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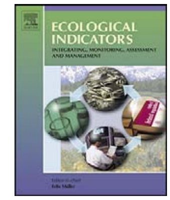

Understory cover and biomass indices predictions for forest ecosystems of the Northwestern United States

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ABSTRACT

The understory community is a critical component of many processes of forest ecosystems. Cover and biomass indices of shrubs and herbs of forested ecosystems of Northwestern United States are presented. Various forest data were recorded for 10,895 plots during a Current Vegetation Survey, over the National Forest lands of entire Pacific Northwest. No significant relationships between the percent canopy cover and understory percent cover and biomass indices were found for the 129 ecoclasses analyzed. Disturbance time and type, and the soil characteristics significantly influenced the shrub biomass indices (*p*-values of <0.001, <0.001, and 0.01, respectively). Only disturbance time and type significantly influenced the shrub percent cover (*p*-values <0.001). There were no significant interactions between these variables. No significant differences were found for herb biomass indices and cover. Climate variables are reasonable predictors of understory cover and biomass indices. Elevation and slope are also influential: understory cover decreases with altitude, while understory biomass increases with slope. Most models showed weak predictive power (adjusted R-squared ≤ 0.27). However, robust models for the maximum/potential understory biomass indices for the forested areas in the Northwestern United States are reported (adjusted R-squared of 0.76 and 0.51 for shrubs and herbs, respectively). Overall, our study provides conceptual and statistical models for the understory of the National Forest lands of the Pacific Northwest. The results are comparable with other models for the area, suggesting that the predictions regarding understory vegetation are inherently difficult.

1. Introduction

The understory community is a major component of any forest ecosystem. It is critical to many system ecological processes, by providing habitat to many organisms, altering the nutrient cycles, protecting against erosion, and contributing to the communities' diversity (Muir et al., 2002; Kerns and Ohmann, 2004). It is the dynamic outcome of intense competition for light, water and nutrients; in turn, is responsible for the establishment and development of tree species at their seedling stage, thus shaping the future overstory plant association (Kabzems and Lousier, 1992; Legare et al., 2002). Understory community structure determine the species present, and their carrying capacity, reproduction, survival rate, and fitness (Leslie et al., 1984; Gonzalez-Fernandez et al., 1998; Ponder, 2008); it is vital for mycorrhizal fungi, invertebrates, and their predators (Muir et al., 2002). Also, it is a major component of the fuel loads, especially of interest in the fire-prone areas of western U.S. and Canada (Arno, 2000). It is responsible for a significant portion of the net carbon and nitrogen fluxes of forests (Moore et al., 2007; Powell et al., 2008), sensible to elevated atmospheric CO_2 and O_3 (Bandeff et al., 2006), and substrate modifications (Six and Halpern, 2008). Understory plant communities are considered good ecological indicators of forest health (Tremblay and Larocque, 2001; Kerns and Ohmann, 2004). Due to the complexity of interactions shaping it, the subcanopy and its characteristics might also be good indicators of biodiversity, habitat potential, umbrella species sustainability, resilience along stress gradients, global change impact, and disturbance risk-assessment. Therefore, robust models predicting the understory vegetation characteristics are important and necessary.

Predictions of vegetation dynamics of forested communities are inherently difficult. These communities are heterogeneous aggregates of various-sized dynamic patches, in various seral stages, influenced by their disturbance history and location, overlapped over a larger-scale temporal variation (Delcourt and Delcourt, 1991). There are few models that predict shrub cover on extensive areas of the Pacific Northwest, including: the COVER model (Moeur, 1985), based on the research of Laursen (1984) and Scharosh (1984), which predicts the probability of occurrence, height, and cover of shrubs in the forest stands of Idaho, NE Washington and NW Montana. McKenzie et al. (2000) modeled shrubs and herbs cover for Southwestern Washington locations,

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and Kerns and Ohmann (2004) modeled shrub cover for the Oregon coastal province. Understory loadings studies include Little and Shainsky (1992) biomass distribution estimates for South-Central Oregon lodgepole pine stands. Olson and Martin (1981) provided estimates of understory biomass in closed-canopy Douglas-fir stands of Central Washington.

