

USE OF A SMOOTHER TO FORECAST OCCURRENCE OF EPIPHYTIC LICHENS UNDER ALTERNATIVE FOREST MANAGEMENT PLANS

BRUCE McCUNE,^{1,4} SHANTI D. BERRYMAN,¹ JOHN H. CISSEL,² AND ALIX I. GITELMAN³

¹Department of Botany and Plant Pathology, Cordley 2082, Oregon State University, Corvallis, Oregon 97331-2902 USA

²Forestry Sciences Laboratory, 3200 Jefferson Way, Corvallis, Oregon 97331 USA

³Department of Statistics, Oregon State University, Corvallis, Oregon 97331-2902 USA

Abstract. We used habitat models to forecast the frequency of occurrence of epiphytic lichen species in a forested landscape under two alternative plans: a literal application of standard prescriptions in the Northwest Forest Plan and a plan patterned in part after natural disturbance regimes. The plans were evaluated for the Blue River watershed in the Cascade Range of Oregon, USA. We used two model types: logistic regression and an ecological neighborhood model using a form of nonparametric regression (SpOcc; Species Occurrence Modeler). Both logistic regression and SpOcc successfully estimated the occurrence of the lichen *Lobaria oregana* in the current landscape, based on elevation and structural classes of forests. Structural classes were defined by combinations of (1) overstory retention of remnant trees, (2) young cohort age, and (3) stream position (upland vs. riparian). *Lobaria oregana* rapidly diminished in frequency in the landscape at elevations above 900–1000 m. Young, even-aged stands had little or no *Lobaria oregana*. Most of the other structural classes, however, were very similar in frequency of *Lobaria*. The differences in lichens between retention levels and between mature and old growth stands were very small compared to the differences with respect to elevation and clearcutting. Similar results, with varying importances of elevation and forest structure, were obtained for most of the 20 species with the strongest models. Many of these species were associated with old growth, and many were forecasted to be more frequent under either management plan than in the current landscape. This is a likely response to the reduction of even-aged management in this landscape. We recommend using SpOcc for flexible nonparametric fitting of species relationships to a multivariate habitat. SpOcc avoids the need to specify response functions and, because it is multiplicative rather than additive, automatically models responses to interactions among predictors.

Key words: ecological neighborhood model; epiphytes; forest planning; habitat model; lichens; *Lobaria oregana*; nonparametric smoothing; Northwest Forest Plan; Pacific Northwest (USA); riparian forests.

INTRODUCTION

The Northwest Forest Plan (NWFP; U. S. Department of Agriculture and U. S. Department of Interior 1994) directs the management of forests on public lands in the Pacific Northwest of the United States. The NWFP departs drastically from previous management plans by emphasizing the long-term maintenance of ecosystem functions, including perpetuation of nontimber species. The NWFP places considerable emphasis on the importance of lichens to old-growth ecosystems.

The NWFP allows experimental departures from its standard prescriptions in “adaptive management areas” (AMA). In the Central Cascades AMA, two proposed management strategies will result in very different future landscapes (Cissel et al. 1999). How will these alternative management strategies affect the long-term survival of lichens within the landscape? The an-

swer is important because lichens are valued for their roles in nitrogen fixation, forage, and contribution to biodiversity (McCune 1993).

We refer to standard prescriptions from the NWFP followed literally as the “Interim Plan” (IP). This plan will result, over time, in old growth primarily allocated to: Riparian Reserves; Late-successional Reserves; administratively or Congressionally withdrawn areas such as Special Wildlife Habitats and Wilderness Areas; and forested areas with soil types not supporting timber production. The remaining areas are designated “matrix,” where younger forests will dominate. Of concern in this future IP landscape will be the loss of the 80–200+ year age class in the matrix. Old-growth-associated lichens in this landscape will need to be able to disperse from propagules emanating from riparian reserves (52 m on both sides of all streams) and “green-tree retention” (15% upland harvest area). Green-tree retention is defined by the NWFP as “stand management practice in which live trees as well as snags and large down wood are left as biological legacies within harvest units to provide habitat components over the next management cycle.”

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⁴ E-mail: Bruce.McCune@science.oregonstate.edu

An alternative management strategy, the "Landscape Plan" (LP), is applied in the Blue River Landscape Study. Under this plan, the forest will be managed for varying levels of retention, a different patch configuration, and much longer rotation lengths, based on the fire history. Low-retention areas will be harvested on long rotations (260 years). Intermittent streams will be buffered for 7.6–9.1 m (25–30 feet) on both sides of the stream to protect trees contributing to streambank stability, a narrower buffer than under the IP.

We modeled the fates of old-growth-associated lichen species under these two plans. Our models use data from Berryman (2002) as a basis for estimating frequency of epiphytic lichens in the Blue River landscape. She compared lichen communities among the same forest structural types that we used to project management strategies in the Blue River watershed. These stand types were based on years since disturbance, retention levels, topographic position, and dominant tree species.

We modeled lichen species responses to alternative forest management plans. Specifically, we evaluate persistence of the species in the landscape, rather than biomass of the species. How will the frequency of particular lichen species change with implementation of the plans? Will one plan promote old-growth-associated species more than the other?

The second goal of this paper is to present a test case for a new method for habitat modeling, a simple form of nonparametric regression based on a smoothing technique. The method was first implemented by Peterson (2000) under the name "SpOcc" for "Species Occurrence Modeler." Our interest in the method derives from the flexibility of SpOcc for modeling complex multidimensional response surfaces, without assuming particular mathematical forms, such as linear, Gaussian, or sigmoid. To illustrate the difference in approach, we contrast SpOcc with a traditional method for habitat modeling, logistic regression.

STUDY AREA

The Northwest Forest Plan designated 10 AMAs as places where the assumptions underlying the plan should be tested, and alternative means of achieving plan objectives are to be developed and evaluated. The Central Cascades AMA, lying in the central part of the Willamette National Forest and the eastern part of the Eugene BLM District (Oregon), was assigned specific objectives of testing the implications of using natural disturbance regimes in management and of integrating upslope and riparian management systems. Managers and scientists responsible for the AMA and for the science program based at the H. J. Andrews Experimental Forest developed the Landscape Plan (LP) for the Blue River watershed, ~23 000 ha. This plan is rooted in information concerning historical fire regimes and watershed processes. Earlier work evaluated the resulting landscape structures under these two plans

and assessed potential ecological and management implications (Cissel et al. 1999). Under the umbrella of the Blue River Landscape Study this approach is being refined, implemented, monitored, modeled, and modified through an adaptive management program.

Maps and description of the topography, vegetation, and climate are in Cissel et al. (1999) and Bierlmaier and McKee (1989). The Blue River watershed lies at 44°15' N, 122°15' W in western Oregon, USA. Elevations range from 450 m to 1500 m. The volcanic bedrock is deeply dissected and overlain with thick mantles of soil and colluvium on the lower slopes and valley bottoms (Swanson and James 1975). Soils are derived from volcanic tuff, breccia, andesite, and basalt. Commonly, soils are Typic Dystrachrepts, ranging from gravelly silty clay loams to very gravelly clay loams (Hawk 1979). Winters are cool and wet, while summers are warm and dry. Annual precipitation averages 240 cm. January and July mean temperatures are about 2° and 22°C, respectively. These conditions result in dominance by fast-growing conifers in the uplands. *Pseudotsuga menziesii* (Mirbel) Franco and *Tsuga heterophylla* (Raf.) Sarg. dominate at lower elevations in the "western hemlock series" of plant associations (Logan et al. 1987). *Abies amabilis* (Dougl.) Forbes, *A. lasiocarpa* (Hook.) Nutt., and *Tsuga mertensiana* (Bong.) Carr. dominate higher elevation forests in the "true-fir series" of plant associations.

