Population biology of sugar pine (*Pinus lambertiana* Dougl.) with reference to historical disturbances in the Lake Tahoe Basin: Implications for restoration

Patricia E. Maloney [a,*], Detlev R. Vogler [b], Andrew J. Eckert [c,d], Camille E. Jensen [a], David B. Neale [d,e]

[a] *Department of Plant Pathology and Tahoe Environmental Research Center, University of California, One Shields Avenue, Davis, CA 95616, USA*
[b] *USDA, Forest Service, Pacific Southwest Research Station, Institute of Forest Genetics, 2480 Carson Road, Placerville, CA 95667, USA*
[c] *Section of Evolution and Ecology, University of California, One Shields Avenue, Davis, CA 95616, USA*
[d] *Center for Population Biology, University of California, One Shields Avenue, Davis, CA 95616, USA*
[e] *Department of Plant Sciences, University of California, One Shields Avenue, Davis, CA 95616, USA*

ABSTRACT

Historical logging, fire suppression, and an invasive pathogen, *Cronartium ribicola*, the cause of white pine blister rust (WPBR), are assumed to have dramatically affected sugar pine (*Pinus lambertiana*) populations in the Lake Tahoe Basin. We examined population- and genetic-level consequences of these disturbances within 10 sugar pine populations by assessing current population structure and trends for 1129 individuals, genetic diversity for 250 individuals, and frequency of WPBR-resistance for 102 families. Logging had occurred in 9 of 10 sites and fire suppression was evident in all stands. High density of white fir (*Abies concolor*) is often an indicator of fire suppression and we found a negative relationship between sugar pine survivorship and white fir basal area ($r^2 = 0.31$). *C. ribicola* was present in 90% of stands (incidence range: 0–48%) and we found a significant relationship between mean host survivorship and disease incidence ($r^2 = 0.46$). We estimated population growth rates (λ) from size-based transition matrices. For six of 10 sugar pine populations λ was $\geqslant 1.0$, indicating that these populations appear to be stable; for four populations, λ was <1.0, indicating populations that may be in decline. A population specific drift parameter, c_i, which is a measure of genetic differentiation in allele frequencies relative to an ancestral population, ranged from 0.009 to 0.048. Higher values of c_i indicate greater genetic drift, possibly due to a bottleneck caused by historical logging, other agents of mortality or much older events affecting population sizes. Effects of drift are known to be greater in small populations and we found a negative relationship between sugar pine density and c_i ($r^2 = 0.36$). Allele frequency of the *Cr1* gene, responsible for WPBR-resistance in sugar pine, averaged 0.068 for all populations sampled; no WPBR infection was found in one population in which the *Cr1* frequency was 0.112. Historical disturbances and their interactions have likely influenced the population biology of sugar pine in the Tahoe Basin; for some populations this has meant reduced population size, higher genetic drift, and poor survival of small- and intermediate-sized individuals. Possible management strategies include restoring population numbers, deploying WPBR-resistance, treating stands to promote natural sugar pine regeneration, and enhancing genetic diversity.

© 2011 Elsevier B.V. All rights reserved.

1. Introduction

Scientists and land managers have rarely considered both the population- and genetic-level consequences of historical disturbances on forest tree species. For more than a century, historical logging, fire suppression, and invasion of the fungal pathogen, *Cronartium ribicola* J.C. Fisch., have influenced populations of *Pinus lambertiana* Dougl. (sugar pine) in mixed-conifer forests of California (Laudenslayer and Darr, 1990; Kinloch et al., 1996;

Maloney, 2000; van Mantgem et al., 2004; Shaw and Geils, 2010 and articles therein). These disturbances and their interactions have the potential to alter the abundance, vital rates (birth, death, and growth), and genetic structure and diversity of sugar pine.

Between c. 1850 and 1910 extensive clearcutting occurred in the Lake Tahoe Basin, providing fuel wood for silver mining of the Comstock Lode in Nevada (Elliot-Fisk et al., 1996; Lindström, 2000). Cutting focused preferentially on large diameter yellow (*P. jeffreyi* and *P. ponderosa*) and white pine (*P. lambertiana*) species (Lindström, 2000). In some locations, sugar pine formerly comprised 20–25% of all trees (e.g., relative density) in a mixed-conifer forest, but at present is only 1–6% (Lindström, 2000; Barbour et al., 2002). Because reforestation was not practiced in the Comstock

period, such losses in sugar pine numbers dramatically altered their abundance and potentially their genetic diversity.

Fire suppression in the Sierra Nevada has resulted in fundamental shifts in forest composition and structure (Kilgore, 1973; SNEP Science Team, 1996; Ansley and Battles, 1998). Lack of fire has increased stand densities of shade-tolerant/fire intolerant tree species and significantly altered stand dynamics and competitive interactions for resources (light, water, nutrients) in these historically pine-dominated communities (Barbour et al., 2002; North et al., 2007; Zald et al., 2008). Because sugar pine is relatively shade-intolerant, the potential for recruitment and small tree survival is greatly reduced in dense forests, which favor shade-tolerant species such as white fir (*Abies concolor*) and incense cedar (*Calocedrus decurrens*) (Zald et al., 2008).

The non-native fungal pathogen *C. ribicola* is a primary management concern in all five-needle white pine ecosystems in western North America. *C. ribicola* (white pine blister rust; WPBR) was introduced into British Columbia around 1910 and arrived in northern California around 1929, the southern Sierra Nevada by 1961 (Smith, 1996), and the Lake Tahoe region during the1980s (K. Jones, pers. comm., USDA Forest Service). While all size classes of sugar pine are susceptible to WPBR, individuals often infected with stem cankers are less than 20 cm in diameter at breast height (measured at 1.37 m height above ground) (Maloney, 2000). Stem cankers are especially lethal to small individuals (Smith, 1996) and can dramatically alter population structure, by reducing or eliminating individuals in smaller diameter size classes.

Although WPBR can be fatal to all white pine species, a gene is present at low frequency in sugar pine that confers immunity from *C. ribicola* (Kinloch et al., 1970). This gene, designated *Cr1*, controls a hypersensitive response in needles that prevents further fungal growth (Kinloch and Littlefield, 1976). *Cr1* is the foundation for naturally occurring resistance in sugar pine to *C. ribicola* in California, and moderate levels of resistance to WPBR are known to exist in the Lake Tahoe region (J. Dunlap and J. Gleason, pers. comm., USDA Forest Service).

Our goal was to determine current population and genetic characteristics of *P. lambertiana* given the history of Comstock logging, fire suppression, and *C. ribicola* in the Lake Tahoe Basin. To better understand both population- and genetic-level consequences of these historical disturbances on sugar pine we have taken an ecological and genetic approach. Given the diversity in forest conditions across the Basin our objectives were to determine: (i) the current population structure and trends of sugar pine in the Basin, (ii) the genetic structure and diversity of extant sugar pine populations, (iii) relationships between stand and sugar pine population characteristics with historical disturbances (logging, fire suppression and WPBR), and (iv) landscape-scale frequency of WPBR-resistance (*Cr1*). Any restoration strategies to potentially mitigate these anthropogenic disturbances will require information on current population, genetic, and stand conditions in the Lake Tahoe Basin.

2. Materials and methods

2.1. Study area

The Lake Tahoe Basin is located in the north-central Sierra Nevada at 120°W and 39°N within the States of California and Nevada (Fig. 1). The Basin is flanked to the west by the Sierra Nevada crest and to the east by the Carson Range. The Lake Tahoe Basin Management Unit (LTBMU, USDA Forest Service) comprises 66,825 ha, ranging in elevation from 1890 to 3292 m, with 85% of the basin in National Forest. The climate is Mediterranean and characterized by warm, dry summers, and cool wet winters. Most precipitation falls as snow between the months of November and

April, with a strong gradient from west to east, with east-side locations influenced by the rainshadow effect of the Sierra Nevada crest. Geology of the region is dominated by igneous intrusive rocks, typically granitic, and igneous extrusive rocks, typically andesitic lahar, with small amounts of metamorphic rock (USDA NRCS, 2007). Study locations are found on both volcanic (including andesite) and granitic bedrock (Table 1).