In our study, we attempted to test if it is possible to use data readily available in USDA Forest Service surveys to predict understory cover and biomass. Many USDA Forest service surveys use similar experimental designs. Thus, if these methods are proved successful, they can be used in predicting understory characteristics for many of U.S. forest ecosystems. In the process, we tried to expand the geographical range of understory cover and biomass estimates models to the forest stands of Northwestern United States. Three different approaches were considered, assembled in the following working hypotheses:

(1) *The understory cover and biomass can be expressed as a function of relative canopy cover at least for species associations belonging to the same ecoclasses.* An ecoclass designates a stable plant association capable of self-perpetuation (Hall, 1998). From a succession theory perspective (Clements, 1916), the early serial events, following a canopy disturbance event, involve the rapid growth and development of opportunistic understory species (Muir et al., 2002). In time, as tree species height and canopy cover increases, the quantity and quality of solar radiation under the forest canopy is modified (Martens et al., 2000) to an extend that might restrict the growth of understory species. Subcanopy vegetation should go through similar stages of rapid expansion after canopy disturbance, followed by decline as canopy closes regardless of the forest association. Therefore, for individual ecoclasses (indicating similar environmental conditions), it might be possible to isolate the dependency relationship of forest understory on overstory.
(2) *The understory cover and biomass can be expressed as a function of relative canopy cover, climatic variables, landscape characteristics and disturbance history of the forest stand for the entire study area.* Environmental gradients may be responsible for evolution and presence of various species in plant associations (Whittaker, 1972), and climate variables can successfully be used in separating biotic communities (Rehfeldt et al., 2006). Also, disturbance is a frequent event in terrestrial communities, and, consequently, it extends a considerable influence on plant association dynamics (Cook, 1996). Any plant community is shaped by its interactions with its biotic and abiotic environment. The overstory canopy, climate, landscape and disturbance should be reasonable representations of the forces that shape these communities.
(3) *The understory biomass can be expressed as a function of maximum understory biomass that a site can sustain given its specific location, and the conditions that might limit this site potential.* The understory biomass is plant community specific which in turn is similar along comparable climatic characteristics (Bailey, 2002). Therefore, each community has a maximum subcanopy biomass based on its location. Competition, predation, disturbance, and/or substrate characteristics are factors that limit the achievement of this potential understory biomass.

2. Methods

2.1. Study area

Study area comprises the Northwestern United States (Washington, Oregon and parts of Northern California and Northwestern Idaho). Although extremely diverse, Pacific Northwest forests can be grouped in three basic ecological regions, based on their location: *West of the Cascades Mountains region*, with high amounts of precipitation, rare and infrequent fires and home of some of the biggest trees in the world; dominant tree species: Douglas-fir (*Pseudotsuga menziesii*), true firs (*Abies*), western redcedar (*Thuja plicata*), Sitka-spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*); *East of the Cascades Mountains region*, with drier conditions and more frequent fires; dominant tree species: lodgepole pine (*Pinus contorta*) at higher elevations and ponderosa pine (*Pinus ponderosa*) at lower elevations; *Northwestern Rocky Mountain region*, with drier conditions (especially summers) and wide-spread stand-destroying wildfires; dominant species: Douglas-fir, true firs, lodgepole and ponderosa pines (Agee, 1993; Christensen et al., 2000).

This study used data collected from 1993 to 1996 during the Pacific Northwest Region's Current Vegetation Survey (USDA Forest Service, 2007). The survey recorded forest data on a grid sample of 10,895 circular plots (1 ha size), with five circular subplots (760 m^2) each, over National Forest lands of the entire Pacific Northwest. The data was analyzed at subplot level. Shrub and herb cover are more heterogeneous, and seemingly, governed by smaller scale parameters than tree cover, and therefore any lack of independence between subplots should not be material to the results, especially for predictor variables derived from subplot measurements (Hurlbert, 1984).

2.2. Data preparation

The understory vegetation data included the transect length and height of shrubs and herbs (herbs, forbs and grasses) vegetation types for each subplot. From these, percent ground covers of shrubs and herbs were calculated for each subplot, equal to the distances the transect runs over the vegetation class as a fraction of total transect length (Martin et al., 1981), and biomass indices (cover multiplied by height) as biomass substitutes.

Olson and Martin (1981) study shows that, generally, understory cover times height (biomass index) is a better biomass predictor than cover alone, because it defines a volume always enclosing the understory plants. Also, individual plants volume decreases with density (Norberg, 1988), and most plants grow along similar geometrical structure (Selvam, 1998). Thus, it can be assumed that the fraction of this volume actually occupied by most understory communities is, more or less, constant. If it is also assumed that the plant material dry weight is similar among species, it can be concluded that the relationship biomass indices–biomass should be fairly similar over a wide range of understory plant associations. The nature of the dataset analyzed prevents the direct calculation or conversion of biomass indices to biomass. But, in the absence of any other information, Olson and Martin (1981) derived conversion factor ($\times 1.57 \times 10^{-2}$) of understory biomass indices to understory loadings (in tons per acre) might be extended from the boundaries of their study area (Central Washington) to entire Pacific Northwest, or at least to the East of the Cascades Mountains region with similar plant associations.