The local lichen communities respond to variation in forest age and topography (McCune 1993, Berryman 2002). *Alectoria*, *Hypogymnia*, *Lobaria*, *Platismatia*, *Pseudocyphellaria*, and *Sphaerophorus* are among the most prominent epiphytic lichen genera.

METHODS

Field data

Topographic variables and forest structures were determined for the Blue River watershed at a resolution of ~1 ha, using a combination of digital elevation models, remote sensing, and ground verification (Cissel et al. 1999). Based on this information, we defined sampling strata based on a combination of age of the youngest major cohort of trees, retention of living trees through the most recent major disturbance, position with respect to streams, and elevation band (Berryman 2002). Within those strata Berryman (2002) sampled lichen communities using a total of 117 0.38-ha plots. Strata were defined by stand types, based on combinations of (1) overstory retention of remnant trees, (2) young cohort age, and (3) stream position (upland, intermittent, non-fish-bearing perennial, and fish-bearing perennial; Table 1).

Some of the strata in the design were empty or nearly empty, because some combinations of stand types are rare or absent in the current landscape. So we collapsed parts of the design to allow five or more plots in each

TABLE 1. Current and predicted areas in landscape strata and estimated frequency of occurrence of *Lobaria* in abundance class 3 or greater in the Blue River landscape.

Response variable	Current and forecasted values		
	Current	+200 yr under LP	+200 yr under IP
Lichens			
Mean $p(\textit{Lobaria} \geq 3)$ using LR model	0.51	0.60	0.58
Mean $p(\textit{Lobaria} \geq 3)$ using SpOcc model	0.51	0.60	0.59
Areas of landscape strata (hectares)			
Young clearcuts, no remnants, upland ($n = 10$)	2079	34	37
Pole timber (21–80 yr), no remnants, upland ($n = 11$)	4556	639	629
Mature timber (81–200 yr), no remnants, upland ($n = 14$)	4367	117	113
Young cuts, 15% retention, upland ($n = 13$)	85	288	2014
Pole to mature, 15% retention, upland ($n = 7$)	1513	2661	6525
Young cuts, 30% or more retention, upland ($n = 5$)	131	889	3
Pole timber, 30% or more retention, upland ($n = 7$)	0	2694	0
Mature timber, 30% or more retention, upland ($n = 5$)	0	2339	0
Old growth, upland ($n = 13$)	7546	10 851	10 939
Recent (<20 yr) cut, variable retention, near stream ($n = 9$)	194	81	<1
Pole trees, variable retention, near stream ($n = 7$)	690	131	65
Mature trees near stream ($n = 8$)	517	380	9
Old growth near stream ($n = 8$)	1066	1649	2387

Notes: Forecasts are made for a 200-yr period under the Landscape Plan (LP) and the Interim Plan (IP). Sample sizes (n) for the training data set are given for each stratum.

stratum (Table 1). Berryman (2002) showed lichen communities differed little between the upland and intermittent streams. Similarly, fish-bearing and non-fish-bearing perennial streams had comparable lichen communities. So we combined the first two stream positions into “upland” and the last two into “near stream.”

Strata 7 and 8 were not in the existing landscape map, but will appear as the forest plan unfolds. They were sampled by using portions of variable stands, the portions meeting the criteria for the strata. Although strata 7 and 8 are sparse, both occur as small managed units with variable retention (variable density of old trees retained in an otherwise young stand) and as parts of old burns with variable survival.

Lichen communities.—The U.S. Forest Health Monitoring (FHM) lichen community method (McCune et al. 1997) was used for the field plots. This method determines the presence and abundance of macrolichen species on all standing woody plants in a large circular plot. The method has been used for over 3000 plots in the FHM program nationwide (McCune 2000). It is also used by the Pacific Northwest Region of the Forest Service for over 1000 plots in western Oregon and Washington (L. Geiser, unpublished data).⁵

Species were assigned abundance on a six-step scale: 0, absent; 1, rare (<3 individuals in plot); 2, uncommon (4–10 individuals in plot); 3, common (>10 but <40 individuals in plot); 4, very common (>40 individuals in the plot but less than half of the boles and branches have that species present); and 5, abundant (more than half of boles and branches in the plot have the subject species present). The population being sampled con-

sists of all macrolichens occurring on woody plants, both living and dead, excluding the 0.5-m basal portion of trees and shrubs. Lichens on fallen branches and other lichen litter are included.

Analysis and modeling

Our overall goal was to project frequency of various lichen species using two alternative landscape management scenarios, the interim plan (IP) and the landscape plan (LP), as described in the introduction. We projected the occurrence of selected species. We first modeled presence of *Lobaria oregana*, a key old-growth-associated cyanolichen, and report trials with two modeling approaches (described in the next two subsections). We chose *Lobaria oregana* because it can develop high biomass (>1 Mg/ha dry mass; McCune 1993), and it is important in nitrogen cycling (Antoine 2001). We then selected one modeling approach and forecasted frequency of various lichen species under both management scenarios.

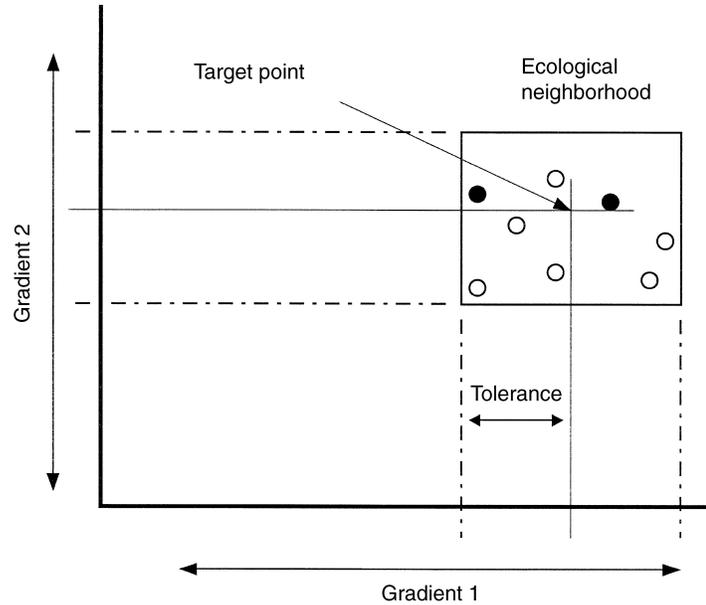
We modeled lichen response variables as a function of elevation and “stratum” based on empirical data for current stand structure. These variables were chosen because of their importance to the lichen communities, as shown by Berryman (2002).

Gridded GIS coverage (for topographic position and stratum) included $\sim 2.2 \times 10^6$ pixels, with an effective resolution of ~ 1 ha. GIS grids for stand structural information were generated from polygons based on stand mapping with practical minimum size of ~ 1 ha. Elevation data were gridded at a 10-m resolution.

We estimated future probabilities for each species under each plan for each pixel in the landscape. We used two fundamentally different kinds of models to

⁵ URL: <<http://www.fs.fed.us/r6/aq/lichen/>>

FIG. 1. Two-dimensional representation of the Species Occurrence Model (SpOcc). The model estimates the likelihood of species presence for the target point. This estimate is based on the frequency of the species in the ecological neighborhood, defined by segments of the two gradients. In this example, eight plots fell within the ecological neighborhood. Filled circles indicate plots that contained the species; empty circles indicate plots that did not. Because two out of the eight sample points within the ecological neighborhood contained the species, the estimate of probability of occurrence at the target point is 0.25.



relate species presence to habitat variables (elevation and stratum). Logistic regression is commonly used for this class of problems. We also used SpOcc, a non-parametric data smoothing technique related to kernel analysis (Bowman and Azzalini 1997). In each case, we tried various sets of predictors.

