing intensities of profile expression) and against vegetation variables (total tree canopy cover, total tree density, total tree basal area, total shrub cover and total herb cover).

Herbarium voucher specimens were pressed in the field and later keyed to species, when necessary seeking the help of specialists (see Acknowledgements). Photographs of representative segments of the transect were taken for future reference.

Disease incidence sampling procedures

Some sampling transects were used for quantifying disease incidence. Upper montane stands, dominated by *Abies magnifica*, were not included. Twenty-two stands were visited in the summer of 1997. In each case, a circular plot (15 m radius) was established around each of the 10 points of the transect. We recorded disease incidence on trees in 3 size classes: 1-50 cm, 51-100 cm and > 100 cm DBH. Individual trees, diseased or not, were counted by species. Trees were noted as alive or dead; if dead, year of death was estimated by decay categories. Live trees were measured for live crown

ratio (span of height of crown as a fraction of total tree height).

Pest signs and symptoms were searched for in the crown, trunk and trunk base (e.g. Furniss & Carolin 1977; Hansen & Lewis 1997; Scharf 1993). Signs included the presence of fungal fruiting bodies, mistletoe and insects. Symptoms included the formation of witches brooms (typically caused by mistletoe, some rusts and *Elytroderma*), chlorosis of foliage, reduced live crown ratio, reduced density of foliage, resinosis and branch dieback.

On living trees, bark beetle attacks were confirmed by the presence of boring dust or pitch tubes. Bark was removed from dead trees to identify characteristic galleries of various bark beetle taxa. Recently dead trees (1-3 yr) were dissected to determine possible mortality agents. Fruiting bodies and the architecture of decayed wood can be used to determine pathogenic species. Tree death is rarely caused by a single agent. A succession of organisms, as well as abiotic stress (such as drought), all contribute to tree death (Ferrell et al. 1994; Filip & Goheen 1982; Worrall & Harrington 1988). However, proximate and ultimate causes of death could sometimes be determined.

Results

Overview characteristics of all the 38 stands

The 38 stands were located throughout the Basin (Barbour et al. 2000). They had a mean area of 25 ha and were < 2407 m a.s.l. (Table 1). All aspects were represented and slopes ranged from 8-62%. Dominant tree taxa included *Pinus jeffreyi, Abies concolor* and *A. magnifica*. Tree cover (overstorey and understorey) was ca. 47%, whereas shrub and herb cover were much less continuous, ca. 20% and < 1%, respectively. Mean density of overstorey trees (> 40 cm DBH) was $107.ha^{-1}$, mean density of understorey trees (1-40 cm DBH) $271.ha^{-1}$ and mean density of saplings $626.ha^{-1}$.

An important issue to resolve is: Are the old-growth sites a non-random assortment of all possible sites or do they represent a biased subset of the original old-growth landscape, perhaps left uncut because they were located on steep slopes with poor soils, difficult to reach or producing inferior timber? The range of topographic positions that our old-growth stands occupied did not appear to be restricted to steep slopes, nor was there any obvious narrowness in soil characteristics relative to sites with seral stands. There may be no way to satisfactorily answer this potential confounding factor of bias, but at least we can state that it remains unanswered.

The range of habitats represented by the stands was

**Table 1.** Environmental traits for 38 old-growth stands in the Tahoe Basin.

Trait	Range	Mean
Longitude (°W; range)	120°10 - 119°55	120°01
Latitude (°N; range)	39°17 - 38°47	39°02
Elevation (m; range)	1920 - 2406	2138
Slope (%; range)	8.0 - 62.5	31.5
Litter depth (cm)	1.8 - 9.7	4.6
Litter cover (%)	55 - 95	75.0
Rock + log cover (%)	5 -16	11.0
Tree cover (%)	20.0 - 71.6	45.3
Tree density (ha-1)	93 - 1102	378
Sapling density (ha^{-1})	0.0 - 5480	626
Tree basal area ($m^2 ha^{-1}$)	16.5 - 98.9	45.0
Shrub cover (%)	0.0 - 50.0	20.0
Herb cover (%)	0.0 - 10.0	0.5

not proportional to western and eastern regions of the basin, as seen in the bar graphs of Fig. 1. Eastern old-growth sites tended to be at higher elevations, on less-developed soils, non-north-facing aspects and on warmer or drier locations where complete snow melt occurred earlier in the year. More old-growth sites were located on the west side than on the east side because logging had historically been more intensive on the east side. The effect of the east side's drier environment on vegetation is dramatic: tree density is only half that on the west side (Fig. 2).

Species richness was 7 conifer, 28 shrub and 78 herb species. On an individual transect, there was a mean of only 4 tree, 5 shrub and 8 herb taxa. There was considerable β-diversity, however, 6 shrub and 30 herb taxa occurring only once.