Our study sites are found within lower montane conifer forests in the Lake Tahoe Basin, which are a mix of white fir (*A. concolor* Gordon & Glend.), Jeffrey pine (*P. jeffreyi* Grev. & Balf.), sugar pine (*P. lambertiana*), ponderosa pine (*P. ponderosa* Laws.), incense cedar (*C. decurrens*), and occasionally lodgepole pine (*Pinus contorta* ssp. *murrayana* Grev. & Balf). Study locations range in elevation from 1971 m to 2128 m (Table 1). Sugar pine is a key component in mixed-conifer forests of the North American mediterranean-climate zone, which extends from northern Baja California, Mexico, to southwestern Oregon, USA (see Plate 1). Sugar pine is found as far north as central Oregon at elevations between 1200 and 2200 m; the southern range limit of the species is in the Sierra San Pedro Martir in Northern Baja California, Mexico (Rundel et al., 1977; Kinloch and Scheuner, 1990). Sugar pine may represent 5–25% of the trees in mixed-conifer stands (Kinloch and Scheuner, 1990), but is a dominant feature due to its large size at maturity (ht. 55 m; diam. 1 m; USDA Forest Service, 1965).

2.2. Current population structure and trends

During the summer of 2008, we selected 10 study populations, with three permanent demographic plots per population (sampling area within a population = 4 ha), for a total of 30 plots (see Fig. 2). For our study a population is defined as an area in which gene flow occurs (pollen and seed dispersal), which for some conifers has been estimated at about 4 ha (Neale, 1983; Adams and Birkes, 1988). Our long-term plot network was established on National Forest System and State Park lands surrounding Lake Tahoe (LTBMU and California and Nevada Sate Parks).

Each of the 10 populations was located in a distinct watershed and distributed around the Basin to capture variation in the physical environment (e.g., climate, geology, topography). Once a population was located, a random starting point was chosen for the first plot; the second and third plots were sited ⩾100 m from the first plot. Within a population, each of three replicate plots were 40 m × 100 m (4000 m^2) with sampling covering approximately 1.2 ha within a 4- ha area (Fig. 2). The following data were recorded for each demographic plot: GPS location (UTM: NAD27 coordinates), slope, aspect, elevation (in meters), visible signs of past fire (i.e., basal fire scar, bole scorch, lightning strike), slope position (ridge-top, upper slope, mid-slope, lower slope, valley bottom, or bench), and land-use history (e.g., historical logging, fire suppression, recent thinning, prescribed fire, wildland fire, recreation, none). Evidence of historical logging was determined by presence of old stumps; remains of tall stumps are characteristic of the style of Comstock-era cutting.

Within each demographic plot, all *P. lambertiana* trees were identified and diameter at breast height (d.b.h. in cm) recorded for all individual stems ⩾1.37 m tall. Seedlings and saplings were all stems <1.37 m in height. All tree positions (*x* and *y* coordinates from the centerline of the plot) were recorded and mapped and data collected for tree status (live or dead), crown condition (rating 1–10 as follows: 1: ⩽10% dead, dying, damaged, infected; 2: 11–20% dead, dying, damaged, infected; 3: 21–30% dead, dying, infected, etc.), and crown position (understory, suppressed, intermediate, codominant, dominant or open). Signs and symptoms of pathogens (including WPBR, dwarf mistletoe, and root diseases) and insects were also recorded. Reproductive output was assessed by counting the number of current and previous years' cones per
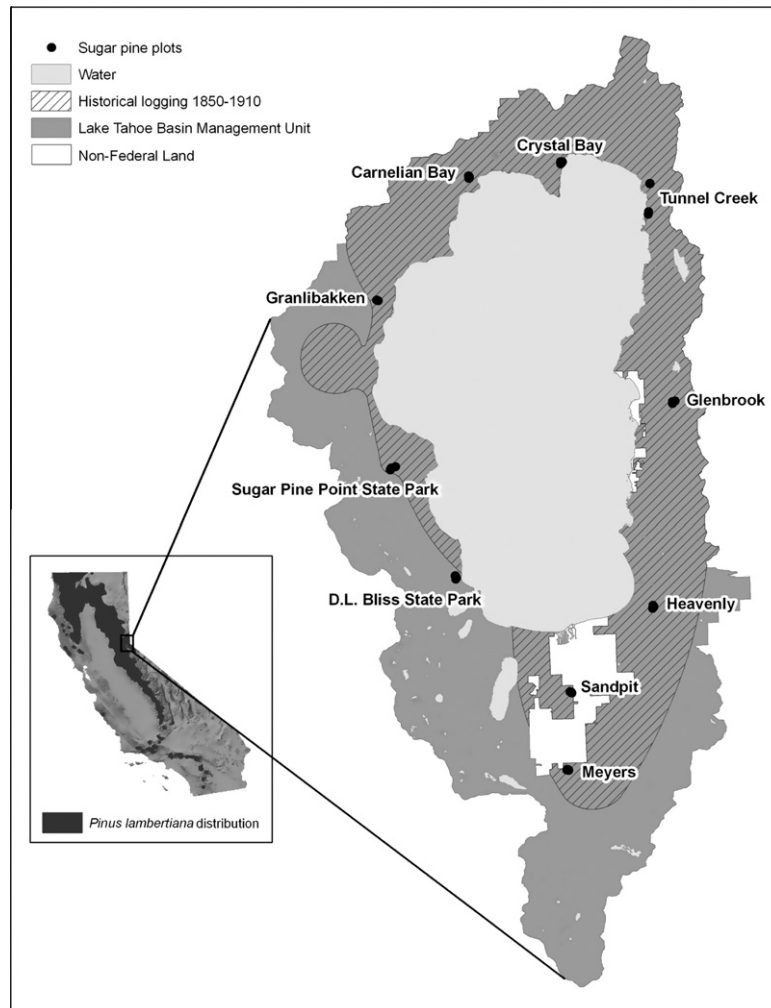
Fig. 1. Location of study area and sugar pine plots in the Lake Tahoe Basin. Areas of historical logging were adapted from Lindström, 2000 (Figs. 2–17). *Pinus lambertiana* distribution in California is shown in insert (distribution map source: USGS 1999 Digital representation of "Atlas of United States Trees" by Elbert L. Little, Jr.).

Table 1
Land-use, environmental, and biological characteristics for 10 stands of *Pinus lambertiana* in the Lake Tahoe Basin. Stands are listed clockwise from north, east, south, and west (refer to Fig. 1).

