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Modeling the distributions of shrub species in Pacific northwest forests

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Abstract

In Pacific Northwest forests, understory species are important elements of forest structure and composition, providing habitat and forage for wildlife and contributing to much of the floral diversity. Knowledge of the factors that control the distribution and abundance of understory species is central to understanding the ecology and dynamics of natural forests and how they will respond to management. Generalized linear models of the binomial family were used, at two spatial scales, to estimate the probability of occurrence of shrub species as a function of environmental variables and the cover of mature and regenerating tree species. Graphical analysis and resampling techniques were used to: (1) examine whether species show unimodal responses to environmental gradients; (2) explore the scale-dependence of model forms; and (3) predict areas of high probability of species occurrence within a multi-dimensional environmental space. Results suggest that the concept of unimodal response to environmental gradients can be used to improve predictions about species' distributions, and to strengthen the biological interpretation of statistical models. They also demonstrate the scale-dependence of model equations and the likelihood that key processes influencing plant distributions may change, or appear different, when viewed at different scales.

1. Introduction

The degree to which physical environment shapes vegetation has been a fundamental theme of ecological inquiry (e.g. Watt, 1947; Mueller-Dombois and Ellenberg, 1974; Whittaker, 1975; Daubenmire, 1978). The distributions of plant species are ultimately constrained by climate (Woodward, 1987; Woodward and McKee, 1991), and species are often assumed to be more robust, and thus more abundant, in the centers of their ranges (Whittaker, 1975). Multivariate methods used in community ecology make the particular assumption that plants show a unimodal response to environmental gradients (Gauch, 1982; ter Braak and Prentice, 1988). This assumption is also implicit in forest successional models, in which tree growth increases, and probability of mortality decreases, toward the center of a species' range (Urban, 1990; Shugart and Prentice, 1992).

Successional models and empirical growth models (e.g. Wykoff, 1990; Hann et al., 1992) generally assume that an increase in competitive inhibition produces a monotonic decrease in tree growth. The response of the understory, however, is likely to be more complex. For example, moderate overstory cover may ameliorate extremes in microclimate that would otherwise be stressful for ground-layer plants (Hammond III, 1969; Cui and Smith, 1991), whereas dense overstory cover suppresses understory species regardless of environmental constraints (Alaback, 1982; Carter and Klinka, 1992). Thus, one might

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assume a unimodal response of understory vegetation to biotic variables, such as overstory canopy cover. In general, however, modeling difficulties and sources of variation increase with the addition of understory layers, and as structural complexity and species diversity increase. Potential interactions among layers increase, as plants respond not only to large-scale environmental variation, but also to microclimatic gradients and multiple sources of competition (Ford and Sorrensen, 1992).

The difficulties in modeling tree growth and succession are substantial (e.g. Bruce, 1990; Shugart and Prentice, 1992; Maguire et al., 1993; Reynolds et al., 1993), but much progress has been made. This has been driven by economic incentives to increase timber production, and the need to estimate species' responses to climatic change (e.g. Urban et al., 1993). In contrast, few efforts have been made to model the distribution or abundance of understory species (but see Laursen, 1984; Klinka and Chen, 1996). Nevertheless there are practical, as well as theoretical, reasons for pursuing research in this area. Understanding the factors that determine the distributions of understory plants is important for:

1. predicting understory composition and structure and its response to natural disturbance, climatic change, and managerial strategies (Alaback, 1982; Halpern, 1988; Halpern, 1989; Alaback and Tappeiner II, 1990; Stein, 1995);
2. conserving plant diversity (Roberts and Gilliam, 1995), particularly in regions, such as the Pacific Northwest, in which the understory is significantly more diverse than the tree flora (Spies, 1991; Halpern and Spies, 1995); and
3. providing for suitable wildlife habitat and forage (e.g. Hansen et al., 1993).

Logistic or fiscal constraints often compel managers to take a coarse-scale approach to applied research and monitoring. Although plant distributions can be site-specific or inherently stochastic at particular scales, coarse-scale predictors that are relatively easy to measure are potentially valuable, but only if they have reasonable predictive power. If easily measured variables are effective surrogates for the 'operational environment' of plants, their predictive power will be sufficient even if a mechanistic understanding is lacking.

In this paper, we illustrate an exploratory approach to understanding the distributions of understory species in Pacific Northwest forests – an approach that has relevance to basic ecological research and to practical application. In particular, we present empirical models that predict the probability of occurrence of nine shrub species that are important structural or compositional elements of Pacific Northwest forests. Our objectives are to:

1. determine whether plant species exhibit a unimodal response to environmental gradients;
2. explore the scale-dependence of model forms and the relationship of spatial scale to the types of variables that are significant for predicting plant responses; and
3. identify, where possible, areas of high probability of occurrence within a multi-dimensional environmental space.

2. Methods

2.1. Study sites and field methods

Plot-level data were obtained from the Area Ecology program, USDA Forest Service, for the Gifford Pinchot, Mt. Hood, and Willamette National Forests in the Cascade Range (Table 1). These forests occupy a latitudinal gradient from southern Washington to central Oregon (Fig. 1). The Area Ecology program has a wide range of objectives (see Hemstrom et al., 1982; Brockway et al., 1983; Halverson et al., 1986; Topik et al., 1986; Topik et al., 1988; Topik, 1989); here, we only describe aspects of data collection relevant to the objectives of this paper.