Saplings of breast height (4 taxa combined) had a weighted mean age of 61 yr (range = 25-110 yr; $n = 72$). There was no statistically significant difference among the species at the $p < 0.05$ confidence level. Ring counts of 40 cm DBH individuals of the same 4 taxa had a weighted mean of 117 rings at breast height (range = 41 to 306; $n = 201$). Again, there was no significant difference for age among the taxa. When sapling age is added to age at breast height, trees 40 cm DBH had a weighted mean age of 178 yr. Thus, our 3 age cohorts were approximately: 20-60 yr, 61-180 yr and > 180 yr. We did not age the largest (and presumably oldest) overstorey trees, but summaries of life spans in Burns & Honkala (1990) and Sudworth (1967) indicate that individuals in these taxa commonly attain ages up to 450 yr.

The overall relationship of DBH to tree age, based on our corings and ring counts for all species combined is: age = 67 + [(3.0) (cm DBH)] yr ($r^2 = 0.48$). Based on this formula, the minimum age of trees large enough to qualify as 'old-growth' by the Forest Service (76 cm DBH) is 295 yr.
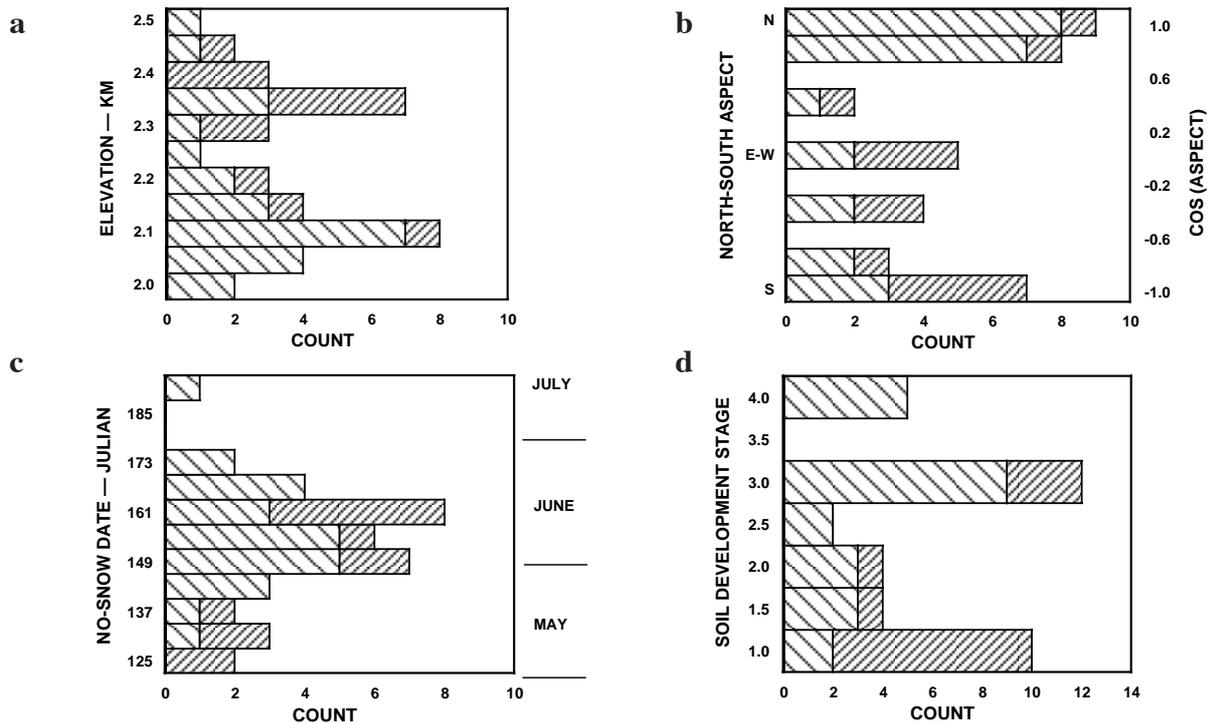
Fig. 1. East-vs-west profiles of old-growth forest stands. Total length of a bar represents all sites; light shading = stands in the western portion of the basin, dense shading = stands in the eastern portion of the basin. Stands are arrayed against **a.** elevation, **b.** aspect, **c.** date of complete snow melt (numbers are Julian dates, 1 being January 1st) and **d.** soil development (1 = rock, 2 = Entisol, 3 = Inceptisol, 4 = Alfisol).

Disease incidence

Some 24 common pathogens and insects on our Basin transects fell into the categories of wood-boring insects, mistletoes, root rots, trunk rots and rusts. The most widespread (present in 22 of the 38 old-growth transects) were the bark beetles *Scolytus ventralis* on *Abies concolor* (100% presence) and *Dendroctonus jeffreyi* on *Pinus jeffreyi* (68% presence). All other pathogens had 5-36% presence. With regard to % occurrence on species, rather than transects, bark beetles were associated with nearly 100% of dead trees of all species. For example, *S. ventralis* was associated with 96% of dead *A. concolor* and *D. jeffreyi* was associated with 91% of all dead *P. jeffreyi*. Live trees had an order of magnitude lower infection percentage.