	Locations									
	Crystal Bay	Tunnel Creek	Glenbrook	Heavenly	Meyers	Sand Pit	D.L. Bliss SP	Sugar Pine Point SP	Granli-bakken	Carnelian Bay
Land-use	hl, fs	hl, fs, rt, pf	hl, fs, rt	hl, fs	hl, fs	hl, fs,rec	fs	hl, fs, pf	fs, hl	hl, fs, rt
A. concolor density (inds. ha^{-1})	152	25	102	46	160	15	107	112	295	201
A. concolor basal area (m^2 ha^{-1})	5.1	0.9	3	2	10	0.5	3	8	26	6
WPBR incidence (%)	10	11	0	3	15	5	5	41	48	30
Ann. ppt. (mm)	605	791	565	715	938	659	1070	869	848	808
Parent material	Granite	Granite	Volcanic	Granite	Granite	Granite	Granite	Mixed sources	Andesite	Andesite
Elevation (m)	1982	1971	2128	1990	2013	2057	2074	2057	2026	1991
P. lambertiana density (inds. ha^{-1})	73	16	141	123	43	48	95	14	37	42
P. lambertiana basal area (m^2 ha^{-1})	7	3	13	10	9	8	13	11	17	9
No. cones ha^{-1}	71	228	930	362	269	307	685	1236	1183	997
Recruitment (inds. ha^{-1})	35	10	835	35	120	54	262	128	25	69
Mortality (%)	9	2	5	1	3	10	8	7	10	2

Notes: Land-use abbreviations: hl = historical logging, fs = fire suppression, pf = prescribed fire, rt = recent thinning, rec = recreational (ohv) area. Increased *A. concolor* (and *C. decurrens*) density and basal area often an indicator of fire suppression and are shown here. Very little *C. decurrens* was present in our stands.

tree. Seedlings and saplings <1.37 m tall were evaluated within each demographic plot by establishing three nested recruitment subplots (15 m × 15 m), for a total of 9 regeneration plots/population (Fig. 2). All recruitment was counted and identified to species.
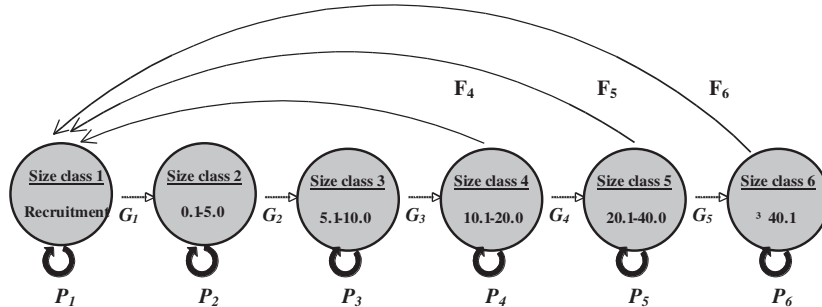
For *P. lambertiana* recruitment, data were collected on basal diameter (cm), height (cm), crown condition, status (live or dead), and disease condition.

A forest vegetation plot (40 m × 40 m) was nested within each of the three demographic plots population^{-1} to obtain tree data for other tree species besides *P. lambertiana* (i.e., d.b.h., status, diseases, insects, crown condition, crown class, etc.) (Fig. 2). All tree and recruitment data at each plot were collected to quantify stand structure, composition, basal area, and density. Positions of all associate trees were recorded and mapped.

For each demographic plot annual precipitation from the period of 1971–2000 were provided by FHTET (USDA FS Forest Health Technology Enterprise Team, Fort Collins, CO) using the PRISM climatic model (Daly et al., 1994). Soil survey data were provided by the South Lake Tahoe office of the USDA Natural Resources Conservation Service (NRCS).

Population trends were assessed by employing transition matrix models for each of the 10 populations of sugar pine. In our study, transition matrices are used to describe and summarize current trends in survivorship, mortality, fecundity, and to a much lesser extent growth. Transition matrix models of populations follow the Lefkovitch (1965) model:
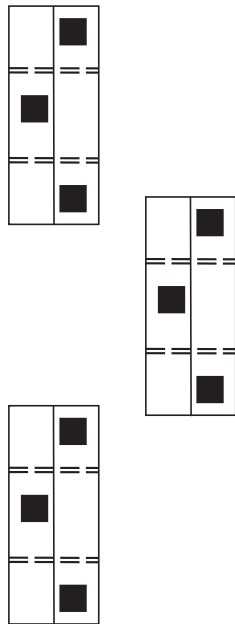
$$\mathbf{n}_{t+1} = \mathbf{A}n_t$$

where $\mathbf{n}_t$ is a column vector corresponding to the size structure at time t on the population classified into s size classes, and **A** is the matrix representing population dynamics. **A** is influenced by survival, growth, and reproduction. Entries in the transition matrix represent the contribution of each size class to every other size class during a specified time interval. We created sized-based models with six size classes: (1) recruits (individuals <1.37 m in height), (2) 0.1–5.0 cm d.b.h., (3) 5.1–10 cm d.b.h., (4) 10.1–20.0 cm d.b.h., (5) 20.1–40.0 cm d.b.h., and (6) ⩾40.1 cm d.b.h. In the diagram below size classes are represented by circles with size class 1 at the left and proceeding to size class 6 at the right, as shown.

matic model (Daly et al., 1994). Soil survey data were provided by the South Lake Tahoe office of the USDA Natural Resources Conservation Service (NRCS).

Transition probabilities for growth (G_1–G_5) are the forward horizontal arrows, survivorship (P_1–P_6) are the bold circular arrows, and fecundity (F_4–F_6) are the long arrows from right to left. Transition probabilities for growth, survival, and fecundity were calculated and estimated from our field data. For growth probabilities, individuals transitioned into the next size class when they were in the upper d.b.h. limit of the size class, or of height for seedlings/saplings. For example, we assumed that an individual with a d.b.h. of 4.9 cm or 5.0 cm would grow into size class 3 in the next time step. Where mortality occurred, survival was calculated using the number of standing dead trees (years dead ranged from 1–12 y) divided by current live and dead stems for each size class. In demographic studies of forest trees where mortality was not observed, mortality was assumed to be 0% or 2% (Ettl and Cottone, 2002; van Mantgem et al., 2004). In our populations where no mortality was observed, we assumed a minimal value of 1% mortality; an average of these previously published estimates. Fecundity was estimated from existing recruitment and cone production data for size classes 4, 5, and 6. We used the following calculation to estimate fecundity (f_i) for each of the three size classes: where r is the number of recruits for the population, c_i is the number of cones for individuals in size class i and n_i is the number of trees in size class i.

$$f_i = \frac{rc_i\left(\sum_{i=1}^{3}c_i\right)^{-1}}{n_i}$$

The population growth rate (λ), as estimated using the dominant eigenvalue of the transition matrix (Caswell, 2001), measures the rate of change in total population size. Population growth rate is a function of size- or age-specific rates of survival, growth and reproduction, with $\lambda > 1$ indicating growing, $\lambda = 1$ indicating stable, and $\lambda < 1$ indicating declining populations. Classical statistical tests using estimates of λ are inappropriate because demographic parameters and estimates of λ are not simple and their distributions are often not known (Caswell, 2001). Therefore, we computed 95% confidence intervals for λ by bootstrapping ($n = 10,000$) across survivorship, growth, and fecundity estimates comprising the transition matrix. All calculations and bootstrapping were performed in Matlab (Mathworks, 2009).

Fig. 2. Illustration of demographic plot layout for each population of sugar pine. Each of the three plots were, on average, 40 m × 100 m (4000 m^2) with sampling covering approximately 1.2 ha. In white is the area in which all sugar pine ⩾1.37 d.b.h. were measured and evaluated. In black are the three nested regeneration plots/plot (15 m × 15 m). The area between the double-dashed lines was the nested forest composition plot (40 m × 40 m).

Simple linear regression analysis was used to relate sugar pine survivorship probabilities (as estimated in transition models) and density to WPBR incidence and genetic diversity parameters. In addition, we related sugar pine survival to white fir basal area. Regression analysis was conducted with the software program JMP, version 8.0.1 (SAS, 2009). For parametric analyses, assumptions of normality and homogeneity of variances were verified and where needed, data were transformed to meet assumptions.