Circular, 0.2-ha plots were established in selected stands encompassing a range of elevations, aspects, and slopes that met the following criteria: (1) >75 years old; (2) relatively undisturbed; and (3) relatively uniform in vegetation composition. Elevation, aspect, and slope were recorded at each plot, and ocular estimates of cover were made for all species, including herbs, shrubs, regenerating trees (<3.5 m tall), and mature trees (>3.5 m tall). For modeling purposes, aspect was transformed into degrees from southwest (range, 0–180) to represent the environmental gradient encountered with the change in slope orientation from SW to NE. Field plots were geo-referenced to UTM

Table 1
Means and ranges of environmental characteristics and tree cover for plots in the model database

Variable		Gifford Pinchot NF	Mt. Hood NF	Willamette NF
Number of plots		859	1219	582
Elevation (m)	Mean	949	903	965
	Range	229–2030	58–2011	320–1768
Annual precipitation (mm)	Mean	2120	1960	1850
	Range	1086–3218	439–3629	1125–3386
Slope (%)	Mean	32	33	31
	Range	0–100	0–83	0–90
Cover of mature Douglas-fir (%)	Mean	32	44	24
	Range	0–95	0–95	0–80
Cover of mature western hemlock (%)	Mean	21	17	12
	Range	0–95	0–90	0–80
Cover of regenerating western hemlock (%)	Mean	5	5	3
	Range	0–80	0–40	0–40

coordinates. The 30-year mean annual precipitation for each plot was extracted from a GIS coverage generated by the PRISM model (Daly et al., 1994).

2.2. *Data analysis*

We had originally intended to develop models at three spatial scales: all three forests; individual forests; and vegetation zones within each forest, characterized by different dominant tree species. Exploratory multivariate analysis revealed no gradients related to species distribution at the smallest scale, so further analysis within vegetation zones was dropped. For each species (Table 2), we used a generalized linear model of the binomial family (McCullagh and Nelder, 1989) to estimate the prob-

Table 2
Species modeled

Species	Common name	Family[a]	Primary reproductive strategy
Tall shrubs			
Acer circinatum	Vine maple	Aceraceae	Layering/basal sprouting
Holodiscus discolor	Oceanspray	Rosaceae	Basal sprouting
Rosa gymnocarpa	Baldhip rose	Rosaceae	Seed
Vaccinium parvifolium	Red huckleberry	Ericaceae	Basal sprouting, layering, seed
Low shrubs			
Berberis nervosa	Oregongrape	Berberidaceae	Clonal spread via rhizomes
Gaultheria shallon	salal	Ericaceae	Clonal spread via rhizomes
Sub-shrubs			
Chimaphila menziesii	Little prince's pine	Ericaceae	Clonal spread via rhizomes
Chimaphila umbellata	Prince's pine	Ericaceae	Clonal spread via rhizomes
Rubus ursinus	Trailing blackberry	Rosaceae	Stoloniferous, seed

[a] Taxonomy and nomenclature follow Hitchcock and Cronquist (1973).

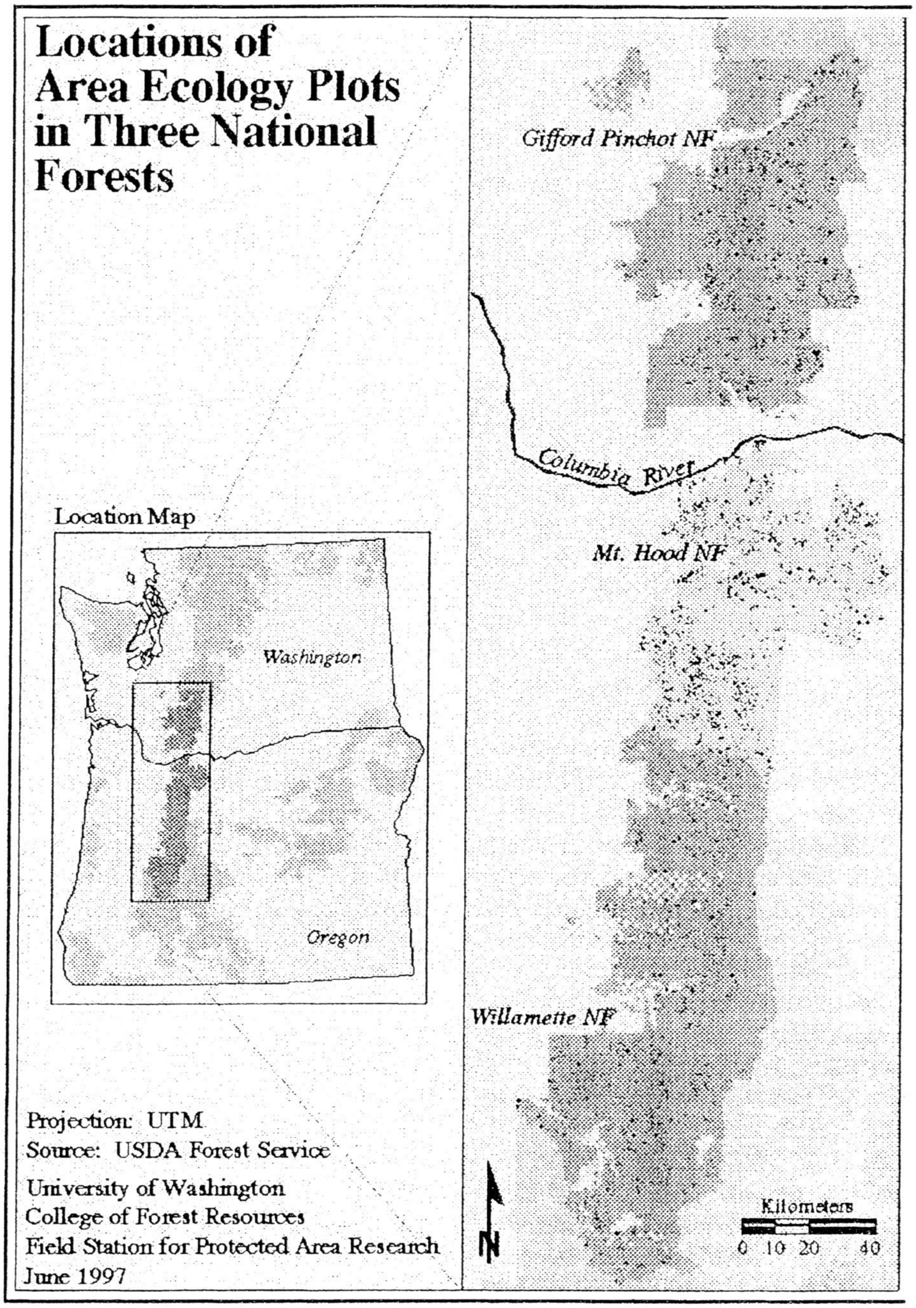

Fig. 1. Geographic locations of area ecology plots. Dots indicate plots.