Logistic regression.—The basic logistic regression model was: $\text{logit}(\pi) = \text{intercept} + \text{slope}(\text{elevation})$, where $\pi = p(\textit{Lobaria oregana} \geq \text{abundance class } 3)$. We fit several variants to this model to include multiple slope and multiple intercept terms. One model used only elevation as an independent variable, describing the overall relationship of *Lobaria* with elevation, without regard to stratum. The second model used all data simultaneously to fit the slope term, but fit a separate intercept for each stratum. The third model fit a different slope term for each stratum, but held the intercept constant. We had insufficient data to fit a separate slope and intercept for each stratum. Many of the slope terms were significant using the third model. All slopes were similar in the third model, but intercepts were variable in the second, so we present the results from the second model rather than the third.

Species occurrence model.—The concepts of the species occurrence model are based on Peterson (2000). The model was implemented as an add-in module “SpOcc” to PC-ORD 4 (McCune and Mefford 1999; free download of the module available online).⁶ SpOcc uses the proportion of a species’ occurrence in an ecological neighborhood to estimate the likelihood of the species occurring at a target site (Fig. 1). SpOcc is thus a local mean estimator at its core, “local” being defined

as the ecological neighborhood. The ecological neighborhood consists of sites nearby in a multidimensional ecological space, the space defined by values for one or more ecological or habitat variables. It can thus be considered an “ecological neighborhood model” for predicting species occurrences. The method requires information on known (sampled) sites, including the presence of species at the sites, and the ecological characteristics of the sites. To estimate the likelihood of species occurrence for a new site (the target site), the model applies data from sites that lie close to the target site in the n -dimensional ecological space (the ecological neighborhood). The ecological neighborhood is defined by a tolerance range around the target site (Fig. 1). One key advantage of the SpOcc model over the logistic regression model is that the former does not assume a specific shape to the relationship between probability of occurrence and explanatory variables. We presume that multiple factors and their interactions will often result in complex response surfaces that are very difficult to fit with regression models.

The neighborhood model has two phases: training and application. In the training phase we use empirical data on species occurrence (0/1) to evaluate the model’s ability to estimate frequency or probability of occurrence (\hat{p}) from the independent variables. The training phase is used to (1) decide which variables to include, (2) select a window size (tolerance) for quantitative variables, and (3) indicate how much we can trust predictions from the model in the application phase. In the application phase, we estimate \hat{p} for sites at which species occurrence is unknown, based on the same data used in the training phase. Because we estimate \hat{p} rather than predict presence/absence per se, we call this “estimating” or “forecasting” rather than “predicting.”

⁶ URL: www.pcord.com

The neighborhood model does not yield an equation with coefficients; rather, the model is completely specified by the following items: (1) the species and environmental data sets used in the training phase, (2) a list of one or more independent variables, (3) specification of whether the independent variables are treated as categorical or quantitative, and (4) a tolerance range for each quantitative variable.

With more than one predictor, SpOcc automatically considers their interaction. For example (Fig. 1), both gradient 1 and gradient 2 must be suitable for the species for that species to occur. If either factor is unsuitable, then the species is absent. Mathematically, this can be represented as a multiplicative combination of two local means. See, for example, the two-dimensional kernel function in Bowman and Azzalini (1997: 6).

We varied the neighborhood size for elevation, then chose a constant tolerance of 203 m, based on optimal fit at a tolerance range of 20% of the observed range in elevations. In other words, the elevation neighborhood consisted of a band 406 m wide around a specific elevation. Because stratum is a categorical variable, it has zero tolerance: a sample point must be in the same stratum as the target stand for it to be considered part of the neighborhood.

To consider the output from this model as probabilities for the occurrence of species, then the sampling of sites must have a random component. If sampling is based on judgement, then one cannot make statements about probabilities of occurrence.

Estimates for sample points near the ends of gradients are weakened by the absence of data for the ecological neighborhood that lies just beyond the end of the gradient. This decreases the accuracy of the model near the ends of the gradient (Bowman and Azzalini 1997: 50), because predictions are made on a truncated range of data. For this reason, our local mean estimator makes estimates near the ends of the gradient somewhat biased toward the overall mean.

We modeled species occurrence in two phases: (1) extensive trials with various models using data on *Lobaria oregana*, and (2) selection of a general model form that was then applied to all major species of epiphytic macrolichens.

We initially modeled the probability of *Lobaria oregana* having an abundance class of three or more, rather than its presence/absence. This guarded against the possibility of "accidental" occurrences, single stray occurrences that would otherwise receive as much emphasis as a large population.

Habitat model evaluation.—We sought a method for evaluating model performance that could be applied to any method of estimating likelihood of occurrence. We chose to evaluate these estimates rather than predictions of presence/absence, because translating likelihood of occurrence to presence/absence unnecessarily sacrifices information. One common method of per-

formance is a pseudo- R^2 statistic (Agresti 1990:110–112):

$$R^2 = 1 - \frac{\sum_{i=1}^n (y_i - \hat{y}_i)^2}{\sum_{i=1}^n (y_i - \bar{y})^2} \quad (1)$$

where \hat{y}_i is the fitted value for the model, representing the likelihood of occurrence, and y_i is the observed value (1 or 0 for presence or absence). This can be applied to the results of any model that predicts values of 1 or 0. Although this is the same form as a traditional R^2 value, we call it "pseudo" because applied in this context it has no fixed lower bound. Negative values are possible when the "regression sum of squares" (the numerator) is larger than the total sum of squares (the denominator).

These drawbacks led us to adopt another method for evaluating model quality. We calculated Bayes factors to express the quality of a model (M_1) relative to a "naïve model" (M_2). In our case the naïve model is simply that our best estimate of the probability of encountering a species in the study area is the mean frequency of occurrence of that species in our data. The likelihood ratio comparing the models is the same as the "Bayes factor," when we assume equal prior probability of the two models (i.e., that a priori, $\Pr(M_1) = \Pr(M_2) = 0.5$). Then, the ratio of the likelihood of the observed value ($\mathbf{y} = y_1, y_2, \dots, y_n$) under the posterior model (M_1) to the likelihood of the result under the naïve model (M_2) is given by

$$\text{Bayes factor} = B_{12} = \frac{p(\mathbf{y} | M_1)}{p(\mathbf{y} | M_2)} \quad (2)$$

where

$$p(\mathbf{y} | M) = \prod_{i=1}^n \hat{p}_i^{y_i} (1 - \hat{p}_i)^{1-y_i} \quad (3)$$

and \hat{p}_i corresponds to the fitted values for the likelihood of occurrence under each model, M_j , $j = 1, 2$.

Kass and Raftery (1995) suggested the following interpretation of Bayes factors as $\log_{10}(B_{12})$, 0–0.5, not worth more than a bare mention; 0.5–1, substantial; 1–2, strong; >2, decisive. Calculating $2\log_e(B_{12})$ puts the Bayes factor on the more familiar scale of likelihood ratio test statistics (for example, G of Sokal and Rohlf 1995:691). One can test the statistical significance of the likelihood ratios using a chi-squared distribution. Conceptually, this requires that the parameter space of one model be considered a subset of, or nested within, the other model. On the contrary, Bayes factors can be applied as easily to nonnested models as to nested ones (Kass and Raftery 1995). Because we are testing models that differ fundamentally in structure, we preferred to avoid the connotation of nesting. So we interpreted our results as Bayes factors [$\log_{10}(B_{12})$] rather than log-likelihood ratios.