2.3. Genetic structure and diversity

Within demographic plots, needle samples were taken from 25 adult sugar pine individuals from each of the 10 populations in the Lake Tahoe Basin. Sampled trees were approximately 30 m apart. Needle samples were stored in vials containing three 0.5 g desiccant packets. DNA was extracted in the laboratory from 50 mg of tissue using DNeasy® Plant 96 Kits following the manufacturer's protocol (Qiagen, Valencia, CA, USA). DNA from sampled trees was genotyped for 1536 single nucleotide polymorphisms (SNPs), which were used as genetic markers. These SNPs were discovered through resequencing of a diversity panel comprising 12 haploid megagametophytes collected across the natural range of sugar pine (Jermstad et al., 2011). All genotyping was carried out at the DNA Technologies Core at the UC Davis Genome Center. Genotypes were called at each SNP locus for each tree using BeadStudio (Illumina) software. Quality thresholds for inclusion of SNPs were the same as those given in Eckert et al. (2009).

For each SNP, we calculated observed (H_O) and expected (H_E) heterozygosity, Wright's inbreeding coefficient (F_{IS}) and hierarchical F-statistics among plots nested within populations. Significance of mean F_{IS} and of mean hierarchical fixation indices across SNPs was assessed using 99% bootstrap confidence intervals (CIs) ($n = 10,000$ replicates sampled over for each SNP). We examined allelic correlations (r^2) between all possible pairs of SNPs to validate our assumption that SNPs were unlinked. Analyses were conducted using the GENETICS and HIERFSTAT (Goudet, 2005) packages in R (R Development Core Team, 2007).

We assessed population structure using the approach outlined by Nicholson et al. (2002) as implemented in the POPGEN library of R (R Core Development Team, 2007). This approach models a set of populations that diverge instantaneously from an ancestral population. Allele frequencies in those diverging populations drift away from those in the ancestral population, and are modeled using a binomial-beta hierarchical structure (Balding and Nichols, 1995). Here, we used the 10 sampled populations of sugar pine. There are three parameters of interest in this model: α_{ilj}, the frequency in population i at locus l of allele j; π_{lj}, the ancestral frequency of locus l of allele j; and c_i, the variance parameter for population i describing the magnitude of drift away from ancestral allele frequencies across loci. Since the c_i parameters are defined in terms of variance in allele frequencies across loci, they are analogous to population-specific estimates of multilocus F_{ST}. Thus, a larger value for an estimate of the c_i parameter indicates more drift away from ancestral allele frequencies, meaning that current allele frequencies within population i (α_{ilj}) are less similar, in terms of variance across loci, to that in the ancestral population (π_{lj}). As with F_{ST}, there are no natural breaks to define easily what is high and what is low. A comprehensive review of F_{ST} estimates for conifers is given elsewhere (Ledig, 1990; Savolainen et al., 2007).

Parameters were estimated in a Bayesian framework using Markov chain Monte Carlo (MCMC), where uniform priors were placed on the c_i and π_{lj} parameters and a Metropolis–Hastings algorithm was used to sample from the posterior distribution of each parameter. The α_{ilj} parameters were integrated out of the likelihood function and thus were not sampled (cf. Nicholson et al., 2002). Markov chains were sampled 10,000 times post burn-in

($n = 10,000$) to estimate posterior distributions, with point estimates reported as posterior means. Convergence was assessed by comparing posterior distributions of the c_i parameters across two replicated runs of the MCMC sampler, using Kolmogorov–Smirnov tests. Posterior distributions of the c_i parameters were visualized using violin plots, with density estimates given, assuming a Gaussian distribution for the smoothing kernel.

2.4. Evaluating disease resistance and Cr1 allele frequency

Cones were collected from 156 sugar pine individuals (from all 10 study locations) from the Lake Tahoe Basin in 2008. Seed were extracted and processed at the USDA Forest Service Placerville Nursery, Camino, CA. One-hundred and two families (none of which exhibited symptoms of WPBR in field evaluations) were screened for presence of the Cr1 allele at the Placerville Nursery's Rust Resistance Program facility, Camino, CA. In the fall of 2008, 56 seeds from each parent tree (family) were soaked in aerated water at 20 °C for 48 h, drained, and placed into cold-stratification at 2 °C for 90 days before sowing in individual containers in March of 2009. In October 2009, test seedlings were inoculated by basidiospore casts from infected leaves of *Ribes nigrum* L., an alternate host to the WPBR pathogen. *Ribes nigrum* plants had been inoculated with aeciospores of *C. ribicola* collected and bulked from forested sites in El Dorado Co., CA. Seedlings with infected *Ribes* leaves suspended over them were incubated in dew chambers for 62 h at 17 °C and 100% relative humidity (J. Gleason, pers. comm., USDA Forest Service). In March of 2010 the frequency of Cr1 was evaluated. When challenged by *C. ribicola*, resistant host needles respond to infection by developing hypersensitive spots (small necrotic flecks) that prevent further fungal growth; these flecks contrast markedly with the bright yellow, expanding spots that develop on the foliage of susceptible *cr1/cr1* genotypes (Kinloch, 1992).

Since the Cr1 allele is dominant and segregates in a 1:1 ratio of resistant to susceptible reactions, its frequency can be estimated for wind-pollinated families by counting the number of seedlings expressing the hypersensitive reaction (Kinloch, 1992). Parents of families that segregate 1:1 resistant:susceptible are assumed to carry one copy of the Cr1 allele (genotype, Cr1cr1). Cr1 allele frequency in a population is calculated by dividing the number of Cr1 alleles identified per family by twice the total number of families tested.

3. Results

3.1. Forest and site conditions

Comstock-era logging was evident in 9 of the 10 sites; only D.L. Bliss State Park, located north of Emerald Bay, did not exhibit obvious, significant harvesting (Lindström, 2000) (Table 1, Fig. 1, see Plate 1). Fire suppression was also evident in most stands, with forest stands characterized by high densities of shade tolerant species like white fir. This was especially the case at Granlibakken (Table 1). Sites with low white fir densities have had recent thinning and/or prescribed fire treatments (e.g., Tunnel Creek, Glenbrook, Carnelian Bay, Sugar Pine Point State Park; see Table 1 "land-use"). Despite the confounding effects of recent stand treatments, we found a moderate and negative relationship between sugar pine survivorship and white fir basal area ($r^2 = 0.31$, $F_{1,10} = 3.57$, $P = 0.09$, slope estimate = -0.01). White pine blister rust was found in 90% of the sites and ranged from 0% to 48% (Table 1). The highest rust levels were found at Carnelian Bay (30%), Sugar Pine Point State Park (41%), and Granlibakken (48%). No rust was found on sugar pine in the Glenbrook population.

Strong environmental gradients exist within the Basin in precipitation, geology, and soil type (Table 1), which can influence stand structure and composition, as well as host-pathogen interactions. WPBR incidence is highest in stands on the west side, which tend to be more mesic than east side locations; mean annual precipitation is 865 mm and 669 mm in west-side and east-side locations, respectively. Moist conditions are required by *C. ribicola* for infection to occur on both hosts; all spore stages require relative humidity >90% and temperatures in the range of 15–18 °C (Hirt, 1942; Van Arsdel et al., 1956; McDonald, 1996). Soil type can influence site characteristics and carrying capacity of sugar pine and other forest associates (Table 1). Populations growing on decomposed granite have relatively lower densities (mean = 150 inds. ha^{-1}) and basal area (mean = 11.9 m^2 ha^{-1}) than neighboring stands growing on soils of volcanic or andesite, which generally have higher available soil moisture, and thus support higher tree densities (mean = 236 inds. ha^{-1}) and basal area (mean = 23.3 m^2 ha^{-1}).

