USING DIGITAL TERRAIN MODELING AND SATELLITE IMAGERY TO MAP INTERACTIONS AMONG FIRE AND FOREST MICROBES

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ABSTRACT

Behavior and biology of many forest pests are tied to major forest disturbances and succession. Fire is the principal disturbance in the forests of the western United States. Fire regimes as well as distribution and behavior of forest pests and beneficial microbes are all strongly associated with plant communities. Thus, mapping of plant communities can facilitate our ability to understand, predict, and manage interaction among these ecological processes. A new procedure to map potential vegetation was assessed on the Priest River Experimental Forest in northern Idaho. Digital terrain modeling and satellite imagery supplied 14 predictor variables to the Most Similar Neighbor (MSN) imputation procedure. MSN uses a multivariate difference function and canonical correlation analysis to impute class designations to unclassified elements, based on the similarity of training samples across a set of global predictor variables. MSN was "trained" with plant community data obtained from 245 delineated stands classified to 8 subseries (groups of habitat types). These subseries were imputed to 27,775 raster cells to create a map of subseries for the Priest River Experimental Forest. MSN statistics indicated a successful classification and the predicted subseries map showed a good overall match with a habitat type map made from ground observation. Accurate mapping of subseries can facilitate analysis of landscape interactions among fire and pests. Such maps would support ecosystem restoration, management, and research. Needed landscape perspective could be added to the design, execution, and analysis of studies directed at understanding ecosystem processes such as gene flow and adaptation in hosts and pests.

keywords: Armillaria regimes, ecological modeling, fire regimes, Idaho, potential vegetation maps, topoclimatic modeling.

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INTRODUCTION

Introduction of *Cronartium ribicola,* the causal agent of white pine blister rust, into western North America in 1910 (McDonald and Hoff 2001) has wrought fundamental ecological change. Significant ecosystem restoration is needed on millions of acres where five-needle pines were once an important forest component (Neuenschwander et al. 1999, Tomback et al. 2001). Reduced stocking of western white pine (*Pinus monticola*) in northern Idaho has relegated a modifier keystone species to a minor role and set in motion a cascade of ecosystem changes (McDonald et al. 2000). At least one change has potential for serious ecosystem consequences. Forest sites capable of supporting western white pine (WWP) also support 2 species of the fungal genus *Armillaria.* This genus is widespread in the WWP forests of the northern Rocky Mountains (McDonald et al. 1987*a*; McDonald 1991*a,b*). One species, *A. ostoyae,* is a well-known root rot pathogen of most conifers (Kile et al. 1991). The other species, undescribed and known as North American Biological Species (NABS) X, appears as a major saprophytic decomposer (G.I. McDonald, unpublished data). This species appears to cause butt rot on climax conifer species in both climax and secondary seral roles (G.I. McDonald, unpublished data). Species affected were grand fir (*Abies grandis*), subalpine fir (*A. lasiocarpa*), western redcedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), and Engelmann spruce (*Picea engelmannii*). Douglas-fir (*Pseudotsuga menziesii*), which can be seral or climax, did not exhibit butt rot. Common seral species in the northern Rockies—WWP, western larch (*Larix occidentalis*), lodgepole pine (*Pinus contorta*), and ponderosa pine (*Pinus ponderosa*)—do not seem to be subject to *Armillaria*-caused butt rot (Kile et al. 1991). NABS X may protect WWP and other seral species against damage by *A. ostoyae* (McDonald et al. 1998). Another closely related species, *A. gallica,* seems to protect its hardwood hosts from infection caused by the principal pathogen of hardwoods in the genus, *A. mellea* (Bruhn et al. 2000). An *Armillaria* species thought to be NABS X (G.I. McDonald, unpublished data) was observed at high frequency as an epiphyte on the roots of most conifer and hardwood species within its range in the northern Rocky Mountains (McDonald et al. 1987*a*).