Bayes factors are sometimes modified to help the analyst select among competing models with differing numbers of parameters and varying sample sizes. One common measure is the Bayesian Information Criterion (BIC). Again, because of the fundamental differences in model form, and working with a fixed sample size, we chose to interpret Bayes factors directly, rather than calculate a BIC. Furthermore, our method for calculating \hat{p}_i in SpOcc penalizes for overfitting a model, rendering a BIC unnecessary.

For both classes of models we use the best available \hat{p}_i . For the logistic regression model this is simply the estimate obtained by applying the coefficients of the regression equation to the observed values for the independent variables. For the neighborhood model, however, we exclude species occurrence at the target point i from the estimation of \hat{p}_i . Conceptually this is a "leave-one-out" strategy (Fielding and Bell 1997) similar to a jackknife estimator: we sacrifice some information to obtain a better estimate of model quality, an estimate with error that is more comparable to the application phase of the neighborhood model. Inclusion of the target point leads to overfitting the model, because as the window size becomes smaller, point i has a larger influence on \hat{p}_i , and that influence is always in the "correct" direction. In other words, the circularity in logic results in \hat{p}_i with the target included always being as close or closer to y_i than \hat{p}_i with the target excluded. On the other hand, if the target point is excluded, we have a built-in penalty for overfitting. If many variables are added to the model, mean neighborhood size becomes very small, and the Bayes factor declines.

Note that if the window is so narrow that it includes a single point, \hat{p}_i cannot be calculated with target excluded, but $\hat{p}_i = y_i$ (identically) with the target included. Including the target point clearly favors narrow windows and leads to overfitting the model. Excluding the target point eliminates that problem and makes the error rate of the training phase more comparable to the application phase.

Excluding the target point does, however, create a computational problem when ($\hat{p}_i = 1$ and $y_i = 0$) or ($\hat{p}_i = 0$ and $y_i = 1$). These cases are undefined when applied to Eq. 3. In these cases, we know that the estimate of \hat{p}_i can be improved by including the target point, and that this contributes useful indication of a failure of the model, because the target point disagrees with the remaining points in the window. In this case, including the target point improves our estimate of \hat{p}_i without contributing toward overfitting the model, so we choose to retain the target point. For example, if the window contains two points, $y = [0, 1]$, and the first point is the target point, then $\hat{p}_1 = 0.5$ with target included, but with the target point excluded the data point cannot be used in Eq. 3 because $\hat{p}_1 = 1$ and $y_1 = 0$.

Application to other species.—We fit habitat models with SpOcc to all of the remaining 71 species that occurred in six or more plots. We used the neighborhood model rather than logistic regression for reasons of flexibility and parsimony of assumptions. Each species was modeled using elevation alone, stratum alone, and elevation and stratum combined. The top 10 species models in each category, based on the highest Bayes factors for improvement over the naïve model, were selected for further summarization. These 30 models included 20 species, because some species were represented in more than one category.

For these 20 species we estimated frequency in the current Blue River watershed by estimating probability of occurrence in each pixel in the watershed. Similar estimates were made under the two future management scenarios. This yielded three maps of probability of occurrence for each species, one map for the current landscape and one map for 200 years later under each scenario.

RESULTS

Changes in frequency of structural classes of forests

Both management plans prescribe large reductions in the area of clearcuts, even-aged pole-sized stands, and even-aged mature stands, as compared to the current landscape (Table 1). Both plans result in an increase in the amount of old growth from ~7500 ha to almost 11 000 ha. In addition, both plans prescribe pronounced increases in mixed-age stands.

One notable difference between plans is in the degree of retention. The Interim Plan (IP) will result in ~8500 ha of young (<80 yr) forest with 15% retention, while the LP will have a third of that area in 15% retention and ~3500 ha of young forest with 30% or 50% retention. This higher level of retention is not represented in the IP.

Another more subtle difference between plans is that the IP will result in more old growth near small streams (~2400 ha under IP vs. 1650 ha under LP). This difference is offset, however, by streamside pole to mature stands with high retention levels under the LP.

Occurrence of Lobaria oregana

Both logistic regression and the Species Occurrence Modeler were successful in estimating the occurrence of *Lobaria oregana* in the current landscape. In both cases the response variable was the presence of *Lobaria oregana* with an abundance class of three or greater. These results are described in the next two subsections.

Logistic regression.—*Lobaria oregana* is less frequently present at higher elevations in the Blue River landscape (Fig. 2; Table 2). The data in this case were fit well by a sigmoid function with *Lobaria oregana* dropping out rapidly above about 1000 m (3280 feet; Fig. 2). The overall relationship between $p(\text{Lobaria})$ and elevation (E) was:

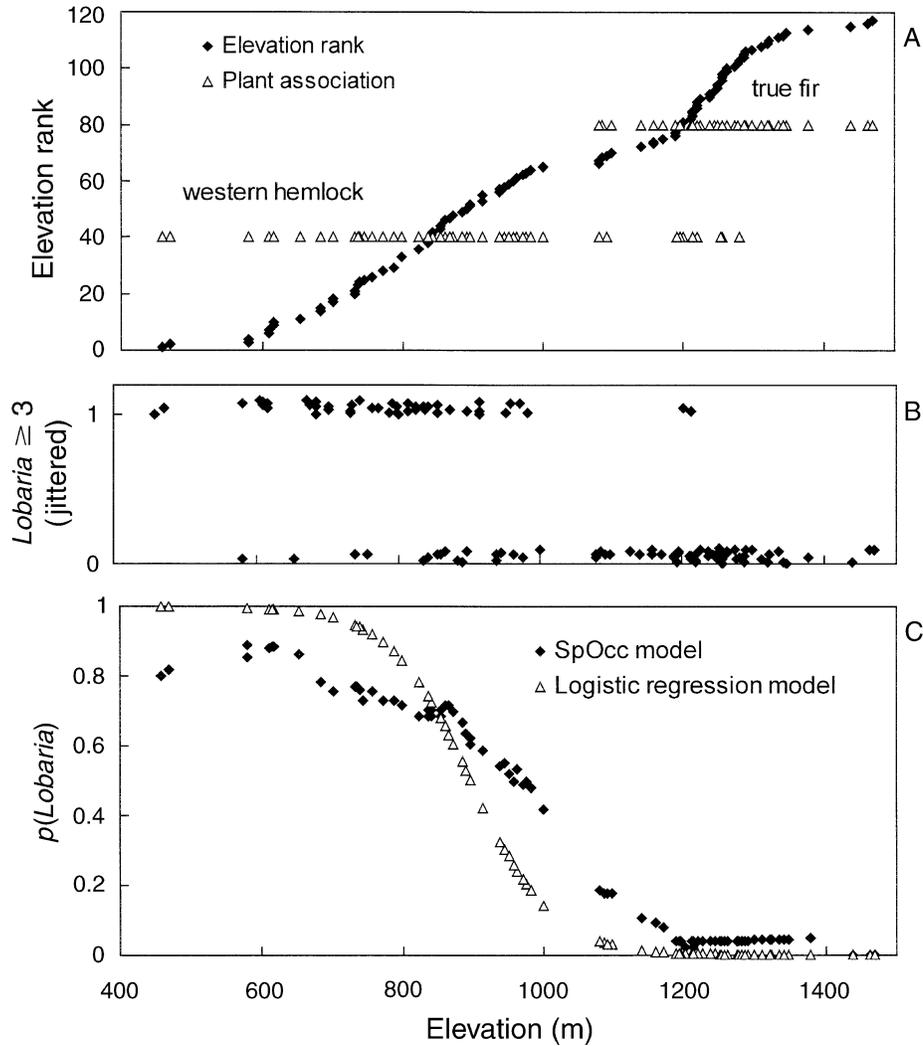


FIG. 2. (A) Relationships of plant associations (western hemlock vs. true fir) and $p(Lobaria\ oregana \geq 3)$ to elevation. The points for “Elevation rank” show the rank order of our sample of 117 plots along the elevation gradient. (B) Presence of *Lobaria oregana* in abundance class 3 or greater along an elevation gradient. Points represent sample plots. Points were jittered to reduce overlap by adding a small random number. (C) Estimated $p(Lobaria\ oregana \geq 3)$ is shown for both the logistic regression model and the Species Occurrence Model (SpOcc). Both models were based on elevation alone, without considering forest structure.