ability of occurrence at each plot as a function of environmental variables and cover of mature and regenerating tree species. This approach produces results similar to logistic regression, except that a maximum likelihood method is used rather than least-squares estimation. The model takes the following form:

$$\nu = \beta_0 + \sum_{i=1}^{p} \beta_i X_i \tag{1}$$

where ν is the linear predictor, X_i ($i=1\cdots p$) the predictor variables, and β_is the estimated coefficients. The logit link function

$$P(\text{occurrence}) = \exp(\nu)/(1+\exp(\nu))$$

then transforms the linear predictor into fitted probabilities.

Wherever possible, we constrained each variable in the linear predictor to a simple unimodal function to approximate the theoretical unimodal response to environmental gradients (Whittaker, 1975; ter Braak and Prentice, 1988). Thus, with appropriate coefficients, plots of the response variable against the predictor variables will appear unimodal within the range of the data. Unimodal functions were either an orthogonal polynomial of degree two, to minimize multicollinearity; or the logarithm plus the square of the predictor, with coefficients fitted to each term (only if the linear/logarithmic coefficient was positive and the quadratic coefficient negative – hereafter indicated ±). We used the Akaike Information Criterion (Akaike, 1974) and Chi-squared statistics, respectively, to determine the most parsimonious models and to check for significant reductions in deviance for each term in the models. Since our objectives were exploratory in nature, we did not search exhaustively through all combinations of variables and model forms. We did, however, calculate the proportional reduction in deviance (PRD) produced by the fitted terms for each model. For models not of the Gaussian family, this proportion roughly corresponds to the multiple coefficient of determination (R^2). Although neither PRD nor R^2 is a good measure of the predictive power of a model (Neter et al., 1990), both provide a means for comparing the amount of unexplained variation in models for different species.

We used graphical analysis to display the expected probability of occurrence of each species with respect to pairs of predictor variables, focusing on the two predictors that are particularly relevant to climatic change, elevation and precipitation. We calculated the probability of occurrence at each plot, replacing the vectors of the other predictors with a vector containing their mean value repeated n times (where n=number of plots). Thus, for elevation and precipitation, the linear predictor is calculated by:

$$Y = \beta_0 + \beta_1\text{ELEV} + \beta_2\text{PRECIP} + \sum_{i=3}^{p} \beta_i \mu_n(X_i) \tag{2}$$

where ELEV and PRECIP are vectors from the data, p the number of predictors, β_i the coefficients, and $\mu_n(X_i)$ a vector equal to the mean of X_i repeated n times. This technique smooths the fitted values from the models so that interpretations from contour plots can be meaningful. Scatterplots of pairs of predictors were used to identify areas of two-dimensional environmental space in which there was a paucity of data, implying that interpretation of smoothed values might be questionable.

With skewed or otherwise irregular distributions, mean values or other summary statistics may be misleading. To check the robustness of our graphical technique, we developed the following resampling technique, applied it to the two-dimensional space of elevation and precipitation at the largest spatial scale (three forests), and visually compared the graphical output (contour plots) to that using Eq. (2). For each predictor variable other than elevation and precipitation, we selected a parametric distribution based on graphical analysis, and randomly generated a vector of length n from the selected distributions. Each of these vectors replaced one of the Xs in Eq. (2) for which the mean values were used. Thus:

$$Y = \beta_0 + \beta_1\text{ELEV} + \beta_2\text{PRECIP} + \sum_{i=3}^{p} \beta_i R_n(X_i) \tag{3}$$

where $R_n(X_i)$ is a vector of random variates from the distribution associated with variable X_i. We then used the mean of 20 realizations of the linear predictor from Eq. (3) as the input to the graphical displays. If contour plots of these predictions were visually similar to those using means of the predictor variables in the model (no obvious differences in shape), we could expect that our simpler graphical technique was robust to distributional anomalies. We assumed that correspondences for elevation and precipitation were indicative of those between graphical output for other variables, at other scales.

Table 3
Signs of coefficients for predictor variables in each model database. 0=coefficient not significant. ±, –/–, or ∓ means that a quadratic term was fit. ± indicates a positive linear or logarithmic term and negative quadratic term. –/– indicates negative–negative, and ∓ negative–positive. ± is taken to indicate a unimodal response (concave down)