Complex interactions among these 3 microbes and 11 conifers occur in a highly heterogeneous environment dominated by repeated occurrence of stand replacement fire. Removal of WWP from these ecosystems by the introduced pathogen, *C. ribicola,* has accelerated mortality caused by *A. ostoyae* in stands of grand fir and Douglas-fir when these species attempt to fill the ecological role of WWP (Monnig and Byler 1992, Byler et al. 1994). Fire in these wet forests also is complex (McDonald et al. 2000). An ignition occurs somewhere in a stand about once every 50 years, yet the return interval for stand-replacement fires is about 200 years. Historically, forests having a significant component of WWP could not have supported much ground fire, since WWP has extreme sensitivity to ground fire (McDonald et al. 2000). These forests competed for light without benefit of fire-caused thinning, thus favoring WWP (McDonald et al. 2000). Reduction of WWP stocking by blister rust moved canopy structure toward development of more fuel ladders (Harvey et al. 1999) at the same time as increased activity of *A. ostoyae* increased fuel loadings. Altered canopy structure also may potentially change hydrologic dynamics by influencing snow accumulation and relocating site nutrient capital to crowns (Harvey et al. 1999). If each ignition has an increased probability of causing a crown fire because of fuel accumulation and altered canopy structure, stand-replacement interval is likely to decrease even without an increased ignition probability. Shorter stand-replacement return intervals could severely impact site productivity through accelerated erosion and depletion of nutrient capital.

Interactions occurring in a heterogeneous environment may have long-term genetic consequences. The ecophysiological maladaptation hypothesis of *Armillaria*–host interaction might explain observed patterns of damage across the landscape caused by *A. ostoyae* (McDonald et al. 1987*b*; McDonald 1991*a,b*). If host populations attain a flexibility–fitness compromise with their most common environments, then the population could be maladapted when it grows on "off modal" sites. A conifer population growing in a particular locale would adjust its genetic architecture to a modal environment according to its species-specific mechanisms. Light–water tradeoff theory (Smith and Huston 1989) states that a population of a given plant species cannot simultaneously evolve high tolerance for low levels of both water and light. Drought-intolerant genotypes adapted to compete for light would dominate, if most of the breeding population were competing for light. Seed from this population that established itself on dry islands (e.g., ridge tops) would be "ecophysiologically" maladapted. Presumably, inefficiencies in carbon metabolism would decrease a tree's tolerance for an opportunistic pathogen like *A. ostoyae* (Harvey et al. 1994). The converse could occur; that is, a population adapted to a sea of high moisture stress would find itself maladapted on islands of low moisture stress. To adequately test this hypothesis, collection points (plots) for data, biotic samples, and abiotic samples must be placed in their landscape perspective to calculate relative proportions of wet and dry environment. Fire behavior is also greatly influenced by the same landscape relations; that is, a given ecosystem will behave one way in a sea of wet and another in a sea of dry (Agee 1993). Thus, the same landscape perspective would also facilitate the study of interaction of the above biological phenomena with fire regimes.

A hierarchical classification of North American ecosystems based on potential vegetation (Brown et al. 1998) facilitated creation of a habitat-type grouping concept to fit a local ecological scale seamlessly into a continental scale (McDonald et al. 2000). Habitat types or plant associations (Pfister and Arno 1980, Cooper et al. 1991) were grouped according to indicator plant occurrence in constancy tables developed for existing classifications (McDonald et al. 2000). This procedure apportioned climax series along moisture gradients signified by understory vegetation to create subseries. Cataloguing ecosystem behavior using correlations among subseries and plot data, in the form of crosswalk tables, provides some useful insight into ecosystem interactions (McDonald 1991*a,b*; McDonald et al. 2000). Placement of plot behavior into a landscape perspective would add real power to crosswalk tables by placing the ecology of forest diseases into explicit scales in time and space (see Hoekstra et al. 1991).

Previous attempts to map potential vegetation (biophysically regulated expected plant community rather than current community) across the landscape were conducted for climax series at a scale of 1 km (Hardy et al. 1998, Hessberg et al. 2000, Keane et al. 2000). Connections between plant associations, *Armillaria,* fire, and other ecological behaviors, based on plot data, point to a finer mapping scale and a subdivision of series (McDonald et al. 2000). Our initial goal is to connect the spatial domain of individual plants at the plot level, about 100 m^2, to its containing landscape, about 100 km^2 (Walker et al. 1993). If this can be successfully done, then we can begin testing various gene–ecological aspects of the ecophysiological maladaptation hypothesis, including the interactions among fire or other disturbances and the microbes, plants, and animals that inhabit said ecosystems.