TABLE 2. Model fit (\log_{10} [Bayes factor]) for lichen response to landscape condition, comparing the indicated model to the naïve model for 117 plots.

Response variable	N	Model type	\log_{10} [Bayes factor]		
			Stratum	Elevation	Elevation + stratum
$p(Lobaria \geq 3)$	117	LR	6.2	16.6	25.7
$p(Lobaria \geq 3)$	117	SpOcc	3.5 (6.2)†	14.1	25.2

Notes: Model types are: LR, logistic regression; SpOcc, species occurrence (neighborhood) model. According to Kass and Raftery (1995) a $\log_{10}(B_{12})$ between 1 and 2 is strong, while $\log_{10}(B_{12}) > 2$ is decisive.

† Value is 6.2 with target point included in estimate; 3.5 with target point excluded.

$$p(Lobaria \geq 3) = \frac{e^{9.48 - 0.0104(E)}}{1 + e^{9.48 - 0.0104(E)}} \quad (4)$$

or

$$\text{logit}[p(Lobaria \geq 3)] = 9.48 - 0.0104(E). \quad (5)$$

The slope term of -0.0104 can be interpreted as an odds ratio. For each 1 m of increase in elevation, the odds of *Lobaria oregana* ≥ 3 increase by e^β , where β is the estimate of the slope. For this model $e^\beta = 1.0$ m, so for every 1 m increase in elevation, the odds of *Lobaria oregana* ≥ 3 decrease by $-0.0104 \times 100 \approx 1\%$.

The model including only elevation was much stronger than the naïve model ($\log_{10}B_{12} = 16.6$). The model was further improved by fitting a separate intercept to

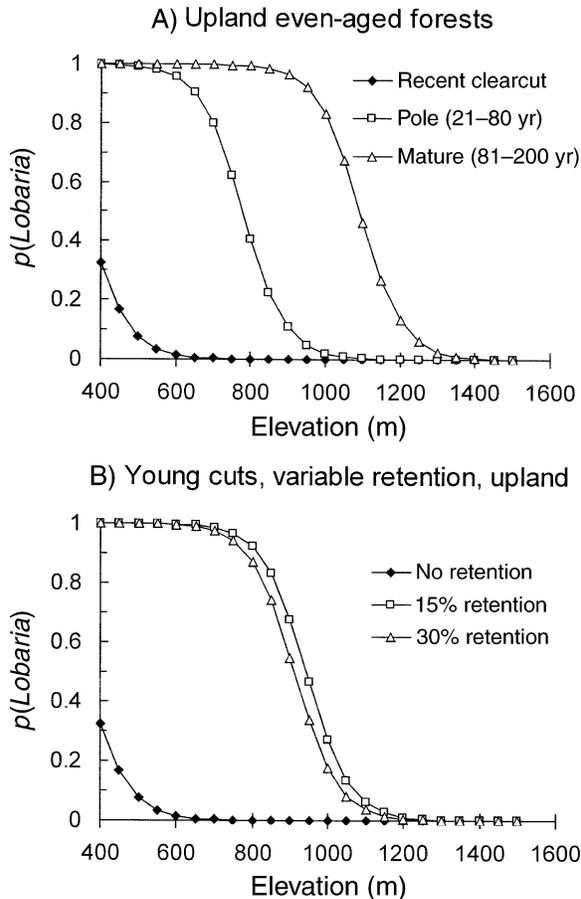


FIG. 3. Curves fit for $p(Lobaria\ oregana \geq 3)$ as a function of elevation, for various forest structural classes, using logistic regression: (A) various ages of even-aged forests; (B) various retention levels in recent cuts.

each stratum, yielding a $\log_{10}B_{12}$ of 25.7 when compared to the naïve model. All strata but one had statistically significant intercepts. Changing the intercept shifts the sigmoid function up or down with respect to elevation. For example, in a stratum unfavorable to *Lobaria oregana* (young clearcuts), the probability of *Lobaria oregana* ≥ 3 is much lower at all elevations, and this is reflected in a negative shift in the sigmoid function (Fig. 3A). As even-aged stands grow older, the intercept becomes higher, and *Lobaria oregana* becomes increasingly probable at elevations below about 1000 m (Fig. 3A).

The $p(Lobaria)$ appears similar between 15% and 30% retention in young cuts, both of which have much higher $p(Lobaria)$ than clearcuts with no retention (Fig. 3B). The similarity of $p(Lobaria)$ between these two retention levels is important, considering that one of the key differences between the LP and IP is the higher retention levels under the LP. Mature stands with 30% retention, however, appeared particularly favorable for *Lobaria*.

By combining the LR model with the planned changes in frequency of structural classes of forests, we estimated the $p(Lobaria)$ in the current landscape, and the landscape in 200 years under the IP and LP. We tabulated the number of landscape cells falling in each of 10 probability classes at 0.1 intervals (Fig. 4), and averaged probabilities across all classes. The current $p(Lobaria \geq 3)$ is estimated to be 0.51 (Table 1). In other words, we expect *Lobaria* with an abundance class of 3 or higher in about half of any number of 0.38 ha plots placed at random in the Blue River landscape. Under both management plans, this would increase over the next 200 years, primarily through a net loss

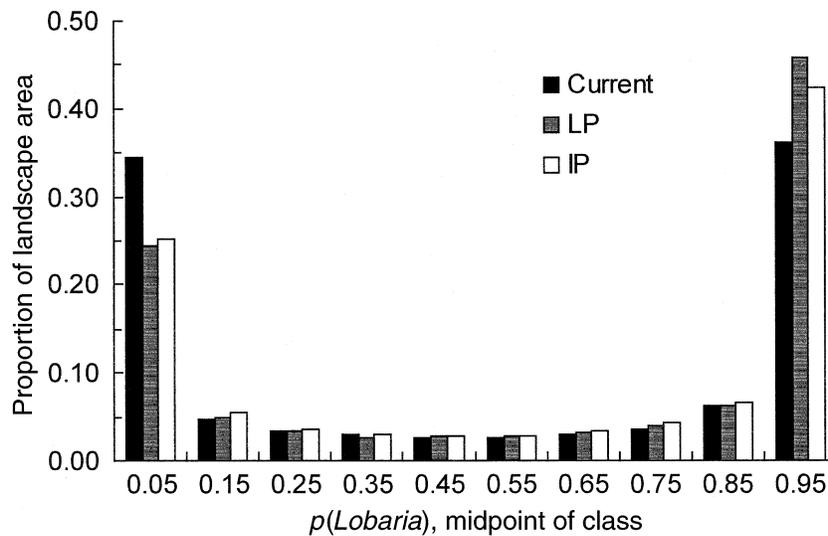


FIG. 4. Landscape area in probability classes for occurrence of *Lobaria oregana* in abundance class 3 or more, based on a logistic regression model. Three landscapes are compared: the current landscape, the landscape after 200 years under the Interim Plan (IP), and after 200 years under the Landscape Plan (LP). Each probability class spans 0.10 and is labeled by the midpoint.