Species	Elevation (m)	Precipitation (mm)	Cover of mature Douglas-fir	Cover of mature western hemlock	Cover of regenerating western hemlock	Aspect in degrees from SW	Slope (%)
All three forests							
Acer circinatum	–/–	±	±	0	±	–	+
Berberis nervosa	±	±	±	0	±	–	+
Chimaphila menziesii	±	–	±	0	±	0	+
Chimaphila umbellata	±	±	±	0	±	–	0
Gaultheria shallon	–/–	∓	±	±	0	–	0
Holodiscus discolor	±	±	±	∓	–	–	0
Rosa gymnocarpa	±	±	±	∓	–	–	0
Rubus ursinus	±	±	±	–/–	–	–	0
Vaccinium parvifolium	±	±	0	+	±	0	+
Gifford Pinchot NF							
Acer circinatum	–	0	+/+	0	0	–	+
Berberis nervosa	–	0	±	+	+	0	+
Chimaphila menziesii	±	0	+	0	+	0	0
Chimaphila umbellata	±	0	0	0	0	0	0
Gaultheria shallon	±	±	±	+	0	0	+
Holodiscus discolor	±	–	+	∓	0	0	0
Rosa gymnocarpa	±	∓	+	0	0	–	0
Rubus ursinus	±	0	±	0	0	–	0
Vaccinium parvifolium	±	±	0	±	0	0	0
Mt. Hood NF							
Acer circinatum	±	±	+	0	0	–	0
Berberis nervosa	±	±	±	0	0	0	+
Chimaphila menziesii	±	±	±	0	0	0	0
Chimaphila umbellata	±	±	0	0	0	0	0
Gaultheria shallon	±	±	+	+	0	0	0
Holodiscus discolor	0	±	±	∓	0	0	+
Rosa gymnocarpa	±	±	±	–	0	0	0
Rubus ursinus	±	±	+	0	0	–	0
Vaccinium parvifolium	±	±	0	±	0	0	0
Willamette NF							
Acer circinatum	–	0	±	0	±	0	0
Berberis nervosa	±	–	+	+	0	0	+
Chimaphila menziesii	+	+	±	0	0	0	0
Chimaphila umbellata	±	±	0	0	+	0	0
Gaultheria shallon	±	–	0	+	0	0	0
Holodiscus discolor	0	0	±	–	–	0	+
Rosa gymnocarpa	0	–	±	∓	0	0	0
Rubus ursinus	–	0	±	0	0	0	0
Vaccinium parvifolium	–/–	±	0	0	±	0	+

3. Results

Significant predictors varied among species and forests Table 3). Elevation, annual precipitation, and cover of mature Douglas-fir were the most frequently significant. For almost every species at the largest spatial scale (all three forests), models included a unimodal function of these three predictors (± coeffi-

Table 4
Percent reduction in deviance for all fitted terms in each model

		National forests		
Species	All three forests	Gifford Pinchot	Mt. Hood	Willamette
Tall shrubs				
Acer circinatum	0.305	0.404	0.354	0.142
Holodiscus discolor	0.314	0.332	0.350	0.340
Rosa gymnocarpa	0.210	0.342	0.198	0.153
Vaccinium parvifolium	0.352	0.342	0.349	0.285
Low shrubs				
Berberis nervosa	0.437	0.518	0.420	0.417
Gaultheria shallon	0.309	0.378	0.315	0.318
Sub-shrubs				
Chimaphila menziesii	0.083	0.136	0.140	0.077
Chimaphila umbellata	0.160	0.184	0.225	0.230
Rubus ursinus	0.211	0.242	0.167	0.200

cients). At the smaller scale (individual forest), elevation was most consistently significant, and the most consistently represented by unimodal functions, except for Mt. Hood NF, in which annual precipitation was significant and consistently unimodal for all species. Aspect in degrees from southwest (SW) and slope never produced significant quadratic terms, and never contributed much to the reduction in unexplained variation. The proportional reduction in deviance for the sub-shrubs *Chimaphila menziesii*, *C. umbellata*, and *Rubus ursinus* was much lower for all four databases than for low shrubs and tall shrubs (Table 4). In general, models for the Gifford Pinchot NF had the highest percent reduction, and models from the Willamette NF the lowest. Models incorporating the entire database (all three forests) were intermediate in PRD. Model forms were more similar among species at the larger than at the smaller scale (Table 3). At the smaller scale, species' responses to each variable were not consistent across forests (Table 3).

The graphical analysis proved to be robust to distributional anomalies. In every case at the larger spatial scale, predicted contours from the resampling method appeared very similar to those from the simple method (examples in Fig. 2). The range of predicted values from the smoothing method corresponded closely to that of fitted values from the models except for one species, *Holodiscus discolor*, for which the distribution of fitted values was highly skewed due to the low proportion of occurrences in the database.

In every case where the signs of coefficients were ± (Table 3) for elevation and precipitation, contour plots displayed an enclosed region of high probability within the range of data (example in Fig. 3). Results were the same when Douglas-fir cover was substituted for elevation or precipitation (not shown). In other cases (i.e. signs other than ± or insignificant quadratic terms), contour plots either revealed linear trends (Fig. 4) or suggested bimodality (Fig. 5). Most species had variations in model forms and predicted contours among forests and between spatial scales (Figs. 6 and 7); on the Willamette NF in particular, enclosed areas of high probability appeared to extend outside the range of the model database (Fig. 6(d) and Fig. 7(d)).

4. Discussion

Both mechanistic and statistical approaches are useful for understanding the factors that affect the distributions of understory plants in a forested landscape. When predictions are desired at larger spatial scales, empirical/statistical methods can be used to identify coarse-scale variables that integrate the multiplicity of factors that shape species' distributions. To be effective surrogates, these variables must be:

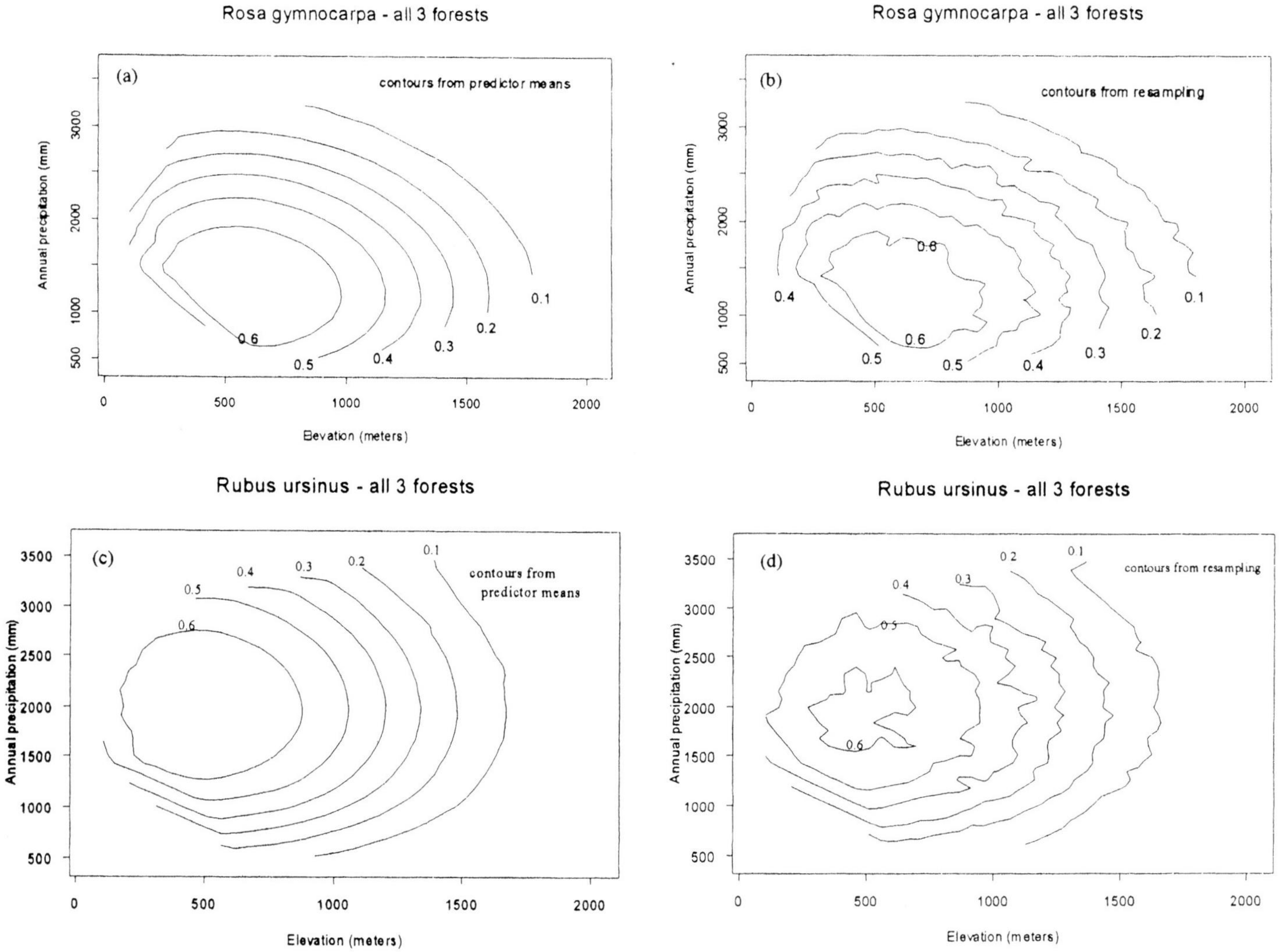

Fig. 2. Predicted contours for *Rosa gymnocarpa* (a,b) and *Rubus ursinus* (c,d) using predictor means vs. resampling technique (see text for explanation).

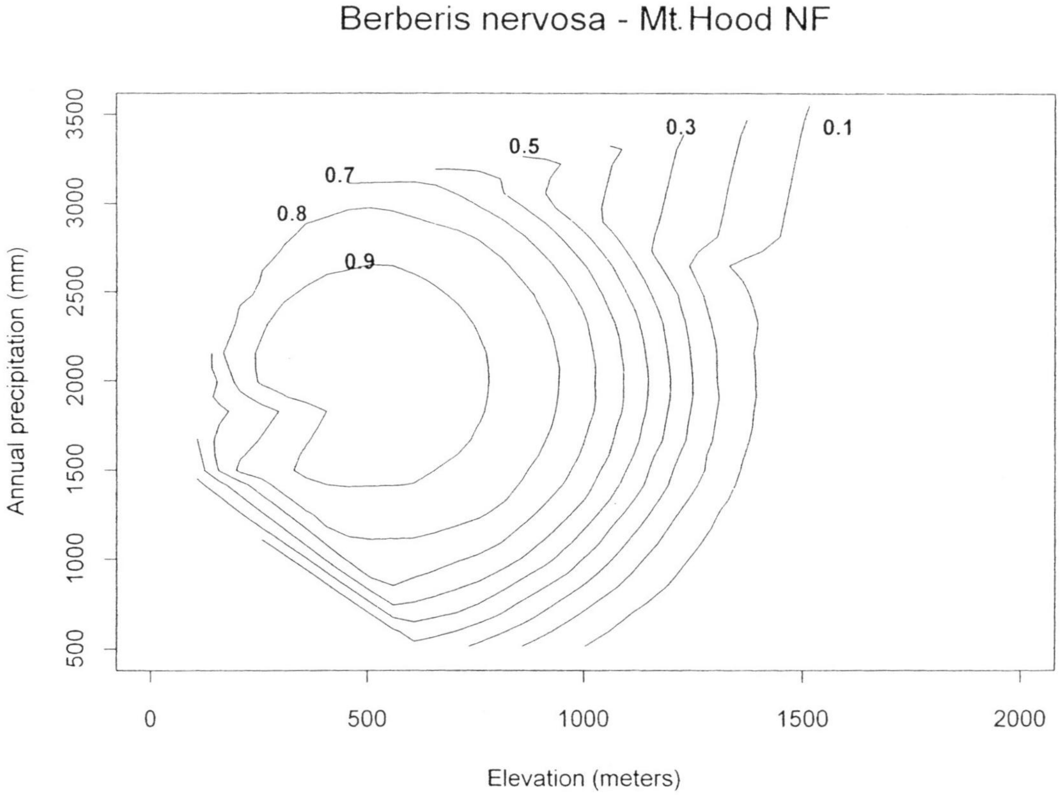

Fig. 3. Area of high probability in two-dimensional environmental space for *Berberis nervosa*.

1. relatively easy and economical to measure at large scales, with large sample sizes;
2. biologically meaningful – i.e. in theory, they should be related to factors whose mechanistic influence on plants is well understood. For example, cover of mature Douglas-fir can be a surrogate for time since disturbance or reduced levels of light; and
3. capable of producing models with reasonable predictive power.