Therefore, further in the study, models for four understory parameters were sought: shrub cover, shrub biomass index (shrub cover multiplied by shrub height) as shrub biomass substitutes, herb cover, and herb biomass index (herb cover multiplied by herb height) as herb biomass substitutes.

The survey recorded 70 tree species. For each tree species, crown widths were estimated using allometric crown width equations as functions of tree diameter at breast height and other variables (Bechtold, 2003, 2004; Crookston, unpublished). From the individual tree crown width, the stand percent crown cover was evaluated for each subplot and corrected for crown overlap (Crookston and Stage, 1999). The missing observations were

Table 1
Independent variables used in regression analysis.

Variable type	Name	Definition
Vegetation	%CC	Corrected stand percent crown cover
Climate variables	MAT	Mean annual temperature
	MTCM	Mean temperature in the coldest month
	MMIN	Minimum temperature in the coldest month
	MTWM	Mean temperature in the warmest month
	MMAX	Maximum temperature in the warmest month
	MAP	Mean annual precipitation
	GSP	Growing season precipitation, April–September
	TDIFF	Summer–winter temperature differential, MTWM-MTCM
	DD5	Degree-days > 5 °C
	DD0	Degree-days < 0 °C
	MMINDD0	Minimum degree-days < 0 °C
	SDAY	Julian date of the last freezing date of spring
	FDAY	Julian date of the first freezing date of autumn
	FFP	Length of the frost-free period
	GSDD5	Degree-days > 5 °C accumulating within the frost-free period
	D100	Julian date of the sum of degree-days > 5 °C reaches 100
	ADI	Annual dryness index, DD5/MAP (formally AMI, annual moisture index, in Rehfeldt et al., 2006)
	SDI	Summer dryness index, GSDD5/GSP (formally SMI, summer moisture index, in Rehfeldt et al., 2006)
	PRATIO	Ratio of summer precipitation to total precipitation, GSP/MAP
Interactions used: MAP × DD5, MAP × MTCM, GSP × MTCM, GSP × DD5, DD5 × MTCM, MAP × TDIFF, GSP × TDIFF, MTCM/MAP, MTCM/GSP, DD5/GSP, ADI × MTCM, SDI × MTCM, TDIFF/MAP, TDIFF/GSP, PRATIO × MTCM, PRATIO × DD5		
Geographic variables	Elevation	Elevation to the nearest 100 feet
	Slope	Stake position slope in percent
	SLASP1	Slope × sine (Aspect)
	SLASP2	Slope × cosine (Aspect)
		Classes
Disturbance	Disturbance time	0–5 years, 5–30 years, >30 years, no disturbance/unknown
	Disturbance type	Fire, exploited plot, no disturbance/unknown
Herbivory	Animal use	Yes, no, unknown
Soil Characteristics	Soil	Stockable, unstockable, unknown

eliminated from the prepared database. The resulting data set contained observations for 31,703 sample points.

2.3. Climatic data

A climatic model developed by Rehfeldt (2006) was used to produce climate estimates for each sample point. This climate model, based on weather data from 1961 to 1990 uses the thin plate splines of Hutchinson (1991, 2000) to yield predictions of monthly precipitation and temperatures for Western United States and Southwestern Canada, based on the study plots' latitude, longitude and elevation. In the study, 35 climatic variables were used including various interactions between temperature and precipitation (Table 1).

In addition, the elevation, slope, and aspect (Stage, 1976) variables were included (Table 1), together with percent canopy cover. The data was analyzed using *R* version 2.5.0 (R Development Core Team, 2007).

2.4. Methods for hypothesis 1

The relationships between percent canopy cover and the understory cover and biomass indices were investigated only for ecoclasses with at least 100 observations recorded. From a total of 899 ecoclasses present in the survey, only 129 of them satisfied this requirement, with observations for 30,219 sample points.

Methods used include linear regression, model diagnostics, data transformations, outlier eliminations (Johnson and Wichern, 2002; Gotelli and Ellison, 2004), and loess smoothing methods (Cleveland and Devlin, 1988).

2.5. Methods for hypothesis 2

To test hypothesis 2, we analyzed the whole data set and a stratified sample of it.

(a) Methods for the whole data set

The original data set containing understory cover, biomass indices and percent canopy cover was amended with 39 environmental variables: 35 climatic explanatory variables, elevation, slope, and aspect variables (Table 1). Missing observations were eliminated.