The percentage of individuals infected with other pathogens was generally low, with considerable variation from stand to stand. *Arceuthobium* spp. (dwarf mistletoe) on *P. jeffreyi* was found in 41% of the stands but only ca. 7% of the trees were infected. *Arceuthobium* on *A. concolor* was found in 24% of the stands but only on 3% of the individuals. There was no significant difference in infection percentage for *Arceuthobium* when comparing live and dead trees. There was a low

incidence of root disease, the most common pathogen being *Heterobasidion annosum* on *A. concolor* with ca. 3% of trees being infected. No incidence of this pathogen was observed on *Pinus* species or *Calocedrus decurrens*. Of the major trunk rot fungi, *Oligoporus amarus* was noted on 11% of *C. decurrens* and *Echinodontium tinctorium* was noted on < 1% of *A. concolor*. Rusts were similarly low in occurrence: 9% of *C. decurrens* trees were infected with the rust *Gymnosporangium libocedri* and 11% were infected with *O. amarus* and fewer than 1% of *Pinus lambertiana* were infected with *Cronartium ribicola* (white pine blister rust).

There were ca. 39 standing dead trees.ha^{-1}, which represented 16% of all trees living and dead that were > 1 cm DBH. Ca. half of the dead trees were > 40 cm DBH and 16% were > 76 cm DBH. Most of the dead trees were *A. concolor* (62%) or *P. jeffreyi* (32%), with *Abies magnifica*, *C. decurrens* and *P. lambertiana* making up the remaining 4%.

Analyses by forest community

Phytosociological analysis of our set of 38 sites × 112 taxa revealed 6 clusters differentiated mainly by abundance of particular tree species. Although shrub
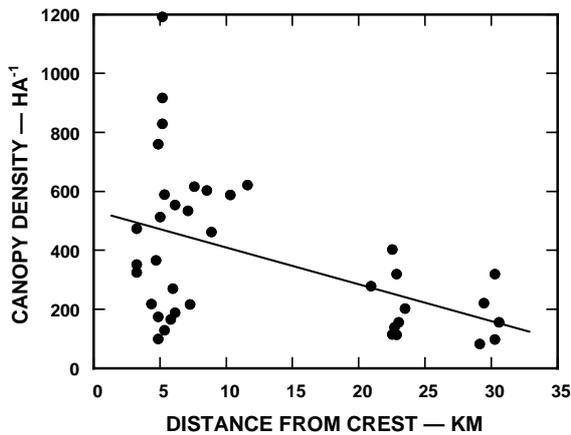
Fig. 2. Regression between tree density (understory + overstory) and easterliness. Each point represents one of the 38 old-growth stands. The slope is significantly different from 0 at $p < 0.003$.

Table 2. ANOVA between floristic- or dominance-defined forest types (clusters) and environmental traits. Floristic types are based on traditional phytosociological analysis of complete floristic lists, whereas series types are based on the importance percentages of overstory tree species. East = distance east of the Sierra Nevada crest; soil = degree of profile development. Only environmental factors with significant F-values (of 12 analysed) are shown.

Classification	No. clusters	Elevation	East	Tree density	Litter depth	Soil
Floristic	6	0.001	0.003	0.02	0.04	
Series	4			0.04	0.02	0.05

and herb cover and composition did separate clusters, their contribution was modest (differences among the 6 clusters in terms of herbs and shrubs was not statistically significant; $p > 0.05$).

We combined the 6 floristic clusters into 4 dominance-defined clusters or series (equivalent to Forest Service dominance types, see Sawyer & Keeler-Wolf 1996), each of which carries the common English name of the dominant (Tables 3-6) Thus we have the *Pinus jeffreyi* series (importance percentage of *Pinus jeffreyi* > 50; 7 sites), the *Abies concolor* series (importance percentage of *A. concolor* > 50; 14 sites), the *Abies magnifica* series (importance percentage of *A. magnifica* > 50; 6 sites) and the mixed conifer series (no species with an importance percentage > 50; 11 sites). These series were much more weakly related to environmental factors, significantly different only with regard to tree density, litter depth and soil profile development (Table 2).

Tree density was highest in the *Abies concolor* series (108 overstorey + 431 understorey trees.ha^{-1}), basal area was highest in the *Abies magnifica* series (59 m^2), both density and basal area were lowest in the *Pinus jeffreyi* series (63 overstorey and 222 understorey trees.ha^{-1}; 31 m^2.ha^{-1}). Sapling density was lowest in the mixed conifer series (425.ha^{-1}) and highest in the *Abies magnifica* series (601.ha^{-1}), but these differences were not significant ($p > 0.05$).

The density of trees > 76 cm DBH was highest in the *Abies magnifica* series (50.ha^{-1}) and lowest in the *Pinus jeffreyi* series (24.ha^{-1}). As a percentage of overstorey trees, however, there was less difference among the 4 series, and those differences were not significant ($p > 0.05$): the *Abies concolor* series was lowest at 13%, the *Pinus jeffreyi* series next at 14%, mixed conifer series at 18% and *Abies magnifica* series highest at 19%. The overall range of absolute density for trees > 76 cm DBH among all 38 stands was 8-89 trees.ha^{-1}.