Our analyses suggest that the concept of a unimodal response of plant occurrence or abundance to environmental gradients is useful for infusing individual-species empirical models with biological meaning. The theory behind this concept is well developed mathematically (ter Braak, 1987), and is widely applied in multivariate analysis of plant communities (e.g. the complex environmental gradients associated with correspondence analysis, ter Braak and Prentice, 1988; Hill, 1991). Here, we have applied it to individual environmental variables, and in most cases found that unimodal functions of predictor variables contributed significantly to the explanatory power of the models. As a result, we may identify a region in environmental space where each species has a high probability of occurrence.

Although our modeling efforts were primarily exploratory, it may be possible, at spatial scales commensurate with current management of forest landscapes in the Pacific Northwest, to identify geographic areas where common species have a high probability of occurrence, based on the empirical niches defined by our graphical analysis. For example, interpolated probabilities for each species, as outlined by our contour plots of elevation and precipitation, could be assigned to pixels on a landscape using Digital Elevation Models and PRISM coverages (Daly et al., 1994). However, model equations change with spatial scale of analysis, without any indications of

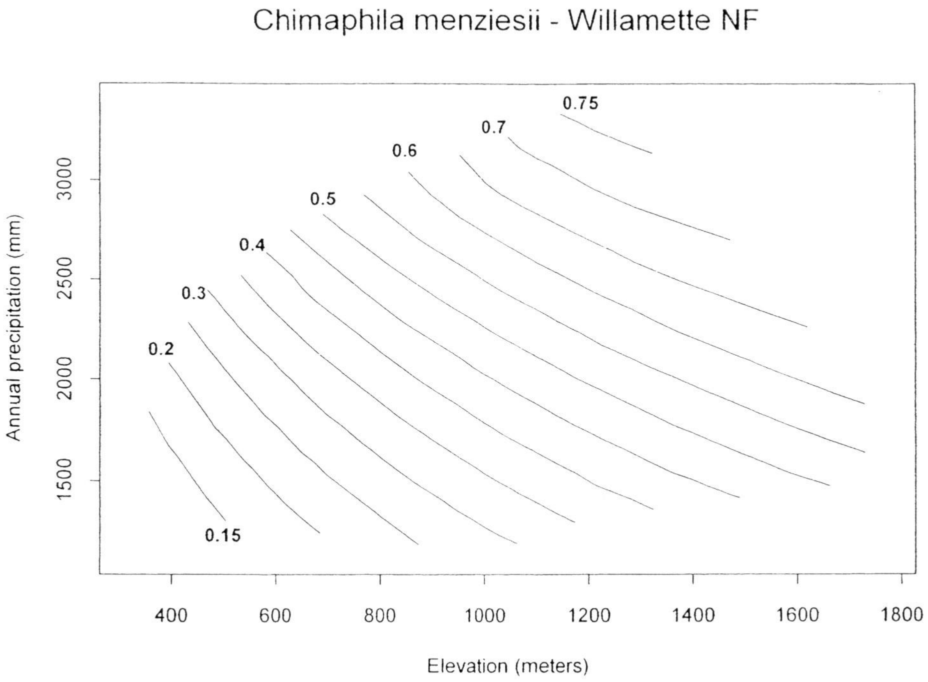

Fig. 4. An example (*Chimaphila menziesii*) of linear trends in response to variables that did not demonstrate a fitted unimodal function.

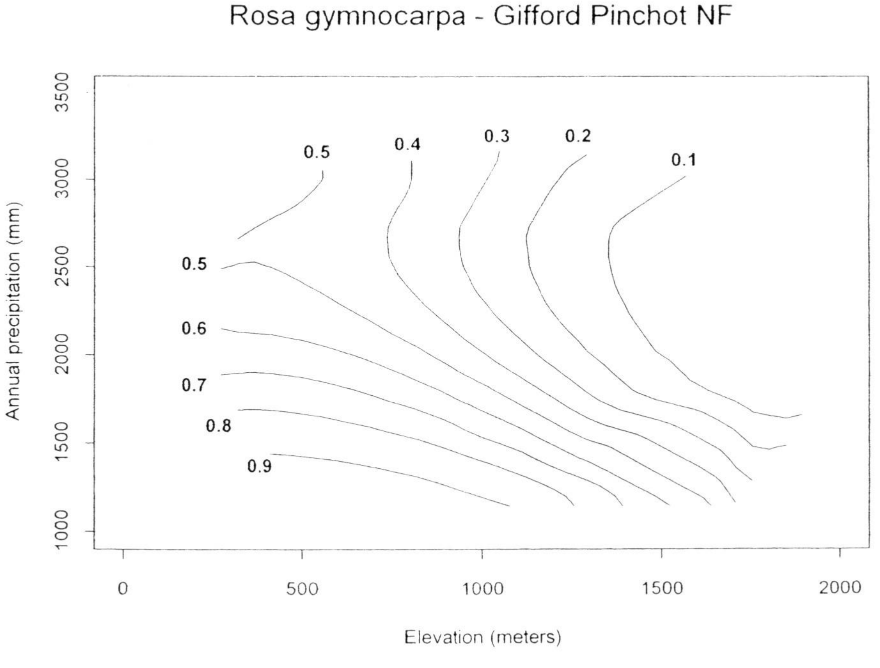

Fig. 5. Apparent bimodality in response of *Rosa gymnocarpa* to elevation and precipitation on the Gifford Pinchot NF.