In many investigations of relationships between heterogeneous topography and vegetation, a close connection between vegetation response and terrain was observed. One attempt to directly map habitat types on north Idaho's Coeur d'Alene National Forest identified precipitation, infiltration, evapotranspiration, growing season, soil depth, wind exposure, and cold air drainage as the major influences on landscape distribution of habitat types (Deitschman 1973). If elevation, as opposed to aspect, was the major factor influencing distribution of habitat types on a slope, ecotones were broad, confused mosaics. On the Coeur d'Alene National Forest most clear changes in habitat type were triggered by aspect. Soil depth (e.g., water-holding capacity) could modify these clear ecotones by displacing boundaries between habitat types (Deitschman 1973). An important characteristic of northern Rocky Mountain forests is the depositional pattern of the ash cap (Geist and Cochran 1991). This may be particularly important regarding north versus south aspects, since the ash deposit tends to be thicker on north as-

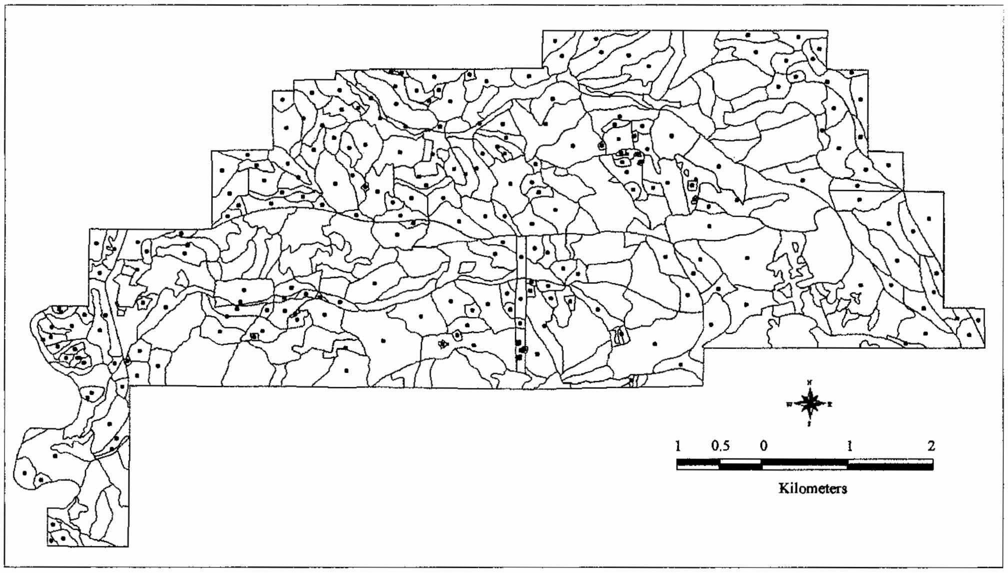


Fig. 1. Boundaries and centers of mass (field plots) of 245 stands on the 2,753-ha Priest River Experimental Forest located in the Idaho Panhandle about 80 km south of the Canadian border. Center of mass not marked for stands lacking habitat type designation.

pects (Nimlos and Zuuring 1982). Perhaps for this reason, south aspects show more heterogeneity and sharper ecotones than do north aspects (Deitschman 1973).

Cross-sectional shape (convex, uniform, or concave) of land configuration was also important. Habitat type ecotones often occurred on ridgelines (Deitschman 1973). Convex conditions were relatively dry, while concave surfaces were relatively wet. Concave surfaces tended to be located on lower slopes, where they would be cooler, owing to cold air drainage. Neighboring terrain was likewise an important consideration, especially regarding wind movement (Deitschman 1973). Others have noted similar influences and have pointed out the importance of cold air drainage (Daubenmire 1980). It is likely that major influences in determining habitat type within a local area would be potential solar radiation, topographic position, and exposure (Allen and Peet 1990). A solar insolation index was used to map habitat types on the Palouse Range in northern Idaho (Plumb 1981). In a recent study of forest structure, the ratio of radiation on a sloping surface relative to the value on a flat surface was an important variable (Lindenmayer et al. 1999). Nieman (1991) modeled landscape drainage to improve Landsat multispectral classification accuracies of vegetation.

If habitat types of geo-referenced plots are available, then the MSN procedure could impute known subseries classifications to locations where subseries is unknown (Moeur and Stage 1995). In an earlier study, MSN was used to build an interpolated data layer of forest species composition (Moeur and Riemann-Hershey 1999). Required data are a set of sample plots at known locations and a global or continuous data layer such as a satellite image or a digital terrain model (DTM) (Moeur 2000). Imputation methods were successfully applied to solve other forest inventory problems (Ek et al. 1997, Van Deusen 1997).