Pinus jeffreyi series stands had the simplest overstory in terms of species composition: *Pinus jeffreyi*, *Abies concolor* and *Calocedrus decurrens* in a density ratio of 2.3 to 1 to 0.05, with virtually no other species (Table 3). The understorey and sapling layers were, however, much more diverse. *P. jeffreyi* declined dramatically in importance percentage from the oldest cohort (overstorey, 68) to the understorey cohort (34) to the sapling cohort (6) – a 10-fold drop. At the same time, *A. concolor* increased in importance value over the same 3 cohorts from 29 to 54 and *C. decurrens* increased from 2 to 38.

In the mixed conifer series, *Pinus jeffreyi* and *Abies concolor* shared dominance and 3 other species were co-equal associates with considerably lower densities, basal areas and frequencies (Table 4). As with stands in the *Pinus jeffreyi* series, the importance percentage of *P. jeffreyi* declined with younger cohorts (29-15-3) while that of *A. concolor* increased (33-55-78). *Calocedrus decurrens* also increased, but not as much as in the Jeffrey pine series (5-20-11). *Abies magnifica* had a strong increase in importance in younger cohorts (4-17-80).

The *Abies concolor* series was strongly dominated by *A. concolor*. *A. magnifica* and *P. jeffreyi* were often present but contributed only ca. 14-25% the density of *A. concolor* (Table 5). Importance of *P. jeffreyi* declined in increasingly younger cohorts (14-7-1), but the importance of other conifers (including *A. concolor*) did not show a consistent pattern of change.

The *Abies magnifica* series was more completely dominated by a single species (importance percentage of *A. magnifica* = 76 in the overstorey; Table 6). *A. magnifica* showed a modest decline in importance in younger and younger cohorts, while *A. concolor* increased 4-fold (7-15-28). No other taxon exhibited any consistent pattern of change with cohort in this series.

Pattern analysis, via the T-squared test, showed that overstorey trees in each of the 4 series were distributed randomly. Understorey trees, however, were clumped in all but the mixed conifer series. The mean C factor for

Table 3. Traits of stands in the *Pinus jeffreyi* series (*n* = 7). DEN = density (ha^{-1}), BA = basal area (m^2.ha^{-1}; FR = frequency (%), IP = importance percentage.

Cohort and species	DEN	BA	FR	IP
Overstorey				
Pinus jeffreyi	43	20	91	68
Pinus lambertiana	0	0	0	0
Abies concolor	19	6	59	29
Abies magnifica	< 1	< 1	1	1
Calocedrus decurrens	1	1	4	2
Others	< 1	< 1	1	1
Total, DBH > 40 cm	63	27		
Density DBH 76-100 cm	15			
Density DBH >100 cm	9			
Understorey				
P. jeffreyi	40	1	55	34
P. lambertiana	3	< 1	10	< 1
A. concolor	137	3	89	58
A. magnifica	< 1	< 1	3	1
C. decurrens	39	< 1	16	7
Others	3	< 1	3	1
Total	222	4		
Saplings				
P. jeffreyi	11		3	6
P. lambertiana	0		0	0
A. concolor	183		21	54
A. magnifica	6		1	3
C. decurrens	234		7	38
Others	0		0	0
Total	434			

Table 4. Traits of stands in the mixed conifer series (*n* = 11). DEN = density (ha^{-1}), BA = basal area (m^2.ha^{-1}), FR = frequency (%), IP = importance percentage.

Cohort and species	DEN	BA	FR	IP
Overstorey				
Pinus jeffreyi	19	12	67	29
P. lambertiana	6	8	31	14
Abies concolor	27	11	76	33
A. magnifica	4	2	15	6
Calocedrus decurrens	5	5	24	10
Others	6	2	24	8
Total, DBH > 40 cm	67	40		
Density DBH 76-100 cm	13			
Density DBH > 100 cm	17			
Understorey				
P. jeffreyi	20	1	35	15
P. lambertiana	4	< 1	9	3
A. concolor	135	4	90	55
A. magnifica	17	< 1	23	9
C. decurrens	20	< 1	19	8
Others	15	< 1	21	11
Total	211	5		
Saplings				
P. jeffreyi	7		2	3
P. lambertiana	0		0	0
A. concolor	327		26	78
A. magnifica	80		5	16
C. decurrens	11		3	5
Others	0		0	0
Total	425			

understorey trees in the 3 clumped series was 0.65 (where C = 0.50 for a completely random distribution and values higher than that indicate clumping). This particular departure from 0.5, although statistically significant (*p* < 0.05), indicates only a moderate degree of clumping. Simulation

testing by Engeman et al. (1994) of distribution patterns that were regular, random, moderately clumped and strongly clumped have shown that moderate clumping underestimates density by ca. 15%. Consequently, understorey tree densities are at least those shown in Tables 3-6 and they

Table 5. Traits of stands in the white fir series (n = 14). DEN = density (ha^{-1}), BA = basal area (m^2 ha^{-1}), FR = frequency (%), IP = importance percentage, 76-100 = density of trees 76-100 cm DBH, >100 = density of trees >100 cm DBH.