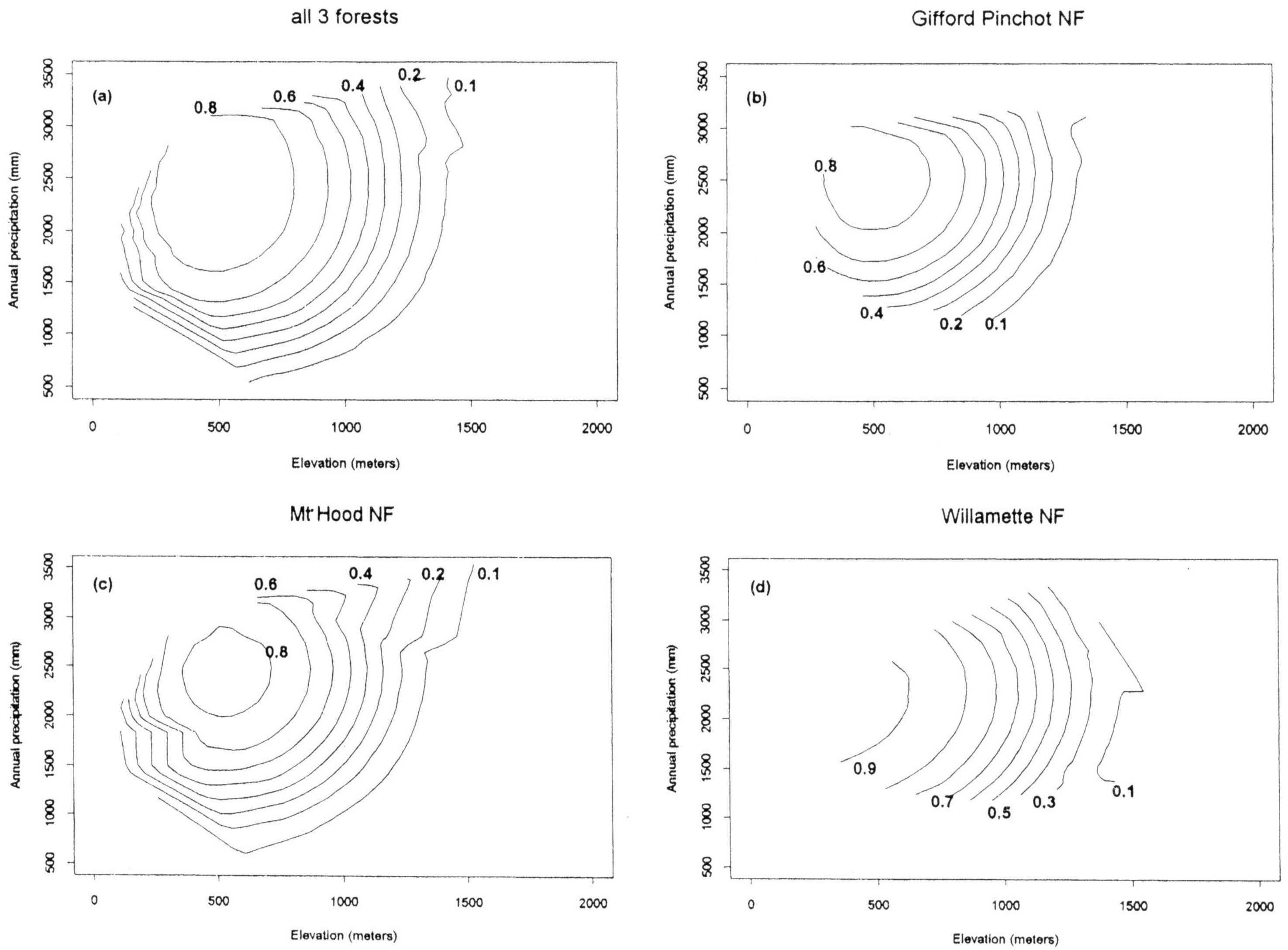

Fig. 6. Responses of *Vaccinium parvifolium* in four models: (a) all three forests; (b) Gifford Pinchot NF; (c) Mt. Hood NF; and (d) Willamette NF.