Methods used include linear regression of raw and transformed data, simple or with restricted cubic splines, distribution assessments, outlier eliminations (Harrell, 2001; Johnson and Wichern, 2002; Gotelli and Ellison, 2004), and loess smoothing methods (Cleveland and Devlin, 1988). Random Forest regression procedures were also performed (Breimen, 2001; Liaw and Wiener, 2002). Although Random Forest regression models compensate for multicolinearity and overfitting present in our data, and, had a percent of variation explained superior to the linear regression models, only the linear regression models were presented because they are easier to understand and apply.

(b) Methods for sample data set

The site history information was available only from the comments associated with each sample plot. From these, four new dummy variables (Kleinbaum and Kupper, 1978) were created: disturbance type and time, animal use, and soil characteristics (Table 1), for a 10% stratified random sample of

Table 2
Linear regression adjusted R-squared and MSE ranges for shrubs and herbs biomass indices and percent cover for the 129 ecoclasses with over 100 observations per class available for Northwestern United States.

Model	All observations/ecoclass datasets		Datasets w/out the top 1% outliers		Datasets w/out the top 5% outliers	
	R-squared	MSE	R-squared	MSE	R-squared	MSE
SBI[a] ~ %CC[b]	−0.01–0.19	3.31×10^2–3.46×10^5	−0.01–0.16	3.14×10^2–3.21×10^5	−0.01–0.08	84.0–2.32×10^5
HBI[c] ~ %CC	−0.01–0.25	41.4–5.76×10^4	−0.01–0.27	26.2–1.10×10^4	−0.01–0.35	9.11–9.22×10^3
HBI ~ %CC + %SC[d]	−0.02–0.25	39.4–5.59×10^4	−0.02–0.27	26.0–1.11×10^4	−0.02–0.37	9.13–9.29×10^3
%SC[e] ~ %CC[e]	−0.01–0.18	0.003–0.20				
%HC[f,e] ~ %CC[e]	−0.01–0.21	0.01–0.17				
%HC[e] ~ %SC[e] + %CC[e]	−0.01–0.22	0.01–0.17				

[a] Shrub biomass index.
[b] Percent Canopy Cover.
[c] Herb biomass index.
[d] Percent shrub cover.
[e] Variables were arcsine-transformed.
[f] Percent herb cover.

the data set. Subplots enclosing roads, trails, rivers and creeks were eliminated from the sample set. The new data set contained 44 predictors (Table 1). In the end, the amended 10% sample data set contained entries for 1871 sample points.

Similar statistical methods as for the whole data set were used to analyze the sample data set. Analysis of variance (ANOVA) procedures and Tukey's HSD test (Hsu, 1996) were used to assess the influence of the new created variables.

To generate the reduced models, first the independent variables with the least predictive power were eliminated one-by-one. In a different approach, the highly correlated predictors were eliminated first, followed by the ones with the least predictive power, until only the statistically significant independent variables were left.

2.6. Methods for hypothesis 3

To model the maximum or potential understory biomass indices on each site, the 99th percentile of shrub and herb biomass indices was sampled separately across 10 equal-length intervals, for each of the 39 climatic variables (Table 1), and joined in one data set; the duplicates were eliminated. The resulting data set for shrubs biomass indices contained 665 sample points, while the one for herbs biomass indices contained 661 sample points. The data was log-transformed, and linear regression analysis procedures were applied. Maximum understory biomass indices and its' constrains: competition, predation, disturbance, and soils quality, were used to predict the actual shrub and herb biomasses.

To evaluate the models, adjusted R-squared values were used because it provides a more honest way to compare multiple regression models than R-squared (Fox, 1997).

3. Results

3.1. Results hypothesis 1

The adjusted R-squared values for the 129 ecoclasses analyzed ranged between −0.02 and 0.25 (Table 2), with values between ±0.01 for most ecoclasses. The maximum values were recorded for the ecoclasses with the lowest number of observations. The outliers elimination (i.e., the top 1% and 5% of the observations), for each ecoclass considered, improved the fit, but not significantly (Table 2).

3.2. Results hypothesis 2

(a) Analysis of the whole data set

The percent of variance explained by Random Forest regression algorithms were 36.8%, 38.0%, 43.8% and 44.0%, for shrubs biomass indices, herbs biomass indices, percent shrub cover, and percent herb cover respectively; and did not improved significantly, no matter how many independent variables were used.

The full linear regression models for the shrubs and herbs percent cover and biomass indices had adjusted R-squared of 0.22, 0.23, 0.27 and 0.14, respectively. The reduced models had only highly significant explanatory variables (Models 1 in Tables 3–6, respectively). Restricted cubic splines models were not significantly better; thus, they were not considered in discussion due to their higher complexity.