We hypothesize that information about potential vegetation attributed to a few cells in a setting can be imputed by MSN to all cells in the setting by using satellite imagery and output from terrain models as variables that describe physical attributes of all individual cells. Our goal is creation of potential vegetation maps of sufficient accuracy to conduct landscape assessments of the ecological ramifications of host–pest–fire interaction. Our purpose is to report a "proof of concept" test of this hypothesis using a common imputation method applied to a USDA Forest Service experimental forest.

STUDY AREA

Priest River Experimental Forest (PREF) (total area 2,753 ha; lat 48°21′N, long 116°47′W) is located in northern Idaho about 80 km south of the Canadian border. Finklin (1983) provided a description of PREF climate. Wellner (1976) described the history and ecology of the forest. Sources of global data were a Forest Service-modified U.S. Geological Survey 30-m digital elevation model (DEM) and a 15 August 1989 Thematic Mapper (TM) satellite image. A stand map (Figure 1) supplied habitat type (Figure 2) as recorded by personnel of the Priest Lake Ranger District, Idaho Panhandle National Forests. In addition, we used a map of habitat types (procedure described by Daubenmire 1973) published by Wellner (1976) (Figure 3).

METHODS

Global Predictor or "X" Variables

GIS and MSN processing (Figure 4) started with assignment of *X* and *Y* Universal Transverse Mercator coordinates and a unique identifier to each cell in the DEM. Aspect (ASP in degrees), slope (SLP in percent), and elevation (ELEV in meters) were generated from the DEM for each 30-m pixel representing PREF

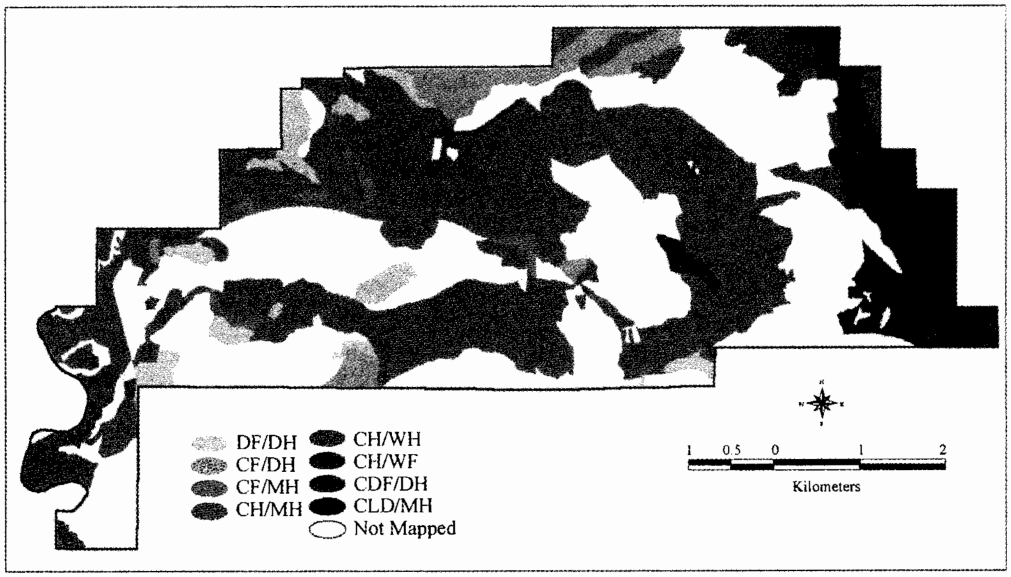


Fig. 2. Potential vegetation subseries (groups of habitat types) on the Priest River Experimental Forest, northern Idaho, as mapped from stand designations of habitat type. Subseries definitions: CDF = cold fir, CF = cool fir, CH = cedar-hemlock, DF = Douglas-fir, DH = dry shrub, MH = moist herb, WF = wet fern, WH = wet herb. (See McDonald et al. [2000] for details.)