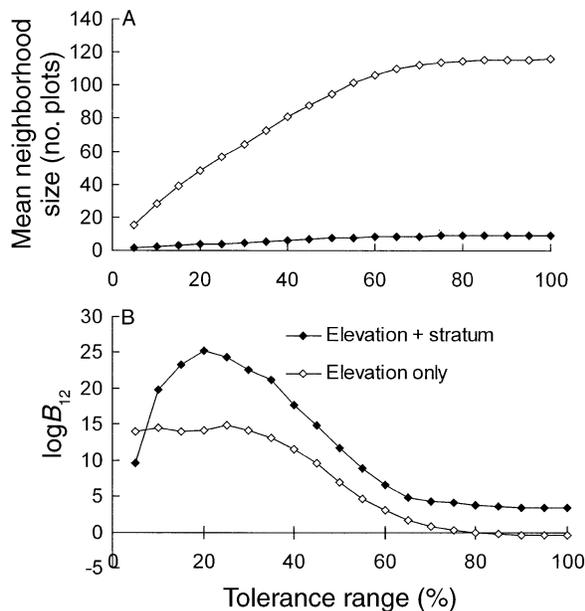


FIG. 5. Curves used to optimize fit of the Species Occurrence (SpOcc) models: (A) mean neighborhood size as a function of tolerance range for elevation, expressed as a percentage of the total range in observed elevation; (B) model fit ($\log B_{12}$) as a function of tolerance range. $\log B_{12}$ is the log of the Bayes factor. Results for two models are shown, one for elevation as the sole predictor, and one combining elevation and stratum.

of young even-aged stands and a net increase in stands with green-tree retention. Under the IP, the estimated mean $p(\text{Lobaria})$ increases to 0.58 after 200 years (Table 1). Under the LP, the mean would be somewhat higher, 0.60. These increases from 0.51 are more significant than they appear at first glance, considering that occupancy of the landscape by *Lobaria* is currently high, and most of the remaining landscape is at elevations too high for *Lobaria*. Mapping $p(\text{Lobaria})$ under both scenarios reveals that in both cases, virtually all stands within the elevational limits of *Lobaria* would be occupied by *Lobaria*. The slightly higher probability under the LP apparently results from prescribing mature stands with higher historical retention levels. These stands were particularly favorable for *Lobaria oregana*.

Species occurrence model.—Optimal fit was provided with an elevation tolerance of 203 m, ~20% of the range in elevation in the Blue River landscape (Fig. 5). The peak in fit was much more pronounced when stratum was included in the model. Best fit was provided with a mean neighborhood size of ~50 plots for the model based on elevation alone, and 3.5 plots for the model including stratum and elevation (Fig. 5).

Using elevation with stratum as predictors yielded a bigger improvement over the naïve model ($\log B_{12} = 25.2$) than either a model using just stratum ($\log B_{12} =$

6.2) or a model using just elevation ($\log B_{12} = 14.1$; Table 2). SpOcc and LR performed similarly (for LR vs. SpOcc, $\log B_{12} = 0.5$).

The LR model based on stratum alone fits a separate intercept for each stratum, but there is no slope. The SpOcc and LR models for stratum alone are identical, if the target point is included in the SpOcc model, both models representing \hat{p}_i as simply the within-stratum frequency. If, however, the target point is excluded from the SpOcc model, but not the LR model, then the fit with SpOcc is expectedly worse than with LR, using stratum alone (For LR vs. SpOcc, $\log B_{12} = 2.7$).

Choosing the best model, which combined stratum and elevation as independent variables, the model fits for LR and SpOcc are remarkably similar (Table 2). Likewise, the estimated landscape-scale frequency of *Lobaria* is nearly identical between the LR and SpOcc models (Table 1). This is true for the current landscape as well as both future landscapes (Table 1).

Application to other species

Based on the flexible, nonparametric form of the neighborhood model (SpOcc) and its good performance with *Lobaria oregana*, we applied the neighborhood model to the other 71 epiphytic lichen species occurring in six or more plots. Although the LR model is, in this case, suitable for *Lobaria oregana*, the response curves for each of the 71 species should be examined both visually and statistically, for confident application of LR. On the other hand, applying SpOcc as a nonparametric smoother allows an automatic fit to any response surface, without having to specify or visualize that surface.

A few species were best modeled with elevation or stratum alone, but most models were improved by including both elevation and stratum as predictors (Table 3). Success of the top 10 species models in each category, based on the highest Bayes factors for improvement over the naïve model, is reported in Table 3. Note that frequency of occurrence in the 117 plots is not the same as the estimated current landscape-level, because the former is based on a stratified random sample rather than a random sample.

For most species, the two landscape management plans made little difference in the frequency of these species after 200 years (Table 3). Several species, however, are forecasted to be more frequent under either management plan than they are now (e.g., *Lobaria oregana*, *L. pulmonaria*, *Nephroma helveticum*, *N. parile*, *Platismatia herrei*, *Pseudocyphellaria anthraspis*, *P. rainierensis*, and *Sphaerophorus globosus*). In all cases, this is a consequence of increasing the amount of old growth and eliminating clearcutting, thereby reducing the frequency of young, even-aged stands. Species forecasted to be more frequent in the current landscape than the future landscape were most frequent in even-aged pole-sized and mature stands (e.g., *Cetraria*

TABLE 3. Fits for epiphytic macrolichen species to habitat models including elevation, stratum, or both.

Species	Frequency	Model fits log(Bayes factor)			Mean <i>p</i> (occurrence)		
		Elevation	Stratum	Elevation + Stratum	Now	IP	LP
<i>Cetraria orbata</i>	0.57	-1.15	3.16	4.35	0.64	0.47	0.44
<i>Cladonia ochrochlora</i>	0.10	-1.02	2.95	2.96	0.17	0.19	0.22
<i>Hypogymnia metaphysodes</i>	0.48	1.46	4.57	8.25	0.50	0.40	0.39
<i>Hypogymnia rugosa</i>	0.16	0.94	2.35	9.41	0.19	0.22	0.23
<i>Lobaria oregana</i>	0.54	17.88	1.53	26.01	0.57	0.63	0.65
<i>Lobaria pulmonaria</i>	0.38	13.96	0.84	21.16	0.53	0.63	0.60
<i>Lobaria scrobiculata</i>	0.25	6.87	-2.29	8.42	0.36	0.37	0.36
<i>Nephroma bellum</i>	0.16	5.80	0.51	8.15	0.25	0.30	0.25
<i>Nephroma helveticum</i>	0.25	9.72	0.72	15.63	0.38	0.48	0.46
<i>Nephroma parile</i>	0.11	2.11	3.07	6.28	0.18	0.26	0.20
<i>Nephroma resupinatum</i>	0.15	4.74	1.04	8.72	0.18	0.13	0.14
<i>Parmeliopsis ambigua</i>	0.15	6.90	2.93	10.68	0.13	0.12	0.12
<i>Platismatia herrei</i>	0.87	1.07	10.12	11.93	0.88	0.98	0.99
<i>Platismatia stenophylla</i>	0.91	-1.16	3.75	6.19	0.92	0.95	0.94
<i>Pseudocyphellaria anomala</i>	0.39	11.73	-0.78	20.19	0.51	0.53	0.51
<i>Pseudocyphellaria anthraxis</i>	0.23	7.92	4.70	15.07	0.34	0.43	0.47
<i>Pseudocyphellaria rainierensis</i>	0.09	2.80	5.38	9.99	0.16	0.29	0.24
<i>Ramalina dilacerata</i>	0.09	-0.11	3.15	7.22	0.09	0.02	0.01
<i>Sphaerophorus globosus</i>	0.71	3.61	10.56	17.51	0.76	0.95	0.94
<i>Sticta fuliginosa</i>	0.14	5.34	-0.03	6.96	0.16	0.15	0.18