Cohort and species	DEN	BA	FR	IP
Overstorey				
Pinus jeffreyi	10	6	25	14
P. lambertiana	< 1	< 1	1	1
Abies concolor	74	28	88	63
A. magnifica	21	5	36	16
Calocedrus decurrens	1	1	4	1
Others	2	1	7	5
Density DBH 76 - 100 cm	108	41		
Density DBH 76 - 100 cm	22			
Density DBH > 100 cm	12			
Understorey				
P. jeffreyi	10	< 1	16	7
P. lambertiana	< 1	< 1	1	< 1
A. concolor	315	7	91	64
A. magnifica	75	1	41	21
C. decurrens	10	< 1	7	3
Others	21	< 1	9	5
Total	431	8		
Saplings				
P. jeffreyi	3		1	1
P. lambertiana	0		0	0
A. concolor	489		32	83
A. magnifica	46		7	13
C. decurrens	0		0	0
Others	11		2	4
Total	543			

Table 6. Traits of stands in the red fir series (*n* = 14). DEN = density (ha^{-1}), BA = basal area (m^2 ha^{-1}), FR = frequency (%), IP = importance percentage, 76-100 = density of trees 76-100 cm DBH, >100 = density of trees >100 cm DBH.

Cohort and species	DEN	BA	FR	IP
Overstorey				
Pinus jeffreyi	3	2	15	6
P. monticola	1	<1	3	2
Abies concolor	6	1	20	7
A. magnifica	86	47	100	76
Calocedrus decurrens	0	0	0	0
Others	11	3	28	10
Density DBH 76 - 100 cm	107	53		
Density DBH 76 - 100 cm	25			
Density DBH > 100 cm	25			
Understorey				
P. jeffreyi	1	<1	5	2
P. monticola	0	0	0	0
A. concolor	34	1	33	15
A. magnifica	155	4	100	67
C. decurrens	0	0	0	0
Others	27	1	38	16
Total	217	6		
Saplings				
P. jeffreyi	7		2	2
P. monticola	0		0	0
A. concolor	167		13	28
A. magnifica	380		27	59
C. decurrens	0		0	0
Others	47		7	11
Total	601			

could be up to 15% higher.

Forest floor surfaces of the 4 series were not statistically different ($p > 0.05$) in terms of percent cover by shrubs, herbs, rock, litter or coarse woody debris (Table 7). Litter covered 80% of the ground; rocks and coarse debris covered 11% of the ground. The *Abies concolor* series was associated with the thickest litter layer and the *Pinus jeffreyi* series was associated with the thinnest, but these were trends without significant differences.

Fuel loads of coarse woody debris (> 25 cm diameter) were high, ca. 58 t.ha^{-1}. This value is well within modern values for mixed conifer, *Abies concolor* and *A. magnifica* stands from throughout the northern Sierra Nevada, which range from 2 to 103 t.ha^{-1} (Blonski & Schramel 1981). We presume, however, that they are much higher than pre-contact values when surface fires recurred every 15-25 yr. A few stands had exceptional fuel loads: 2 *A. concolor* stands had 156 and 162 t.ha^{-1} of coarse woody debris. There was no statistically significant difference ($p > 0.05$) in the amount of coarse woody debris among the 4 series, but there was a definite trend: Jeffrey pine and mixed conifer series stands had ca. 50-33% of the fuel biomass of *A. concolor* and *A. magnifica* series stands (Table 7). We did not measure debris smaller than 25 cm diameter. According to tables in Blonski & Schramel (1981), such debris would contribute another 60%, or 34 t.ha^{-1}.

Snags of all diameters were ca. 70.ha^{-1}, equivalent to 14% of total (live and dead) tree density. Snag density was lowest in the red fir series (46.ha^{-1}, 12% of all trees) and highest in the *Pinus jeffreyi* series (109.ha^{-1}, 28% of all trees; Table 7). Most of the snags were < 76 cm DBH, implying that relatively young/small trees have been more at risk than older/larger trees. Mixed conifer and *Abies magnifica* series showed the highest percentages of snags > 76 cm DBH: 25 and 33%, respectively, vs 10% in *Pinus jeffreyi* and *Abies concolor* series.

Analyses by tree species

We calculated correlation values between the importance percentage of the 4 most common conifer species and 9 environmental factors. The relatively few significant correlations are summarized in Table 8. For a given species, at least 2 of the 3 cohorts performed equally. For example, *A. concolor's* overstorey tree, understorey tree and sapling importances were all significantly and negatively correlated with elevation (Table 8). *A. concolor* was thus favoured by low-elevation mesic sites; *A. magnifica* by high-elevation, north-facing, late-melting sites; *P. jeffreyi* by south-facing, eastern, arid sites with an early date of snow melt and *Calocedrus decurrens* by low-elevation sites with little snow and early date of snow melt.