(b) Analysis of the sample data set

For each new variable (i.e., disturbance time and type, animal use and soil characteristics), ANOVA procedures indicated no significant differences for herb biomass indices and cover. For shrub biomass indices, all categories were significant, with p-values <0.001 for disturbance time (F-value = 11.25, $df = 3$) and type (F-value = 8.80, $df = 2$), 0.001 for animal use (F-value = 7.21, $df = 2$), and 0.01 for soil characteristics (F-value = 5.69, $df = 2$). For biomass cover, only disturbance type and time, and animal use were significant ($p < 0.001$, F-values: 11.97, 8.20, and 17.23; and df of 2, 3, and 2, respectively). There were no significant interactions between variables. Tukey's HSD test indicated that, for disturbance type, only the level "exploited plot" was significantly different from the others; for disturbance time, the level ">30 years" was significantly different from the others; for animal use, levels "yes" and "unknown" were significantly different; and, for soil characteristics "stockable" and "unstockable" were significantly different. The results were similar for shrub cover, with only one exception: no categories were significantly different for soil characteristics.

The one-by-one elimination of least predictive independent variables resulted in the Models 2 in Tables 3–6. The elimination of highly correlated predictors first, followed by the one-by-one elimination of least predictive remaining independent variables resulted in the Models 3 in Tables 3–6. The reduced models had only highly significant explanatory variables.

The reduced models for the whole data set and the sample data set, presented in Tables 3–6: Models 1, 2, and 3, are compared with other models developed for Northwestern United States forests (Table 7).

3.3. Results hypothesis 3

The full linear regression model for the maximum shrub biomass indices (MSBI) had an adjusted R-squared of 0.82. The reduced model had five significant climatic predictors and an

Table 3
Multiple regression models for total percent shrub cover in the Northwestern United States.

Model 1: ln(%SC[a]) Coefficient		Model 2: ln(%SC) Coefficient		Model 3: ln(%SC) Coefficient	
7.34	Intercept	7.03	Intercept	−12.26	Intercept
−0.09	ln(%CC)	0.37	ln(MMIN + 14)	−0.07	ln(%CC)
1.18	ln(MAT + 1)	0.71	ln(GSDD5)	−2.59	ln(MTWM)
0.83	ln(GSP)	−0.72	ln(GSP × MTCM + 3800)	0.72	ln(SDI)
−4.40	ln(MTCM + 11)	−0.41	ln(DD5 × MTCM + 12000)	1.61	ln(MAP × TDIFF)
2.03	ln(MMIN + 15)	−0.39	ln(DD5/GSP + 1)	1.03	ln(PRATIO × DD5)
5.56	ln(MMAX)	0.62	ln(ADI × MTCM + 32)		
−4.64	ln(TDIFF)	−0.39	ln(Elevation)		*Disturbance time:*
−0.73	ln(MAP × MTCM + 15000)			−0.33	0–5 years
−0.36	ln(DD5 × MTCM + 12000)			0	5–30 years
54.23	ln(MTCM/MAP + 1)			0.07	>30 years
				0.03	No disturbance/unknown
	RSE[b] = 1.07 Adj.-R^2 = 0.22**		RSE = 1.05 Adj.-R^2 = 0.24**		RSE = 1.05 Adj.-R^2 = 0.24**

** Significant at $p < 0.01$.
[a] Percent shrub cover.
[b] Residual standard error.

adjusted *R*-squared of 0.76 (Table 5: Model 4). The realized shrub biomass indices (SBI) reduced model (Table 5: Model 5) had three significant predictors, and an adjusted *R*-squared of 0.15 (identical with the full model).

The full linear regression model for the maximum herb biomass index (MHBI) had an adjusted *R*-squared of 0.52, while the reduced model had 11 significant climatic predictors, and an adjusted *R*-squared of 0.51 (Table 6: Model 4). The actual herb biomass indices (HBI) reduced model (Table 6: Model 5) had three significant predictors, and an adjusted *R*-squared of 0.05 (identical with the full model).

4. Discussion

4.1. Discussion hypothesis 1

For all response variables and regression procedures, the maximum adjusted R-squared was 0.37 (Table 2), recorded for the ecoclass with least observations. It suggests that some other underlying causes might be responsible for the result than the predictive power of canopy cover. Hypothesis 1 intended to expose the relationship between understory cover and biomass, and relative canopy cover, under similar environmental conditions. Yet, most models displayed an extremely weak predictive power.

Loess methods indicate high values of residuals, and unproportionally high influence of extreme observations. Negative or Gaussian-type relationships between the understory and overstory were observed for some ecoclasses investigated, but for the majority of them, no relationship was evident.