Notes: All results are for neighborhood (SpOcc) models. The top 10 species in each class of models are included in the following table. Model fits are expressed as \log_{10} [Bayes factor] ($\log B_{12}$). "Frequency" is the overall frequency of occurrence in 117 plots. The last three columns are the mean probability of each species occurring in a grid of two million, 0.38-ha plots, for the current landscape, the landscape under the Interim Plan (IP) after 200 years, and the landscape under the Landscape Plan (LP) after 200 years; these were estimated from the elevation + stratum neighborhood models. Values in bold have landscape-scale probabilities at least 0.1 greater than one of the other categories.

orbata and *Hypogymnia metaphysodes*). Similarly, because *Ramalina dilacerata* was most frequent on shrubs in pole stands near streams, this species is forecast to decline under both plans.

Maps for *Pseudocyphellaria rainierensis* illustrate the modeling results (Fig. 6). Like *Lobaria oregana*, *P. rainierensis* is old-growth associated and probably dispersal limited (Sillett and Goward 1998, Sillett et al. 2000). At a mean probability of occurrence of 0.17 in plots in the current landscape (Table 3), it is less frequent than *Lobaria oregana* (mean probability = 0.57). Because *Pseudocyphellaria rainierensis* is concentrated in low-elevation old growth, much of the current landscape is unlikely to support it (Fig. 6, upper). The major drainage in the southeastern part of the watershed (Fig. 6) is the H. J. Andrews Experimental Forest, to be managed as "Late-successional Reserve" (LSR), as opposed to the remaining "matrix" lands. Because there is more old growth remaining in the LSR than in the matrix, we are currently more likely to encounter *P. rainierensis* in the LSR than in the matrix. In the future, *P. rainierensis* should increase in both the LSR and matrix. Because the LSR is to be managed the same under both management scenarios, our forecast for *P. rainierensis* in the LSR appears the same under both the interim plan (IP) and landscape plan (LP; Fig. 6).

The contrast between the two management plans can be seen in the 200-yr forecasts for *Pseudocyphellaria*

rainierensis (Fig. 6). Because *P. rainierensis* favors low topographic positions, and the IP maintains a relatively broad riparian buffer along all streams, we see a pronounced dendritic pattern of occurrence in the forecast (Fig. 6, middle). In contrast, the LP eliminates buffers along intermittent streams, pruning the finest branches of the dendritic pattern of occurrence (Fig. 6, lower). Furthermore, riparian buffers are narrower under the LP than under the IP. This loss of habitat is partially offset by higher green-tree retention levels in the cutting units, such that the resulting mean probability of occurrence in the whole watershed is only slightly higher under the IP ($P = 0.29$ for the IP and $P = 0.24$ for the LP).

DISCUSSION

Habitat of Lobaria oregana

Lobaria oregana rapidly diminishes in frequency in the landscape at elevations above 900–1000 m (Fig. 2). Young, even-aged stands have little or no *Lobaria oregana*. However, most of the other structural classes are similar in frequency of *Lobaria*. The lichen differences between different levels of retention and between mature and old-growth stands are small compared to the differences with respect to elevation and clearcutting. In the Blue River landscape, *Lobaria oregana* is a predictable component of the lichen flora in mature to old-growth or mixed-age stands 400–1000 m in elevation.

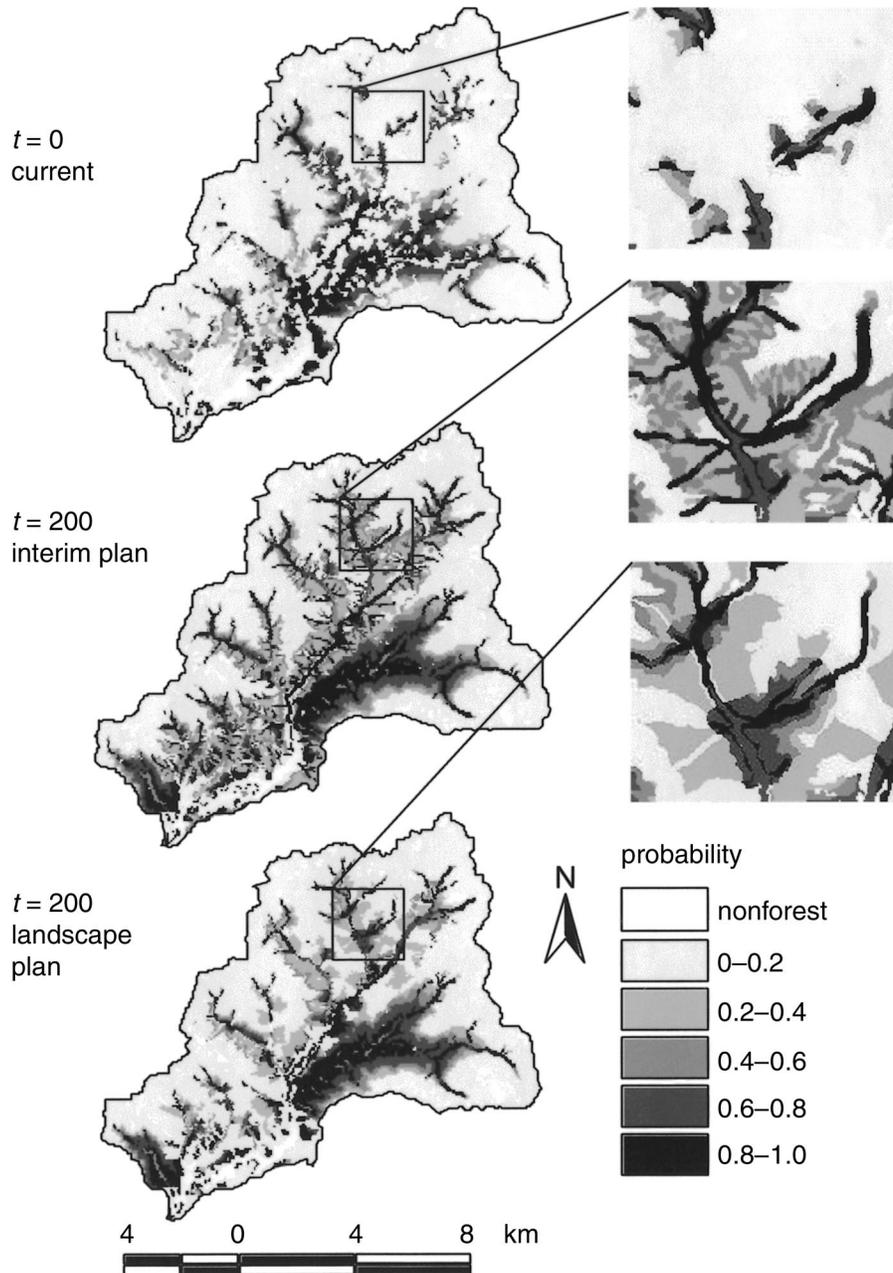


FIG. 6. Probability of occurrence of *Pseudocyphellaria rainierensis* in the Blue River watershed. The top panel shows the current landscape; middle panel, 200 years later, managed under the Interim Plan; and bottom panel, 200 years later, managed under the Landscape Plan. Inset maps show details for a portion of the watershed. The major subwatershed in the southeast part of the map is to be managed as a Late-successional Reserve under both plans.