Correlations with tree density, rather than importance percentage, revealed additional relationships between species and environmental gradients. *A. concolor* density was significantly and negatively correlated with easterliness and significantly and positively correlated with coarse woody debris biomass. The other taxa had no significant relationships with any factors.

Saplings were only somewhat more sensitive to environmental gradients than were trees. Those of *A. concolor*, *A. magnifica* and *P. jeffreyi* had greater importance beneath the cover of their own species, but saplings of the remaining 3 taxa exhibited no overstorey preferences. *A. concolor's* sapling importance was positively correlated with overstorey canopy cover of itself ($p < 0.01$) and negatively correlated with canopy cover by *A. magnifica* ($p < 0.0003$). *A. magnifica's* sapling importance was the mirror image, positively correlated with canopy cover of itself ($p < 0.0001$) and negatively with canopy cover of *A. concolor* ($p < 0.02$). Finally, *P. jeffreyi's* sapling importance was positively correlated with canopy cover of itself ($p < 0.0005$) but not negatively correlated with any other overstorey species.

Sapling importance was unrelated to physical factors except in the case of *A. concolor* being positively correlated with litter depth ($p < 0.009$) and *A. magnifica* being negatively correlated ($p < 0.01$). This relationship reflects the known tolerance to litter by *A. concolor* seedlings (Burns & Honkala 1994). Neither saplings nor trees were related to the biomass of coarse woody debris. Sapling importance was not significantly correlated with total shrub cover or N-fixing shrub cover, nor was it correlated with coarse woody debris biomass.

Table 7. Forest floor attributes of the 4 series. LD = Litter depth, CWD = Coarse woody debris for all material > 25 cm diameter. ANOVA of series vs physical traits were significant ($p < 0.05$) only for LD, but no pair of individual values was significantly different. ANOVA of series vs snag density was significant ($p < 0.05$) only for the < 76 category and mixed conifer-red fir series were significantly different from *Pinus jeffreyi-Abies concolor* series ($p < 0.05$).

Series	Cover (%)				LD (cm)	CWD (t.ha^{-1})	Snag density ha^{-1}		
	Shrub	Herb	Litter	Rock+log			< 76 cm DBH	76 - 100 cm DBH	> 100 cm DBH
Pinus jeffreyi	27	27	5	15	3.8	33.5	97	8	4
Mixed conifer	21	2	77	12	4.2	24.5	28	3	6
Abies concolor	17	4	84	9	6.1	102.6	80	5	3
Abies magnifica	16	1	86	0	3.4	53.5	31	6	9

Discussion

Estimation of total remaining old-growth area

Old-growth stands do exist in the Basin, but they occupy a small percentage of the landscape. Our field check of 400 potential old-growth polygons revealed only 38 that were unentered old-growth stands. The total combined old-growth area of lower and upper montane forest is 1030 ha. The area of lower and upper montane forest in the basin, including all seral phases, is 38 340 ha based on our assessment of current Forest Service vegetation maps. Thus, old-growth forest today accounts for 2.7% of the forested area.

How many of those 38 340 ha were in late-successional, old-growth status prior to Euroamerican contact? The best estimate comes from an examination of old-growth landscapes in Sierran national parks located in the same ecological zones. Franklin & Fites-Kaufmann (1996) analysed Lassen Volcanic, Yosemite and Sequoia and Kings Canyon National Parks and concluded that 55% of the modern forested landscape was in old-growth status and the rest was seral. As logging had never occurred in those parks, they deduced that the present landscape was equal to the past. Applying 55% to the Tahoe Basin gives 21,087 ha as old-growth in the past. Today's 1030 ha represents a 95% reduction of the pre-existing old-growth area.

Modern vs. pre-contact old-growth forest

How does the structure and composition of modern old-growth vegetation compare with pre-contact old-

growth forest? Three kinds of indirect evidence in the Basin can be used to reconstruct the pre-contact vegetation: (1) analysis of stumps still remaining from logging in the late 1800s (Taylor 1998), (2) surveys of the General Land Office (GLO) (Barbour et al. 2000) and (3) data from other old growth forests in the area.

One type of evidence is the density, size distribution and species identity of stumps still remaining from clear-cuts of old-growth forest accomplished in the late 1800s. Taylor (1998) examined 17 such logged sites on the east side of the Basin that had been harvested between 1875 and 1902. The relatively cool and dry conditions preserved stumps down to a diameter of 10 cm. Half-hectare samples were taken of 11 *Pinus jeffreyi* and 6 *Abies magnifica* stands, the data consisting of stump diameter, location and species identity.

An abstraction of Taylor's results shows pre-contact *P. jeffreyi* stands with a *Pinus* : *Abies* ratio of 4 to 1, 68 trees.ha^{-1}, a basal area of 26 m^2.ha^{-1} and importance percentages of *P. jeffreyi* = 79, *A. concolor* = 19 and *A. magnifica* = 2. These values are within 7% of the values for modern *P. jeffreyi* stand overstories in the Basin (Table 3). Total tree density (understorey and overstorey), however, is much higher today (131 understorey trees ha^{1}, after subtracting trees < 10 cm DBH, plus 63 overstorey trees.ha^{-1} = 194), almost 3 × pre-contact density.