3.2. Sugar pine characteristics

Sugar pine densities were highest at Crystal Bay, D.L. Bliss State Park, Heavenly, and Glenbrook, respectively, and lowest at Sugar Pine Point State Park and Tunnel Creek (Table 1). Basal area of sugar pine was highest at Granlibakken, followed by Glenbrook, D.L. Bliss, and Sugar Pine Point State Park (Table 1). Sugar pine cone production and recruitment varied considerably from site to site (Table 1). High cone production was found at Glenbrook, Carnelian Bay, Granlibakken, and Sugar Pine Point State Park (Table 1). High reproductive output did not always correspond to higher numbers of recruitment, with the exception of the Glenbrook population, with 835 recruits per hectare (Table 1). Cone production at Granlibakken was high (1183 cones ha^{-1}) but only 25 seedlings and saplings were found per hectare. D.L. Bliss State Park had moderate cone production (685 cones ha^{-1}) and the second highest number (262) of seedlings and saplings per hectare. Evidence of cone-damaging insects was found at all sites (Maloney, unpubl. data). Sugar pine mortality was moderate, ranging from 1–10% (Table 1). The highest mortality levels were at Granlibakken and the Sand Pit (Table 1). High mortality at Granlibakken corresponded with very high rust incidence.

3.3. Current population structure and trends

The structure and density of sugar pine in the Lake Tahoe Basin differed greatly from site to site (Table 1, Fig. 3). Size structure

Plate 1. Lower montane mixed-conifer forest at D.L. Bliss State Park which has a significant sugar pine component. The area around and north of Emerald Bay experienced little to no Comstock era logging. The characteristic tree architecture of sugar pine has long sweeping limbs. Photo credit: C.E. Jensen.

ranged from relatively even (Crystal Bay, Heavenly, and D.L. Bliss State Park) to uneven (Glenbrook) (Fig. 3). These four sites also correspond with higher sugar pine densities, >70 trees ha^{-1} (Table 1, Fig. 3). The size structures at Tunnel Creek, Meyers, Sand Pit, Sugar Pine Point State Park, Granlibakken, and Carnelian Bay were highly skewed, with higher representation of large diameter trees, high basal area (except Tunnel Creek), and very few smaller individuals (Fig. 3 and Table 1). Overall, each of these six sites had relatively low sugar pine densities, <50 trees ha^{-1} (Table 1).

Variation in fecundity, which is a function of cone production and the number of recruits that successfully established, was found among populations (Tables 1 and 2). Overall fecundity was highest at Glenbrook, due to a combination of good cone production and successful recruitment (Tables 1 and 2). Despite high cone production at Sugar Pine Point State Park and Granlibakken, both populations had moderate to low fecundity, possibly due to stand conditions and high WPBR incidence (Tables 1 and 2).

Survivorship varied due to differential mortality between size classes and populations (Table 2, Appendix A). Mean survivorship probabilities were >0.850 for 8 of 10 sugar pine populations, but were substantially lower for Sugar Pine Point State Park (0.621) and Granlibakken (0.729) (Table 2). In both latter populations survivorship was low in size classes 2 (0.1–5.0 d.b.h.), 4 (10.1–20.0 d.b.h.), and 5 (20.1–40.0 d.b.h.) (Appendix A). Mean survivorship probability and WPBR incidence were significantly and negatively related ($r^2 = 0.46$, $F_{1,10} = 6.72$, $P = 0.03$, slope estimate = −0.04).

Estimated growth rate (λ) for 6 of the 10 sugar pine populations was $\lambda \geqslant 1.0$, indicating that these populations are stable, if not slightly growing (Fig. 3). Sugar Pine Point State Park, Tunnel Creek, Granlibakken and Crystal Bay had $\lambda < 1.0$, indicative of populations that may be in decline. All upper limit confidence intervals for λ were greater than 1, suggesting stability in most populations. However, for most populations the lower confidence interval was <1.0 (Table 2); whether this is cause for concern is difficult to assess, given that λ was estimated from a one-time sampling.

3.4. Genetic structure and diversity

Of the 1536 SNP marker loci, 493 were segregating in our sample of 250 trees and were of high quality. Genetic diversity measures (H_O and H_E) ranged from 0.307 to 0.350 and 0.303 to 0.332, respectively (Table 3). Expected heterozygosity was slightly higher than what was reported by Conkle (1981) in a sampling of sugar pine in California, across a range of forest conditions ($H_E = 0.275$). The inbreeding coefficient (F_{IS}) ranged from −0.049 to 0.010, with two populations having positive values and six with negative values (Table 3). High positive values of F_{IS} often indicates inbreeding; with fewer heterozygotes than expected. Most values reported here are within range of zero and appear to be in Hardy–Weinberg equilibrium. The drift parameter (c_i) ranged from 0.009 to 0.048 (Table 3), which is consistent with the multilocus estimate of F_{ST} across all populations ($F_{ST} = 0.0179$, 99% CI: 0.0152–0.0206). The highest value of c_i was at Sugar Pine Point State Park (0.048), followed by Tunnel Creek (0.027), Meyers (0.026), and Crystal Bay (0.023) (Table 3, Fig. 4). Moderate and negative relationships exist between sugar pine density and c_i ($r^2 = 0.36$, $F_{1,10} = 4.50$, $P = 0.06$, slope estimate = −0.0002) as well as sugar pine survivorship and c_i ($r^2 = 0.37$, $F_{1,10} = 4.79$, $P = 0.06$, slope estimate = −3.49). High values of c_i may be the result of a bottleneck: Comstock logging or WPBR-mediated mortality may have drastically reduced the population size.

3.5. Frequency of disease resistance

Of the 102 families (maternal parents) screened for *Cr1*, 14 were heterozygous (*Cr1cr1*), yielding an overall *Cr1* allele frequency of
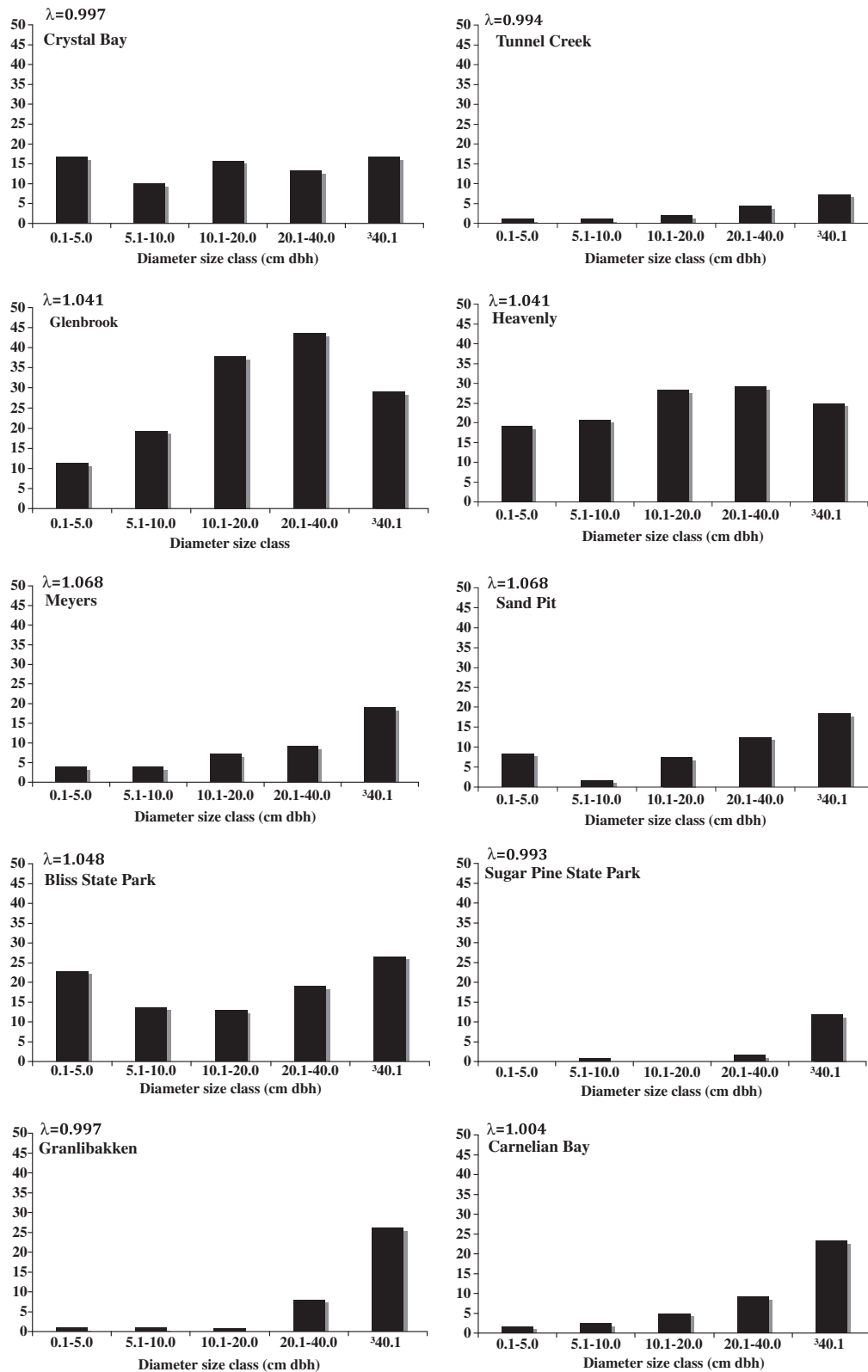
Fig. 3. Size structure and population growth rate (λ) for ten populations of *Pinus lambertiana* in the Lake Tahoe Basin.