The loss of *Lobaria oregana* with increasing elevation roughly corresponds with the transition from western hemlock to true firs as the predominant shade-tolerant trees (Fig. 2). There are some exceptions, however. Ten of the 117 stands with considerable western hemlock occurred above the transition zone for *Lobaria oregana*, at elevations ranging from 1100 to 1300 m.

Difference in lichen response to alternative management plans

The LP will produce more late-successional habitat (71% of the watershed vs. 59%) in a less fragmented landscape as compared to the IP (Cissel et al. 1999). More complex stand structures are favored by the LP due to generally higher overstory canopy retention lev-

els. The LP also maintains a substantial component of mature forest (80–200 yr old). In contrast, the IP nearly eliminates the mature forest component, because almost all lands are either in a reserve, where all stands grow old and large-scale disturbance is eliminated, or in matrix lands where a relatively short rotation (~80 yr) prevents regrowth of mature forest.

Our neighborhood model of lichen responses to management scenarios does not include components of patch size or edge effects, but it is potentially responsive to green-tree retention levels, stand age, and riparian management. Larger patches in the LP create more interior habitat, thought to benefit some wildlife species such as the Northern Spotted Owl (*Strix occidentalis caurina*), but of questionable significance to lichens. Existing evidence on lichen response to edges is ambivalent: subtle negative and positive effects have been seen for various species (Sillett 1994, 1995, Renhorn et al. 1997, Esseen and Renhorn 1998, Kivisto and Kuusinen 2000). If increased exposure kills old-growth-associated lichens along new edges of old forest, then less edge between old and young forests in the LP may reduce mortality of these species. On the other hand, less edge will reduce habitat for species that favor edges.

In contrast, positive effects on old-growth-associated lichens are known for green-tree retention (Rominger et al. 1994, Neitlich and McCune 1997, Peck and McCune 1997, Peterson and McCune 2001) and stand age (examples from the Pacific Northwest: McCune and Antos 1982, Lesica et al. 1991, McCune 1993, Neitlich 1993, Neitlich and McCune 1997, Ruchty 2000, Peterson and McCune 2001, Pipp et al. 2001).

Lobaria oregana showed minimal differences in frequency of presence in 0.38-ha plots between management plans after 200 years. Assuming climate and air quality do not change much, and assuming no extensive wildfires, *L. oregana* should be present in virtually all stands below ~1000 m. The similarity of the two plans for lichen habitat derives from the fact that neither plan prescribes even-aged management. Even 15% retention is sufficient to ensure the presence of *Lobaria oregana* in most stands. An increase in retention from 15% in the IP to 30% and 50% in the LP might enhance *Lobaria* biomass considerably, but make little difference in the presence of *Lobaria* throughout the landscape. Influences of landscape features such as patch size, shape, and connectivity are probably minor compared to the pronounced influence of a nearby retention tree.

The retention of lichen biomass through a cutting operation should be approximately proportional to the degree of tree retention. Therefore, we hypothesize that the biomass of lichens will be more responsive to a difference between 15% vs. 30% retention than the presence of a particular species would be. In terms of preserving a species' frequency across the landscape, both plans may do well, because even the lower level of retention is apparently a good way of retaining pres-

ence of epiphytes. But in terms of functionality (e.g., contribution of fixed N), it seems likely that the higher retention levels under the LP would promote biomass, and therefore functional contributions, of *Lobaria oregana*.

Retention trees in the IP will be younger and smaller due to shorter rotations in the matrix, as compared to the LP. Our model does not consider characteristics of retention trees, but as their mean age decreases we anticipate smaller contributions to future lichen populations.

Similar to *Lobaria oregana*, most other species showed only slight differences in frequency between management plans. Many of these species were old-growth-associated or riparian-associated cyanolichens or forage lichens. About half of the species examined, however, are predicted to be more frequent under either management plan than in the current landscape. This is a likely response to the demise of even-aged management in this landscape.

The outcome under either management plan could differ greatly from our long-range forecasts, depending on changes in factors outside our models, such as climate and air quality. If the current trend toward increasing population in the Willamette Valley continues, air pollution is likely to reduce the presence of *Lobaria oregana* and other cyanolichens in the Blue River landscape. Air pollution effects are already apparent in the presence of pollution-tolerant lichens and near-absence of pollution-sensitive lichens in the Cascades east of Portland, Oregon (Neitlich and McCune 1997).

If lichen species exist that require continuous old-growth forests near intermittent or small non-fish-bearing streams, then the IP would favor those species. There is no evidence, however, that such lichen species exist. The riparian lichens of the Central Cascades AMA do not appear to be restricted to old-growth stands in the headwaters. In fact, the difference in lichen communities between upland stands and stands along non-fish-bearing streams are so subtle as to be virtually undetectable with multivariate analysis of lichen community data (Berryman 2002). The lichens with the strongest riparian association in this area are most frequent along larger streams (McCune et al. 2002). The IP and LP prescribe almost identical management practices along large streams.

Comparison of modeling methods

The most important difference between our logistic regression model and the SpOcc model was that logistic regression requires the analyst to specify a response function that relates the probability of occurrence to habitat variables. This model is usually sigmoid, but see Huisman et al. (1993) for using logistic regression to fit other forms, including a bell-shaped response for species data. On the other hand, SpOcc fits a model to the data without assuming any particular response shape. Adopting SpOcc means foregoing the represen-

tation of the response as a simple function. This is a sacrifice only if a simple function can realistically represent the response. A simple function is easily adapted to a GIS framework, while predictions under SpOcc require a nonformulaic application to every point in the landscape. This cannot be done with standard GIS software, but could be done with extensions or scripts for GIS or spreadsheet software.

Will logistic regression models be generally useful for modeling species occurrences on the landscape? Probably not, if we assume that many species will have variously hump-shaped or irregular distributions on environmental gradients. Simple response surfaces are unrealistic for most multifactor habitat problems.

Despite the good fit of the *Lobaria* data to elevation using logistic regression, the results cannot be extrapolated to lower elevations in the Cascades. *Lobaria oregana* apparently becomes less frequent below the study area, such that the broader response of *Lobaria oregana* to elevation is hump-shaped rather than sigmoid. This means that our sigmoid function is inappropriate for a broader span of elevations extending below the low end of our data set (400 m). Using SpOcc allows flexible fitting of a response, without examining each species' relationship to each predictor. Furthermore, SpOcc automatically models responses to interactions among predictors, while those must be consciously and sparingly introduced into regression models.

SpOcc provides a particular method of nonparametric regression (compare with Bowman and Azzalini 1997: Chapter 3), with several innovations useful for habitat modeling: (1) we used the simplest possible specification of a window into a multidimensional ecological neighborhood; (2) we adopted a Bayesian statistic for comparing model performance to a naïve model, giving us a common basis for evaluating estimates of the probability of species occurrence generated by any means; (3) our "leave one out" strategy for estimation minimizes overfitting. Nonparametric regression for habitat modeling deserves further exploration, in particular using improved kernel functions, such as local logistic regression, in place of our local mean estimator.

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