That canopy structure can influence the understory environment, through changes in the quantity and quality of radiation, is a long-held tenet of forest ecology. Therefore, if relative canopy cover is a good quantifier of the irradiance environment, stronger relationships between understory and overstory structure were expected. Lhotka and Loewenstein (2006) determined that canopy cover calculated as in the current study explains 44.4% of the variation in radiation transmittance; while the canopy cover estimated using a vertical sighting tube explains 72.7% of the variance in radiation transmittance. Tree basal area and density have even weaker predictive power, and were used in the canopy cover calculations.

Table 4
Multiple regression models for the total percent herb cover in the Northwestern United States.

Model 1: ln(%HC[a]) Coefficient		Model 2: ln(%HC) Coefficient		Model 3: ln(%HC) Coefficient	
24.09	Intercept	7.23	Intercept	−33.38	Intercept
−0.24	ln(%CC)	−0.27	ln(%CC)	−0.28	ln(%CC)
−1.69	ln(MAP)	2.89	ln(MAT + 1)	−4.22	ln(GSP)
4.29	ln(MTCM + 11)	−8.74	ln(MAP)	−24.72	ln(MTWM)
−1.64	ln(MMIN + 15)	−2.15	ln(MTCM + 11)	3.90	ln(MMAX)
−38.06	ln(MTWM)	10.75	ln(MMAX)	8.24	ln(MAP × TDIFF)
6.01	ln(MMAX)	4.18	ln(SDAY)	−2.66	ln(GSP × TDIFF)
7.97	ln(SDAY)	1.03	ln(FFP)	9.87	ln(PRATIO × DD5)
−10.33	ln(FDAY)	−1.78	ln(MMINDD0)		
2.94	ln(FFP)	−9.84	ln(ADI)		*Animal use:*
8.59	ln(DD5)	2.68	ln(PRATIO × DD5)	0	Yes
−0.92	ln(DD0)	−1.30	ln(Elevation)	−0.31	No
−4.54	ln(MMINDD0)			−0.06	Unknown
20.56	ln(TDIFF)				
−2.70	ln(DD5/GSP + 1)				
−1.02	ln(SMI × MTCM + 88)				
	RSE[b] = 1.06 Adj.-R^2 = 0.24**		RSE = 1.09 Adj.-R^2 = 0.22**		RSE = 1.61 Adj.-R^2 = 0.24**

** Significant at $p < 0.01$.
[a] Percent herb cover.
[b] Residual standard error.

Table 5
Multiple regression models for the total shrub biomass index and maximum shrub biomass index in the Northwestern United States.

Model 1: ln(SBI[a])		Model 2: ln(SBI)		Model 3: ln(SBI)		Model 4: ln(MSBI[b])		Model 5: ln(SBI)	
Coefficient		Coefficient		Coefficient		Coefficient		Coefficient	
3.47	Intercept	18.28	Intercept	−24.05	Intercept	32.13	Intercept	−5.47	Intercept
1.23	ln(MAT + 1)	0.99	ln(MMIN + 14)	−0.15	ln(%CC)	1.54	ln(MAT + 1)	1.32	ln(MSBI)
−3.77	ln(MTCM + 11)	−1.56	ln(GSP × MTCM + 3800)	2.49	ln(MAP × TDIFF)	0.78	ln(GSP)		
3.55	ln(MMIN + 15)	−1.34	ln(Elevation)	1.64	ln(DD5/GSP + 1)	−21.01	ln(MMAX)		*Disturbance type:*
−0.67	Elevation	0.24	ln(Slope + 1)	0.24	ln(Slope + 1)			0	Fire
0.22	ln(Slope + 1)					−16.48	ln(FFP)	0.05	Exploitation
					Disturbance time	16.04	ln(GSDD5)	−0.35	None/unknown
				−0.72	0–5 years				
				0	5–30 years				*Disturbance time:*
				0.26	>30 years			−0.97	0–5 years
				0.08	No disturbance/unknown			0	5–30 years
								0.27	>30 years
								0.03	No disturbance/unknown
	RSE[c] = 1.80		RSE = 1.57		RSE = 1.61		RSE = 0.64		RSE = 1.89
	Adj.-R^2 = 0.24**		Adj.-R^2 = 0.27**		Adj.-R^2 = 0.24**		Adj.-R^2 = 0.76**		Adj.-R^2 = 0.15**

** Significant at $p < 0.01$.
[a] Shrub biomass index.
[b] Maximum/potential shrub biomass index.
[c] Residual standard error.