0.068 for sampled sugar pine in the Lake Tahoe Basin. Kinloch (1992) reported *Cr*1 frequency in the LTBMU to be 0.018, more than 3-fold lower than what we found. *Cr*1 was found in 6 of 10 sugar pine populations and ranged from 0.045 to 0.125 per

population (Table 3). No evidence for *Cr*1 was found at Crystal Bay, Tunnel Creek, Meyers, or Granlibakken. The highest *Cr*1 frequencies were found at Glenbrook (0.114), Sand Pit (0.125), and Sugar Pine Point State Park (0.125) (Table 3).

Table 2
Mean fecundity, survival and growth from transition matrices for ten sugar pine populations. Population growth rate, λ, is shown along with 2.5% and 97.5% confidence intervals (CI, in parentheses).

Population	Fecundity	Survival	Growth	λ (2.5%, 97.5% CI)
Crystal bay	0.119	0.907	0.042	0.997 (0.624, 1.559)
Tunnel creek	0.038	0.960	0.020	0.994 (0.567, 1.690)
Glenbrook	1.482	0.943	0.048	1.041 (0.409, 1.749)
Heavenly	0.075	0.987	0.041	1.041 (0.755, 1.540)
Meyers	0.284	0.969	0.076	1.068 (0.663, 1.594)
Sand pit	0.176	0.886	0.074	1.068 (0.690, 1.535)
D.L. Bliss state park	0.507	0.964	0.040	1.048 (0.596, 1.699)
Sugar pine point state park	0.577	0.621	0.010	0.993 (0.0794, 1.808)
Granlibakken	0.052	0.729	0.012	0.997 (0.420, 1.735)
Carnelian bay	0.167	0.967	0.018	1.004 (0.725, 1.636)

Table 3
Genetic summary and diversity patterns for *P. lambertiana* from 493 marker loci and *Cr1* allele frequency (standard deviation for H_O, H_E, F_{IS}, and 95% credible intervals for c_i in parentheses).

| Population	H_O	H_E	F_{IS}	c_i	$Cr1$
Crystal bay	0.307 (0.179)	0.313 (0.166)	0.010 (0.207)	0.023 (0.017–0.029)	0.000
Tunnel creek	0.321 (0.192)	0.314 (0.167)	−0.015 (0.217)	0.027 (0.021–0.033)	0.000
Glenbrook	0.328 (0.171)	0.326 (0.158)	−0.013 (0.190)	0.009 (0.005–0.013)	0.114
Heavenly	0.324 (0.184)	0.321 (0.165)	−0.008 (0.213)	0.011 (0.007–0.015)	0.059
Meyers	0.317 (0.189)	0.318 (0.168)	0.007 (0.228)	0.026 (0.019–0.032)	0.000
Sand pit	0.320 (0.179)	0.318 (0.157)	−0.003 (0.211)	0.009 (0.006–0.014)	0.125
D.L. Bliss state park	0.333 (0.183)	0.328 (0.161)	−0.009 (0.209)	0.018 (0.013–0.023)	0.071
Sugar pine point state park	0.321 (0.213)	0.303 (0.178)	−0.049 (0.231)	0.048 (0.038–0.059)	0.125
Granlibakken	0.321 (0.187)	0.318 (0.167)	−0.003 (0.214)	0.015 (0.010–0.020)	0.000
Carnelian bay	0.350 (0.192)	0.332 (0.159)	−0.042 (0.222)	0.013 (0.009–0.018)	0.045
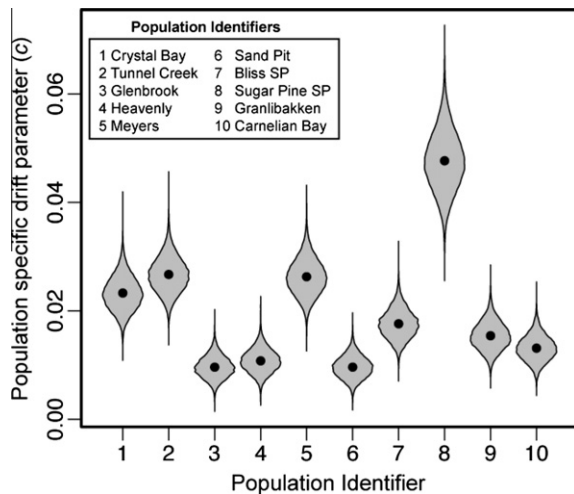
Fig. 4. Posterior distributions are plotted for parameter c_i. The larger the value of c_i the more a population has drifted (i.e. diverged) away from a set of ancestral allele frequencies as estimated from the data. Posterior means are given by the black points.

4. Discussion

Population- and genetic-level consequences of historical disturbances on forest tree populations are rarely considered or described. Here we assessed population and genetic characteristics of sugar pine in the Lake Tahoe Basin as they relate to stand conditions, given historical logging, fire suppression, and WPBR. For four populations we documented negative population trends and genetic consequences associated with these disturbances. These populations have low estimated growth rates (λ), small population sizes, relatively high genetic drift, high levels of WPBR, and poor survival of small- and intermediate-sized individuals. In contrast,

six currently appear to be stable ($\lambda \geqslant 1.0$), most likely because of large population sizes, low disease levels, presence of resistance to WPBR, and, in some instances, recent thinning and/or prescribed fire treatments.

A major issue in trying to understand the influence of historical logging is that most of what we know about it is anecdotal; we have little or no detailed information on numbers, size, and species removed. Logging was widespread throughout much of sugar pine's distribution in the Basin (Fig. 1) and historical populations may have been larger and more extensive in some locations than at present. Since the effects of genetic drift are greater in smaller populations, we believe that a population bottleneck is a likely explanation for diversity patterns at Sugar Pine Point State Park (as pointed out by Nicholson et al. (2002) as a possible cause of higher c_i values). This could possibly have been caused by historical logging and other agents of mortality. Sugar pine at this site has low density (14 inds. ha^{-1}), the highest value for c_i (0.048), high WPBR incidence (41%), and poor survivorship (mean = 0.621), mainly due to WPBR-mediated mortality. At Tunnel Creek and Crystal Bay, the consequences of historical logging may explain the small population sizes and higher levels of genetic drift. Tunnel Creek has the second lowest population growth rate (λ = 0.994) and density (16 inds. ha^{-1}) following Sugar Pine Point State Park. This population has moderate levels of WPBR (11%), very low recruitment (only 10 recruits ha^{-1}), and the second highest drift parameter (c_i = 0.027). Similarly, Crystal Bay has relatively low population growth rate (λ=0.997), the fourth highest drift parameter (c_i = 0.023), but moderate population numbers.