using ARC/INFO GIS (geographical information systems) software. ASP was transformed to radians for calculation of SLPCOSASP, a linear relationship between slope and aspect (Stage 1976), where SLPCOSASP = SLP (percent/100) × cos (ASP in radians). We also calculated SLPSINASP (Stage 1976), where SLPSINASP = SLP (percent/100) × sin (ASP in radians). Slope curvature (SLPCURV), an index of relative slope convexity and concavity, planform curvature (PLFCURV), an index of divergence and convergence of water flow on the landscape, and profile curvature (PROCURV), an index of acceleration and deceleration of landscape water flow, were calculated from the DEM using ARC/INFO. Wetness index (WETIND) was calculated using a model (Nieman 1991) to create a landscape–water-holding index based on flow direction, flow accumulation, and slope curvature. Insolation (INSOL) at each pixel was calculated as annual global solar radiation in kWh/m^2 by Solar Analyst (an ArcView extension) (Fu and Rich 1999). This model views the terrain through a simulated hemispherical lens placed at each cell, tracks the sun

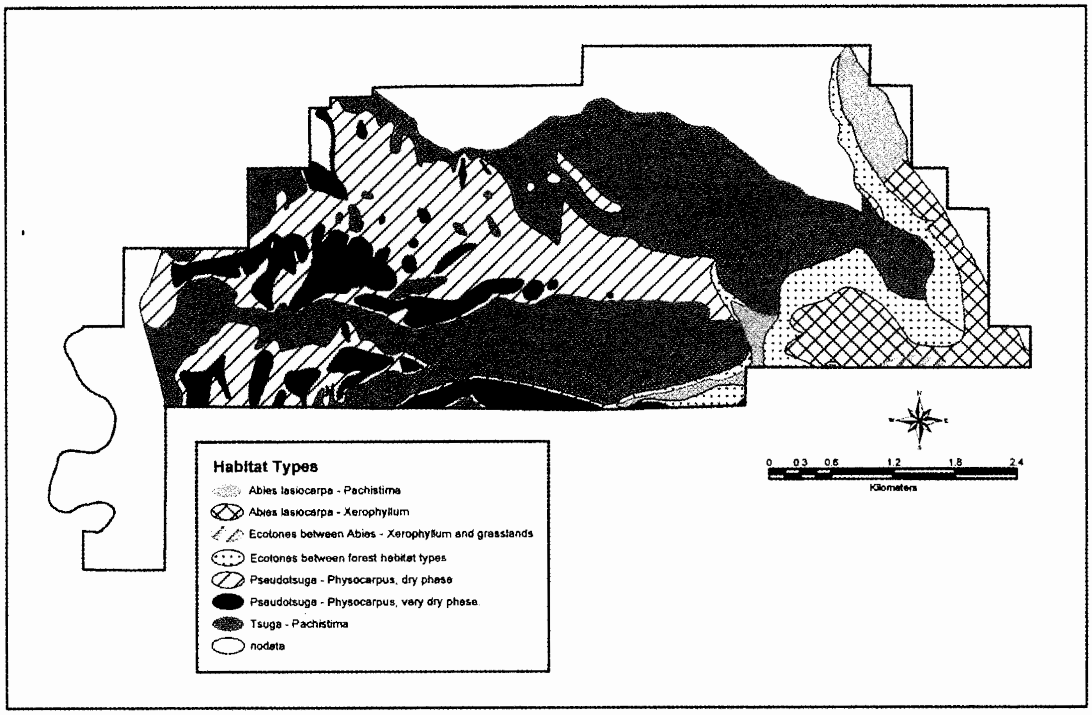


Fig. 3. Priest River Experimental Forest, northern Idaho, habitat types mapped by R. Daubenmire (see Daubenmire 1973 for details).

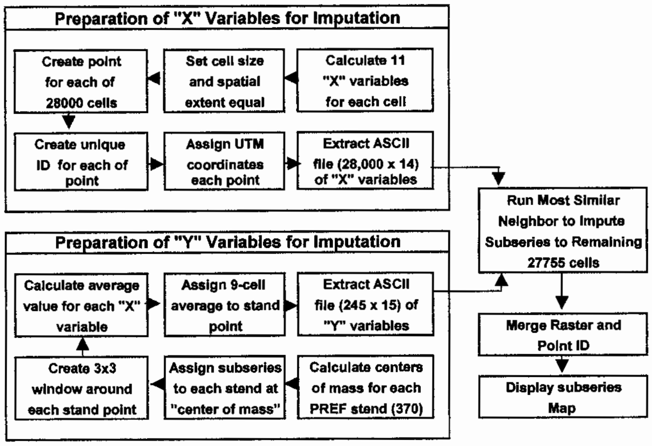


Fig. 4. Process diagram showing preparation of "X" and "Y" variables used to impute subseries to raster cells of the Priest River Experimental Forest, northern Idaho, digital elevation model.