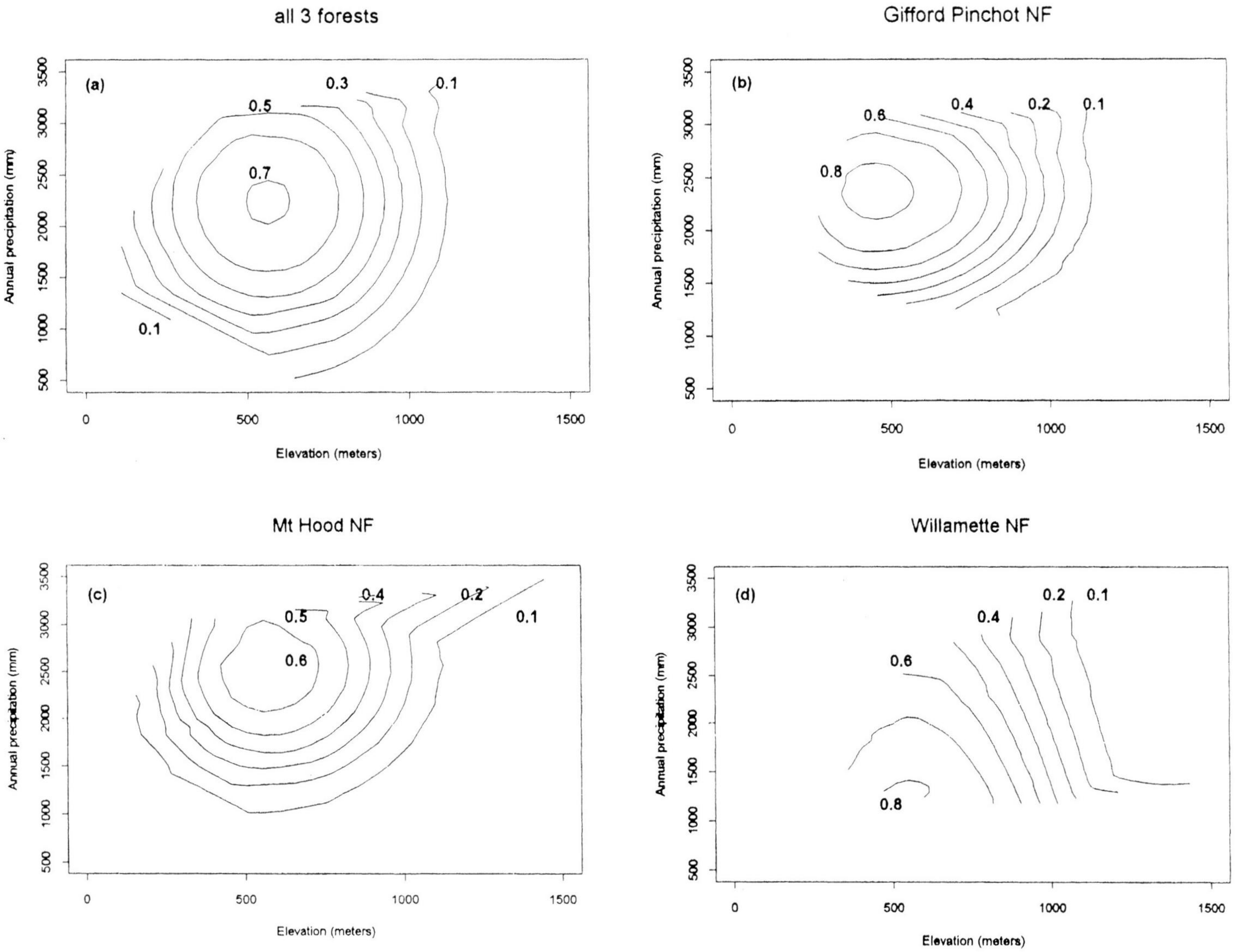

Fig. 7. Responses of *Gaultheria shallon* in four models: (a) all three forests; (b) Gifford Pinchot NF; (c) Mt. Hood NF; and (d) Willamette NF.

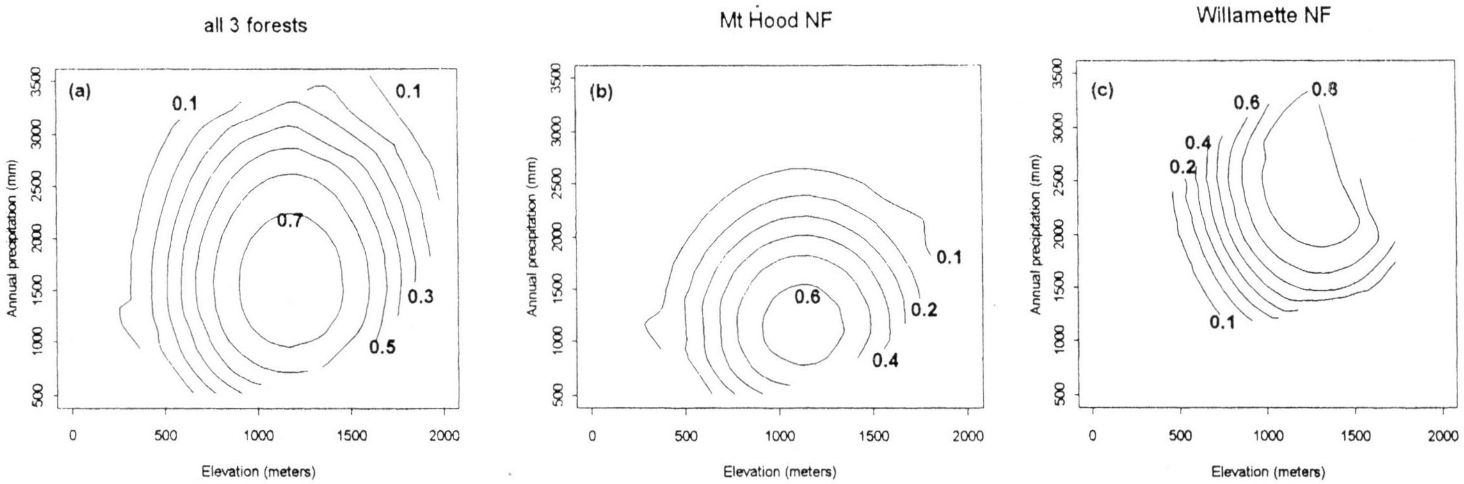

Fig. 8. Contrasting responses of *Chimaphila umbellata* to elevation and precipitation in three different models: (a) all three forests; (b) Mt. Hood NF; and (c) Willamette NF.

changes in predictive power (Table 4), suggesting that the notion of a 'best' predictive model is scale-dependent. Likewise model equations change with geographic location. Thus, distributional maps generated by models like ours must be carefully validated.

Each species may respond individually to the multiplicity of variables represented by a latitudinal gradient. Examining outputs from models developed at different scales of resolution may lead to different inferences about the determinants of species' distributions. For example, *Chimaphila umbellata*, when viewed at a large scale, appears to have a unimodal response to both elevation and precipitation (Fig. 8(a)). Smaller scale analysis, however, suggests that it is more likely to be found on drier sites at more northerly latitudes (Mt. Hood NF) and on moister sites at more southerly latitudes (Willamette NF) (Fig. 8(b) and Fig. 8(c)). In the absence of a conceptual framework for understanding how ecological processes change across scales (Levin, 1992; Reynolds et al., 1993), empirical models (both multivariate and single species) should be explored at multiple scales. As understory components are incorporated into forest simulation models, we must remain cognizant of the scale-dependence of model equations and predictions, and be cautious about applying models at scales different from those at which they were developed.

5. Conclusions

Our modeling approach suggests that, for common shrub species in the Pacific Northwest, the concept of a unimodal response to environmental gradients can be used to improve predictions about the distributions of species, and to strengthen ecological interpretations of statistical models. It also demonstrates the scale-dependence of model equations, and the likelihood that key processes influencing plant distributions change, or at least appear different, when viewed at different scales. An important application of models like ours is to delineate a multi-dimensional environmental space with high probabilities of occurrence for individual species, rather than to make detailed predictions at small spatial scales. Using existing methods that are widely available (e.g. GIS and geostatistical interpolation (Isaaks and Srivastava, 1989)), output can be mapped into geographic information.

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