Caution is recommended, however, in the interpretation of the c_i values, as any changes in the local effective population sizes will affect these estimates and they are based on a particular model of population divergence (see Nicholson et al., 2002). For example, we have not explicitly modeled gene flow or hierarchical divergence of populations, both of which could reflect our conclusions. With respect to gene flow, the overall levels of drift that were inferred are small and likely so because of gene flow in combination with large

effective population sizes and recent population divergences. The estimates of c_i, however, are constrained by variation in the data, which are a product of those aforementioned processes. Thus, the relative trends should still hold, regardless of the mechanism that we have modeled. With respect to hierarchical structure, the correlations of c_i with density and survivorship would be hard to explain unless these co-varied along the unknown and underlying tree-like structure describing the divergence history of the sampled populations. We feel that this is unlikely given the entire spectrum of ecological and environmental determinants of tree density and survivorship. Lastly, we have not estimated a time associated with putative bottlenecks, so that the trends we observed may be due to much older events; however, the genetic data will reflect recent events as long as the change in effective size is large enough and/or statistical power is high enough (see Wakeley, 2009).

Infection by *C. ribicola* is highest on sugar pine at Granlibakken (48%). At present, Granlibakken seems to have little or no naturally occurring disease resistance. This population also appears to be declining ($\lambda = 0.997$) because of high levels of WPBR resulting in low survival of small and intermediate sized trees (0.1–5.0 and 20.1–40.0 d.b.h.). Lack of sugar pine recruitment (e.g., seedlings) at Granlibakken, despite the presence of large reproductive individuals, may be a function of the combined effects of fire suppression and stand densification. We found the highest white fir densities (295 inds. ha^{-1}) and white fir basal area (26 m^2 ha^{-1}) at this site, which has resulted in a dense canopy and low light levels, which are unfavorable conditions for sugar pine recruitment (Zald et al., 2008).

In spite of anthropogenic disturbances, six populations appear to be maintaining, given current population characteristics and genetic structure. Populations at Glenbrook, D.L. Bliss State Park, and Heavenly have little or no WPBR, good representation across all diameter classes (Fig. 3), relatively high survival, high fecundity (except Heavenly), moderate frequencies of *Cr1*, and relatively high genetic diversity. Sand Pit, Meyers, and Carnelian Bay, which have low population numbers, are showing somewhat positive estimated growth rates, more than likely because of relatively high survival across diameter classes and moderate levels of fecundity.

Because population growth, λ, was calculated from a one-time sampling, our estimates may not reflect intrinsic variation in rates of survivorship, mortality, growth, and fecundity. Year to year variation in climate, cone production, cone and seed predation, recruitment success, tree mortality, and conditions favorable for WPBR infection can be considerable. Our intent was not to predict future population growth but to describe current population conditions. Another limitation of our study is that the confidence intervals are very large for λ, which is a cause for concern, but it is difficult to assess the magnitude of this concern as λ was estimated from a one-time sampling that likely resulted in the large variances around the point estimate. Obtaining long-term demographic data for long-lived tree species is difficult, but will be necessary to accurately access population dynamics of sugar pine in the Lake Tahoe Basin in the future.

5. Restoration implications

Restoration strategies to mitigate anthropogenic influences should be based on strong evidence of negative population and genetic effects, as well as an assessment of risk factors for a population (e.g., how much disease at a site, frequency of resistance, and frequency of infection periods). Of the 10 sugar pine populations evaluated in the Lake Tahoe Basin only three appear to be in need of restoration. Restoring population numbers, disease resistance, and genetic variation may require out-planting seedlings that are genetically diverse and WPBR-resistant, as well as, forest treat-

ments (e.g., thinning and/or prescribed fire) that promote natural sugar pine regeneration. Despite recent prescribed fire treatments at Sugar Pine Point State Park, this location still may require restoring sugar pine numbers, as well as genetically diverse and WPBR-resistant material. Even though frequency of *Cr1* (0.125) is moderate at Sugar Pine Point State Park, the remaining 87% of the individuals are susceptible and under strong disease pressure (WPBR incidence = 41%). Deploying resistance at least to present levels (0.125) would be advisable. Given recent thinning and prescribed fire treatments at Tunnel Creek, a similar strategy, as stated above, of restoring sugar pine numbers by facilitating recruitment and planting genetically diverse and resistant seedlings may be warranted. Future fuel treatments of thinning and prescribed fire are proposed at Granlibakken (D. Fournier pers. comm., USDA Forest Service) and will be key to promoting natural sugar pine regeneration. Because this sugar pine population is in a high-risk site and very little disease resistance has been found, deploying WPBR-resistant material from nearby locations is warranted. Frequency of *Cr1* being deployed should be within the range of frequencies currently found in the Lake Tahoe Basin (0.045–0.125). Deploying resistance will have positive effects on sugar pine survival in high-risk sites, despite the risk that virulence to *Cr1* may evolve in the pathogen (Kinloch et al., 2007).

Regional and National plans such as the Sierra Nevada Forest Plan Amendment (USDA Forest Service, 2004) and the Healthy Forests Initiative (http://www.healthyforests.gov) have made forest restoration a priority. The primary goals of forest restoration treatments (e.g., thinning and/or prescribed fire), is to generally increase tree size and shift forest composition toward fire tolerant pine species, particularly in historically pine-dominated communities (North et al., 2007). We have shown from our study that it is not only about restoring numbers of sugar pine or desirable forest conditions (e.g., reduced stem densities and representation of fire intolerant species) but also restoring genetic diversity and moderate levels of disease resistance, so rarely considered.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2011.05.011.

References

Adams, W.T., Birkes, D.S., 1988. Estimating mating patterns in forest tree populations. In: Hattemer, H.H., Fineschi, S. (Eds.), Proceedings International Workshop on Plant Biology, Biochemical Markers in Population Genetics of Forest Trees, Porano-Orvieto, Italy. Inst. Agroforestry Nat. Res. Council Italy (CNR). SPB Academic Publishing, The Hague, pp. 152–172.

Ansley, J., Battles, J.J., 1998. Forest composition, structure, and change in an old-growth mixed conifer forest in the northern Sierra Nevada. J. Torr. Bot. Soc. 125, 297–308.

Balding, D., Nichols, R., 1995. A method for quantifying differentiation between populations at multi-allelic loci and its implications for investigating identity and paternity. Genetica 96, 3–12.

Barbour, M., Kelley, E., Maloney, P., Rizzo, D., Royce, E., Fites-Kaufman, J., 2002. Present and past old-growth forests of the Lake Tahoe Basin, Sierra Nevada, US. J. Veg. Sci. 13, 461–472.

Caswell, H., 2001. Matrix Population Models, second ed., Sinauer Associates, Sunderland, MA, USA.

Conkle, M.T., 1981. Isozyme variation and linkage in six conifer species. In: Conkle, M.T. (Ed.), Proceedings of a Symposium on Isozymes of North America Forest Trees and Forest Insects. USDA Forest Service General Technical Report PSW-48, pp. 11–17.

Daly, C., Neilson, R.P., Phillips, D.L., 1994. A statistical model for mapping climatological precipitation over mountainous terrain. J. Appl. Meteorol. 33, 140–158.

Eckert, A.J., Ersoz, E.S., Pande, B., Wright, M.H., Rashbrook, V.K., Nicolet, C.M., Neale, D.B., 2009. High-throughput genotyping and mapping of single nucleotide polymorphisms in loblolly pine (*Pinus taeda* L.). Tree Genet. Genomes 5, 225–234.