Thus, one reason for the poor results is that calculated relative canopy cover might be an inadequate predictor for the radiation environment under the canopy, and, thus, of understory structure. Also, it is possible that relative canopy cover might not have a prevalent influence on the understory community. The radiation environment represents only one resource gradient through which the overstory stand can affect the understory community; soil nutrient content, moisture, and allelophatic effects should also be considered (Lodhi and Johnson, 1989).

Even if relative canopy cover can be estimated better, the problem of homogeneity and scale remains. While the dominant canopy species are more homogeneous within an ecoclass, the understory community seems more heterogeneous and responsive to finer-scale environmental conditions. For example, less than 100% canopy cover for a sample plot suggests the existence of gaps in the canopy, but does not say anything about the type of gap (one coarse-scale gap, or many small gaps); gap type is responsible for the irradiation, moisture and temperature gradients at the ground, and, consequently, for the understory plant associations and growth rates (Wayne and Bazzaz, 1993; Coates and Burton, 1997). Moreover, the shrub vegetation patterns are also related with specific landforms, topography and microsite hydrology (Pabst and Spies, 1998).

Therefore, even though the hypothesis that the understory cover and biomass should decrease with increasing canopy cover was not refuted, was not supported either by the data analyzed here. More precise measurements of canopy cover or its environmental effects on subcanopy might yield different results.

4.2. Discussion hypothesis 2

Climate variables are reasonable predictors of understory cover and biomass. When present in models, percent canopy cover increases leads to understory cover and biomass decreases. Elevation and slope are extremely significant predictors: understory cover and biomass decrease with elevation; understory biomass indices increase with slope, while understory cover is not influenced. The slope orientation was not significant in these

Table 6
Multiple regression models for the total herb biomass index and maximum herb biomass index in the Northwestern United States.

Model 1: ln(HBI[a])		Model 2: ln(HBI)		Model 3: ln(HBI)		Model 4: ln(MHBI[b])		Model 5: ln(HBI)	
Coefficient		Coefficient		Coefficient		Coefficient		Coefficient	
29.23	Intercept	−8.7	Intercept	−31.06	Intercept	−0.05	Intercept	−0.67	Intercept
−0.41	ln(%CC)	−0.39	ln(%CC)	−0.40	ln(%CC)	2.90	ln(MAT + 1)	0.61	ln(MHBI)
−1.03	ln(MAP)	10.00	ln(MTWM)	−4.61	ln(GSP)	−19.59	ln(MTWM)	−0.02	PCC
−4.72	ln(MTCM + 11)	3.96	ln(SDAY)	−22.34	ln(MTWM)	9.54	ln(MMAX)		
−3.21	ln(MMIN + 15)	−0.77	ln(DD0)	−0.52	ln(SDI)	2.05	ln(GSDD5)		*Disturbance type:*
−4.92	ln(MMAX)	−2.27	ln(GSP × DD5)	9.26	ln(MAP × DIFF)	1.32	ln(D100)	0	Fire
−3.93	ln(D100)	−29.29	ln(MTCM/GSP + 1)	−4.08	ln(GSP × TDIFF)	1.88	ln(MAP × MTCM + 13858)	0.32	Exploitation
5.83	ln(TDIFF)	−4.56	ln(DD5/GSP + 1)	11.22	ln(PRATIO × DD5)	−2.19	ln(GSP × MTCM + 3896)	0.06	None/unknown
−1.79	ln(DD5/GSP + 1)	1.91	ln(PRATIO × DD5)	0.13	ln(Slope + 1)	−33.40	ln(MTCM/GSP + 1)		
−0.59	ln(Elevation)	−1.40	ln(Elevation)			0.49	ln(SDIXMTCM + 88)		*Disturbance time:*
0.13	ln(Slope + 1)	0.11	ln(Slope + 1)		*Animal use:*	−0.44	ln(Elevation)	0.09	0–5 years
				0	Yes	0.43	ln(SLASP2 + 103)	0	5–30 years
				−0.40	No			0.27	>30 years
				−0.06	Unknown			0.28	No disturbance/unknown
	RSE[c] = 1.75		RSE = 1.27		RSE = 1.29		RSE = 0.55		RSE = 1.82
	Adj.-R^2 = 0.13**		Adj.-R^2 = 0.20**		Adj.-R^2 = 0.20**		Adj.-R^2 = 0.51**		Adj.-R^2 = 0.05**

** Significant at $p < 0.01$.
[a] Herb biomass index.
[b] Maximum/potential herb biomass index.
[c] Residual standard error.

Table 7
Selected models of understory cover for Northwestern United States.