Taylor's pre-contact *A. magnifica* stands had 160 trees.ha^{-1}, a basal area of 57 m^2.ha^{-1} and importance percentages of *A. magnifica* = 66, *Pinus monticola* = 29 and *P. contorta* = 5. Modern *A. magnifica* stands (Table 6) have a total tree density (overstorey and understorey) only 20% greater and an overstorey basal area only 7% lower; thus, the magnitude of change in the upper montane has been much less than in the lower montane.

A second source of data for the reconstruction of 19th century forests in the Basin is GLO records by surveyors who annotated their routes and section corners by recording the identity of the nearest large tree. Fites-Kaufmann recently summarized GLO data ca. 1870-1890 (Barbour et al. 2000) and concluded that the ratio of *Pinus* : *Abies* in the lower montane zone throughout the Basin was then 1 to 1. Taylor's 4 to 1 ratio (above), thus may have represented only the drier east side of the Basin. Anecdotal accounts by 2 turn-of-the-century foresters, Lieberg (1902) and Sterling (1904), ratify the GLO ratio. They wrote that *Abies concolor* accounted for 25-40% of all trees in lower montane forests, that *Pinus lambertiana* and *P. jeffreyi* each accounted for 20-25% of all trees and that *P. contorta* and *Calocedrus decurrens* accounted for the rest. Excluding *P. contorta*, the *Pinus* : *Abies* was 1.5 to 1.

A third type of evidence for pre-contact Basin forests comes from modern mixed conifer forests in the Sierra San Pedro Martir (SPM) described by Minnich et

Table 8. Correlations between tree importance percentage and environmental traits. Only significant relationships are shown, from the environmental factors tested and only those 4 species exhibiting more than one significant relationship are shown. Not shown: *Pinus lambertiana* overstorey trees were negatively correlated with elevation ($p < 0.05$) and *P. monticola* saplings were positively correlated with date of snow melt ($p < 0.05$). The + or - shows the direction of the correlation; one symbol = $p < 0.05$; two symbols = $p < 0.01$.

Species/cohort	Elevation	Aspect	Eastern liness	Snow depth	Snow melt
Abies concolor/overstorey	-				
A.c./understorey	- -				
A.c./saplings	- -				
Abies magnifica/overstorey	+	+			+
A.m./understorey	+	+			+
A.m./saplings	++				
Pinus jeffreyi/overstorey		-	+		-
P.j./understorey		-	+		-
P.j./saplings					
Calocedrus decurrens/overstorey	-			-	-
C.d./understorey	-			-	-
C.d./saplings					-

al. (2000). The SPM is the southern-most portion of the Peninsular Range, which extends from southern California south across the international border for 250 km into Baja California Norte. Mixed conifer forests in the SPM are ecologically analogous to those in the Basin (Minnich 1986; Minnich et al. 1995, 2000): *Pinus jeffreyi, P. contorta, P. lambertiana, Abies concolor* and *Calocedrus decurrens* dominate a rolling plateau at 1900-2500 m a.s.l.; mean annual precipitation is 65 cm, more than 50% of which falls as snow. Fire suppression management has never been practised in SPM and fire-scar studies indicate a mean fire return interval over the past 400 yr of 26 yr, with no evidence of any increase during that time.

Minnich and his colleagues quantified 21 forest stands comparable to those of the Tahoe Basin, using a restricted-random method of stand selection and the same point-centered quarter method we used in the Tahoe Basin. Tree density (understorey and overstorey, all individuals > 3 cm DBH) ranged from 78.ha^{-1} in *P. jeffreyi* forest to 156.ha^{-1} for *A. concolor* forest. The size-class distributions were various, but no stand had peak density in the youngest cohort, in contrast to modern Tahoe Basin old-growth forests. SPM forests had 20-25 trees.ha^{-1} of size > 76 cm DBH (17-28% of all trees). Basal area for all trees combined ranged from a low of 21 m^2.ha^{-1} in *P. jeffreyi* stands to 34 m^2.ha^{-1} in *A. concolor* stands.

These SPM data are remarkably similar to overstorey data for modern Tahoe stands. Overstorey tree density in *Pinus jeffreyi* stands in the Basin is within 20% of SPM density and within 30% for *Abies concolor* stands. Overstorey basal area in Basin *P. jeffreyi* stands is within 30% of SPM basal area and within 21% for *A. concolor* stands. Some 30% of all trees were > 76 cm DBH in the 2 series in the Basin. Although the overstories are similar, the understories are different. SPM understorey and sapling species composition show no trends toward increasing importance of *A. concolor* and *Calocedrus decurrens* and decreasing importance of *P. jeffreyi*, whereas Basin forests have 4 times as many understorey trees, an importance of *A. concolor* and *C. decurrens* 2-3-fold higher and an importance of *P. jeffreyi* 50% lower. The implication is that future SPM forests will remain with the density and species balance they currently exhibit, but that Basin forests will become more and more densely homogeneous, dominated by *A. concolor* in all age cohorts.