Elliot-Fisk, D., Rowntree, R.A., Cahill, T.A., Goldman, C.R., Gruell, G., Harris, R., Liesz, D., Lindström, S., Kattelmann, R., Machida, D., Lacey, R., Bucks, P., Sharkey, D.A., Ziegler, D.S. 1996. In: Lake Tahoe Case Study. Sierra Nevada Ecosystem Project: Final Report to Congress. Addendum, University of California Centers for Water and Wildland Resources, Davis, CA, US, pp. 217–276.

Ettl, G.J., Cottone, N., 2002. Whitebark pine (*Pinus albicaulis*) in Mt. Rainier National Park, Washington, USA: response to blister rust infection. In: Akçakaya, H.R. (Ed.), RAMAS GIS. Applied Mathematics. Setauket, NY, pp. 36–48.

Goudet, J., 2005. Hierfstat, a package for R to compute and test hierarchical *F*-statistics. Mol. Ecol. Notes 5, 184–186.

Hirt, R.R., 1942. The Relation of Certain Meterological Factors to the Infection of Eastern White Pine by the Blister-Rust Fungus. The New York State College of Forestry. Tech. Pub. No. 59.

Jermstad, K.D., Eckert, A.J., Wegrzyn, J.L., Kinloch, B.B., Mix, A.D., Davis, D.A., Burton, D.C., Neale, D.B., 2011. Comparative mapping in Pinus: Sugar pine (*Pinus lambertiana Dougl*) and Loblolly pine (*Pinus taeda* L.). Tree Genet. Genomes 7, 457–468.

Kilgore, B.M., 1973. The ecological role of fire in Sierran conifer forests. Quart. Res. 3, 496–513.

Kinloch Jr., B.B., Parks, G.K., Fowler, C.W., 1970. White pine blister rust: simply inherited resistance in sugar pine. Science 167, 193–195.

Kinloch Jr., B.B., Littlefield, J.L., 1976. White pine blister rust: hypersensitive resistance in sugar pine. Can. J. Bot. 55, 1148–1155.

Kinloch Jr., B.B., Scheuner, W.H., 1990. *Pinus lambertiana* Dougl., sugar pine. In: Burns, R.M., Honkala, B.H. (Eds.), Silvics of North America. USDA Forest Service, Washington, DC, USA., pp. 370–379.

Kinloch Jr., B.B., 1992. Distribution and frequency of a gene for resistance to white pine blister rust in natural populations of sugar pine. Can. J. Bot. 7, 1319–1323.

Kinloch Jr., B.B., Marosy, M., Huddleston, M.E. (Eds.), 1996. Sugar Pine: Status, Values, and Roles in Ecosystems: Proceedings of a Symposium presented by the California Sugar Pine Management. University of California, Division of Agriculture and Natural resources, Davis, CA. Publication 3362.

Kinloch Jr., B.B., Davis, D.A., Burton, D., 2007. Resistance and virulence interactions between two white pine species and blister rust in a 30-year field trial. Tree Genet. Genomes 4, 65–74.

Ledig, F.T., 1990. Genetic variation in *Pinus*. In: Richardson, D.M. (Ed.), Ecology and Biogeography of *Pinus*. Cambridge University Press, Cambridge, UK, pp. 251–280.

Lefkovitch, L.P., 1965. The study of population growth in organisms grouped by stage. Biometrics 21, 1–18.

Laudenslayer Jr., W.F., Darr, H.H., 1990. Historical effects of logging on the forests of the Cascade and Sierra Nevada ranges in California. Trans. West. Sect. Wild. Soc. 26, 12–23.

Lindström, S., 2000. A contextual overview of human land use and environmental conditions. In: Murphy, D.D., Knopp, C.M. (Eds.), Lake Tahoe Basin Watershed Assessment, vol. 1, Gen. Tech Rep. PSW-GTR-175. Pacific Southwest Research Station, USDA Forest Service, Albany, CA, pp. 23–127.

Maloney, P.E., 2000. Topics in Forest Pathology and Ecology in the Sierra Nevada and the Sierra San Pedro Martir, Baja. Ph.D. Dissertation, University of California, Davis.

Mathworks, Inc., 2009. 3 Apple Hill Dr. Natick, MA 01760, USA.

McDonald, G.I., 1996. Ecotypes of blister rust and management of sugar pine in California In: Kinloch Jr., B.B., Marosy, M., Huddleston, M.E. (Eds.), Sugar Pine: Status, Values, and Roles in Ecosystems: Proceedings of a Symposium presented by the California Sugar Pine Management. University of California, Division of Agriculture and Natural resources. Publication 3362, Davis, CA, pp. 137–147.

Neale, D.B., 1983. Population Genetic Structure of the Douglas-fir Shelterwood Regeneration System in SOUTHWEST OREGON. PhD dissertation, Oregon State University.

Nicholson, G., Smith, A.V., Jonsson, F., Gustafsson, O., Stefansson, K., Donnelly, P., 2002. Assessing population differentiation and isolation from single-nucleotide polymorphism data. J. Roy. Stat. Soc. B 64, 695–715.

North, M., Innes, J., Zald, H., 2007. Comparison of thinning and prescribed fire restoration treatments to Sierran mixed-conifer historic conditions. Can. J. For. Res 37, 331–342.

R Development Core Team, 2007. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.

Rundel, P.W., Parsons, D.J., Gordon, D.T., 1977. Montane and subalpine vegetation of the Sierra Nevada and Cascade Ranges. In: Barbour, M.G., Major, J. (Eds.), Terrestrial Vegetation of California. J. Wiley & Sons, New York, pp. 559–594.

SAS Institute, 2009. JMP Start Statistics: JMP Statistics and Graphics Guide, Release 8.0.1. SAS Institute Inc., Cary, NC.

Savolainen, O., Pyhäjärvi, T., Knürr, T., 2007. Gene flow and local adaptation in forest trees. Ann. Rev. Ecol., Evol., Systemat. 38, 595–619.

Shaw, C.G., Geils, B.W. (Eds.), 2010. Special Issue: White Pines, *Ribes*, and Blister Rust. For. Pathol., vol. 40, pp. 145–418.

Smith, R.S., 1996. Spread and intensification of blister rust in the range of sugar pine. In: Kinloch Jr., B.B., Marosy, M., Huddleston, M.E. (Eds.), Sugar Pine: Status, Values, and Roles in Ecosystems: Proceedings of a Symposium presented by the California Sugar Pine Management. University of California, Division of Agriculture and Natural resources, Publication 3362, Davis, CA, pp. 112–118.

SNEP Science Team, (Eds.), 1996. Status of the Sierra Nevada: Final Report to Congress of the Sierra Nevada Ecosystem Project, 3 vols. Wildland Resources Center, University of California, Davis, Calif. Rep. 36.

Unites States Department of Agriculture, Natural Resources Conservation Service, 2007. Soil Survey of the Tahoe Basin Area, California and Nevada.

USDA Forest Service, 2004. Sierra Nevada Forest Plan Amendment: Final Environmental Impact Statement, vols. 1–6. USDA Forest Service, Pacific Southwest Region, Vallejo, California.

Van Arsdel, E.P., Riker, A.J., Patton, R.F., 1956. The effects of temperature and moisture on the spread of white pine blister rust. Phytopathology 6, 307–318.

van Mantgem, P.J., Stephenson, N.L., Keifer, M., Keeley, J., 2004. Effects of an introduced pathogen and fire exclusion on the demography of sugar pine. Ecol. Appl. 14, 1590–1602.

Wakeley, J., 2009. Coalescent Theory. Roberts and Company Publishers, Greenwood Village, CO.

Zald, H.S.J., Gray, A.N., North, M., Kern, R.A., 2008. Initial tree regeneration responses to fire and thinning treatments in a Sierra Nevada mixed conifer forest. For. Ecol. Manage. 256, 168–179.