No.	Model predictions:	Predictor variables	R^2/adjusted R^2	Study area	Citation
1.	1st probability of shrub cover; 2nd total shrub cover; 3rd probability of occurrence and height for shrub species; 4th individual species cover, weighted, and summed up to a total understory cover.	Slope, elevation, basal area, disturbance, understory union group, physiography, geographic location	0.11–0.47	Idaho, NE Washington and NW Montana	Laursen (1984), Scharosh (1984), Moeur (1985)
2.	Total shrub cover, vine maple and herbs cover	Stand density index, quadratic mean diameter of trees, percent canopy cover, coefficient of variation of tree diameter, sapling density	0.20–0.57	SW Washington	McKenzie et al. (2000)
3.	Total shrub cover and deciduous shrub cover on private and federal lands	Basal area of *Tsuga heterophylla*, trees per hectare, stand age, quadratic mean diameter, basal area of all trees, slope, solar radiation, mean annual precipitations	0.14–0.49	Coastal Oregon	Kerns and Ohmann (2004)
4.	Shrubs and herbs cover, biomass indices, and maximum biomass indices	Climate variables, slope, elevation, percent canopy cover, disturbance	0.05–0.76	National Forests of entire Pacific Northwest	Current study

models. Thus, the increase of shrub biomass with slope might not be caused by the orientation-associated microclimate conditions (Auslander et al., 2003), but maybe by different understory and overstory growing capacities on slopes.

The disturbance, herbivory and soil characteristics variables were based on rather inconsistent personal comments of the people collecting the data, instead of carefully collected historical data. Many sample plots could not be allocated to specific categories. For example, the status of 14%, 37%, 45%, and 54% sample plots, respectively, was unknown for the four dummy variables that represent disturbance history. Thus, the results of the study might be weak due to poor data quality.

Briefly, contrary to other studies (e.g., Laursen, 1984; Scharosh, 1984), disturbance did not have the explanatory power expected. Interestingly, only exploitation disturbance (e.g., clearcut, thinning, logging, etc.) is significantly different from the other disturbance types, suggesting that fire impact might resemble the natural dynamics of a forest, while exploitative disturbance has a fundamentally different effect. Shrub biomass indices and cover were not significantly different between freshly disturbed sites (<5 years) and sites disturbed 5–30 years ago, suggesting that shrubs might establish and reach their potential fairly fast, and remain at that level in the community for a long period of time.

Disturbance, animal use and soil characteristics did not have a significant impact on the herb biomass and cover. Perhaps the herbaceous community is more resilient, the effects are more subtle (e.g., changes in species composition), or our measurements were too coarse and/or inaccurate to reveal any underlying relationship.

4.3. Discussion hypothesis 3

Climatic factors have a reasonable predictive power of the maximum/potential understory biomass indices (Models 4 in Tables 5 and 6). But, interestingly enough, predictions of the existent understory biomass indices from potential biomass indices were not successful: shrub and herb biomass indices adjusted R-squared of 0.15 (Table 5: Model 5) and 0.05 (Table 6: Model 5), respectively. It suggests that human influence and stand history may have a bigger effect that we previously considered. Based on our results, it seems that their influences should be investigated with at least the same level of detail as environmental parameters. Unfortunately, the quality of the disturbance, predation and soil characteristics information for this data set was questionable, preventing any further investigation of this new-raised hypothesis.

Regardless, the potential understory biomass indices by themselves can be useful in a series of applications. For example, they can serve as basis for worst-case-scenarios in net carbon and nitrogen fluxes, fire, and global change impact models. Or, can be adapted as baseline in evaluating forest health, with every measurement below being considered as indicative of potential ecological stress, or substrate modifications. Also, they can be indicative of the potential carrying capacity and sustainability of various communities.

5. Conclusion

Understory characteristics are good candidates for ecological indicators of many processes in forested ecosystems. Therefore, robust models predicting the subcanopy characteristics are important and necessary. Unfortunately, it seems difficult to predict understory attributes based only on the common forest data available. Although we employed a wide range of statistical methods, our final models display weak predictive power; but, without denying their need for improvement, at this moment they are the only models for the entire region (Table 7). Maybe experimental designs focused on the understory structure coupled with detailed information about human intervention and stand disturbance history, instead of just canopy structure, might provide more pertinent data. Climate, landscape, substrate, disturbance, dominant trees characteristics are shaping the understory plant community, but neither one seems to be ultimately determinant of the subcanopy dynamics. While in theory it seems possible, studies suggest that many understory interactions are at a scale and of a complexity difficult to be captured by deterministic models, like the ones presented here. If understory cover and biomass are excellent indicators of many forest processes, the "indicators" of the understory remain elusive.

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