Health of modern old-growth forests

One measure of health is disease incidence and mortality, as compared with the less-impacted SPM forest of Baja California. Maloney & Rizzo (2002) quantified disease incidence in 16 SPM stands domi-

nated by *Abies conolor, Calocedrus decurrens, Pinus Jeffreyi, P. lambertiana* or a mixture.

Individual Tahoe stand mortality ranged from a low of 3% to a high of 33%, whereas the range of mortality in SPM was narrower, only 4-15% (Savage 1997; Maloney & Rizzo 2002). The majority of standing dead trees in the Basin had died during a drought of 1988-1992, judging from decay classes, whereas the majority of deaths in the SPM were older. SPM forests appear to have endured the 1988-92 drought without the epidemic bark beetle outbreaks and mortality experienced in the forests of Alta California. Bark beetle mortality in the Basin was similar to that in forests of the Modoc Plateau, Southern Cascades, entire eastside of the Sierra Nevada and mountains of southern California (Smith et al. 1994; Dale 1996) and also to that in the Transverse Range of southern California where Savage (1997) reported a mean mortality of 14%, compared to only 4% mortality in SPM forests.

Patterns of distribution of old-growth forests and dominant species within the Basin

Forest types – whether floristic associations or dominance-based series – were generally poorly correlated with the environmental factors we chose to quantify. Possibly, this situation can be ascribed to the relatively few number of old-growth stands still in existence, leading to noisy statistical relationships. Also, the Basin's modest range and gradients of environments, coupled with the wide distribution of *Abies concolor*, may have combined to minimize vegetational diversity and relationships with environmental factors. The only environmental gradients statistically linked to clusters were elevation, easterliness, tree density, litter depth and soil development. All of these factors, ultimately, are expressions of aridity and warmth during the growing season.

The link between conifer species and environmental factors was only somewhat richer than community types based on dominance, adding aspect, maximum snowpack depth and date of complete snow melt for the 4 most common tree taxa. The distribution of less common *Pinus lambertiana* and *P. monticola* exhibited almost no relationship to the environmental factors, perhaps because data were less intensive/ extensive than for the common species or because they had broader environmental tolerances. Royce & Barbour (2001a) showed very close relationships between conifer species importance and snowpack depth and melt dates in the southern Sierra Nevada, but the gradients there were much broader and steeper than those within the Tahoe Basin.

Old-growth definition: a moving target

Relictual old-growth forest stands in the Tahoe Basin exhibit the same demographic trends shown by mixed conifer stands elsewhere in California: an increasing dominance by *Abies concolor* and a declining importance of *Pinus jeffreyi* and several other pine species. The increase in dominance is lowest in stands of the *A. magnifica* series, but even there the importance percentage of *A. concolor* has tripled in the last 150 yr. This pattern of declining *Pinus* importance and increasing *Abies* importance has been indirectly documented for other parts of the Californias, such as the west slope of the Sierra Nevada (Barbour & Minnich 2000; Bouldin 1999; Feldman 2000) and the Transverse Ranges (Minnich et al. 1995), but ours is the first study of the phenomenon in drier, more continental habitats such as the east slope of the Sierra Nevada. If active management were to include thinning of young trees and prescribed fire, it is probable that succession could be set back and that the pre-contact landscape might be approached in the Tahoe Basin and elsewhere in Alta California. Otherwise, the shift from *Pinus* to *Abies* and from open to closed forests will continue into the near future.

Modern old-growth relictual stands in the Tahoe Basin have neither pre-contact nor near-future attributes. If we wish to quantitatively define the attributes for old-growth status today, we should keep in mind that the definition is a moving target.

Minimum criteria for current old-growth forest

Based on our data, and adopting a protocol that 'minimum' or 'maximum' shall be 2 standard deviations from the mean, then we propose that a given ha of current old-growth Basin forest must have: (1) a minimum of 5 snags of > 76 cm DBH (mean = 16), 10 living trees of > 76 cm DBH or > 295 yr of age (the average is 50), and 25 living trees > 40 cm DBH or > 180 yr old (mean = 107) and (2) a maximum of 400 understorey and overstorey trees for all forest types except *Abies concolor* (mean without *A. concolor* = 296) or 625 for *A. concolor* stands (mean = 539) and 35% cover by shrubs and herbs (mean = 21%).

This definition is much more quantitative than the definition adopted a few years ago by the Tahoe Regional Planning Agency governing body. Because of its more quantitative nature, the success of future management attempts to move seral forest to old-growth status can be measured. The rate of change towards a target and the direction of change toward a target can now be quantified and judged to be appropriate or inappropriate, allowing a process of adaptive management to proceed. Our definition complements the current Forest Service focus on management objectives that define a healthy forest as being within its 'historic range of variation'.

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