through its annual cycle for that location, and then accumulates the result. Annual duration of light (LDUR) was computed for each pixel by Solar Analyst. Wetness (WET) was principal component 3 generated from a Tasseled Cap Transformation (Crist et al. 1984) of the Landsat TM satellite data. This variable reflects relative canopy and soil moisture contents. Finally, an ASCII file of global predictor variables for individual pixels (28,000 × 14) was generated for input into the MSN imputer.

Training or "Y" Variables

Out of 370 stands delineated at PREF, 125 were removed from the coverage because of absence of a habitat type determination (Figure 2). The remaining 245 stands were assigned to a subseries based on plant occurrence listed in published constancy tables for each habitat type (McDonald et al. 2000). Subseries assignments were Douglas-fir/dry herb (DF/DH), cool fir/dry herb (CF/DH), cool fir/moist herb (CF/MH), cedar-hemlock/moist herb (CH/MH), cedar-hemlock/wet herb (CH/WH), cedar-hemlock/wet fern (CH/WF), cold fir/dry herb (CDF/DH), and cold fir/moist herb (CDF/MH). These subseries are described in McDonald et al. 2000. The shape-weighted center cell of each of the remaining 245 stands was determined (Figure 1), and assigned *X*- and *Y*-coordinates and a unique pixel identifier. Mean values of computed global variables were calculated for the center pixel and its 8 surrounding pixels. This matrix (245 × 15) of training observations was input to MSN (Crookston et al. 2002) along with the previously produced global matrix of "X" variables. MSN then imputed subseries to all 28,000 cells representing PREF using a Euclidean distance measure weighted by the canonical correlations between subseries and the global matrix of "X" variables. Raster and MSN output was merged by point identification (Figure 4) to map imputed subseries (Figure 5).

RESULTS AND DISCUSSION

MSN Validation

The Most Similar Neighbor imputer calculates accuracy assessment statistics between observed and predicted values for training cells to guide the user in assessing overall classification results. Overall, fit for predictor variables between the training cells and assigned most similar neighbors or "predictions" was good (Table 1). Similar means and standard deviations for observed and predicted values and large R^2 indicated field plots and their assigned neighbors were alike on that predictor variable. MSN validation results (Table 1) show $R^2 > 0.5$ for the *X*-coordinate, SLP, ELEV, SLPCOSASP, PROCURV, and INSOL. In fact, R^2 for variables SLPCOSASP, ELEV, *X*-coordinate,

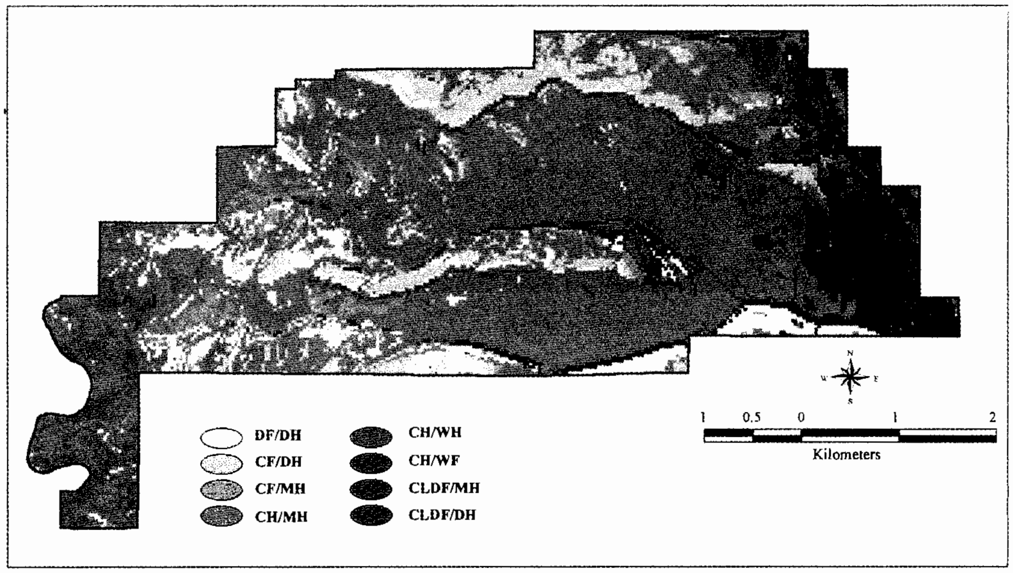


Fig. 5. Most Similar Neighbor imputation of subseries to the Priest River Experimental Forest, northern Idaho. Subseries designations are as in Figure 2.

Table 1. Most Similar Neighbor validation results based on 245 stands at Priest River Experimental Forest, northern Idaho, used for subseries training.

Variable[a]	Observed		Predicted		Fit statistics	
	Mean	SD	Mean	SD	R^2	Prob > t
X-coordinate	515228.384	2386.766	515405.290	2368.171	0.8277	0.257
Y-coordinate	5355830.318	1045.047	5355898.445	1021.524	0.4990	0.322
Slope	30.144	12.634	30.724	12.314	0.6262	0.568
Elevation	1038.473	294.610	1058.886	287.791	0.8312	0.299
SLPCOSASP	0.109	0.220	0.117	0.218	0.8313	0.823
SLPSINASP	−0.112	0.154	−0.118	0.157	0.3066	0.552
Slope curvature	0.031	0.214	0.036	0.185	0.3787	0.771
Planform curvature	0.021	0.107	0.019	0.097	0.0439	0.782
Profile curvature	−0.010	0.146	−0.017	0.122	0.5738	0.599
Insolation	1058471.000	136333.000	1057254.000	136261.000	0.8005	0.949
Light duration	3534.000	294.000	3545.000	281.000	0.4961	0.658
Wetness	9.882	12.889	9.347	14.247	0.1769	0.519
Wetness index	8.784	2.085	8.891	1.812	0.4348	0.511

[a] See text for definition of variables.

and INSOL were >0.8. The lowest R^2 (0.044) was for PLFCURV. All R^2, except PLFCURV, indicate significant contribution to the classification. Small probability for the paired t-tests between predicted and observed means indicate serious lack of fit. For this MSN imputation, significant differences (≥0.05) were not observed (Table 1).

Canonical Correlation Report

Weights or canonical coefficients assigned by MSN can be helpful in interpreting which specific variables are driving the MSN classification. Values (Tables 2 and 3) indicate relative "loadings," or importance, of individual variables in the MSN assignments. Relatively large values indicate variables that receive more weight in the MSN weighted distance function. The same variables with the best performance in the validation step (Table 1)—SLPCOSASP, ELEV, *X*-coordinate, and INSOL—had canonical loading values of 0.9 and higher (Table 2). Other potentially important drivers include SLP and LDUR (0.6 and higher). Based on relative loadings for the subseries classes (Table 3), we might expect best classification results for CDF/MH, CDF/DH, CF/DH, and CH/MH (0.2 and higher).

MSN Error Matrix

The Error Matrix (Table 4) shows the ability of the MSN procedure to predict (or classify) subseries for the field plots data, both overall, and for individual loci (cells). The MSN classification approach correctly classified 171 of 245 field plots, for an overall accuracy of 0.7. Individual results were best for CDF/MH (13/14 = 0.93), CH/MH (134/163 = 0.82), CF/DH (9/16 = 0.56), and CDF/DH (8/15 = 0.53). These are the same subseries classes identified as being most "predictable" according to their loading values (Table 3). Evaluation of misclassifications may be important. Correct classification of all observations would be best, but misclassification into adjacent (or "next best") classes might be acceptable (e.g., 10/14 = 0.71 CH/WH observations were misclassified as CH/MH). Serious misclassifications (DF/DH into CH/MH, 8/15 = 0.53) probably happened because the class was not well represented in the field data (Figure 2). High R^2 values between observed and predicted classes indicate assigned most similar neighbors closely resemble the field plots for that variable. Presumably, these variables are most closely related to the classification variable, subseries, which is our primary classification objective. Variables having low correlations, such as

Table 2. Weights assigned by Most Similar Neighbor routine to 5 eigenvectors for 13 terrain variables calculated for Priest River Experimental Forest stands, northern Idaho. Relatively large eigenvector loadings are in bold.

Variable[a]	Eigenvector				
	1	2	3	4	5
X-coordinate	−0.20288	0.37836	**1.29270**	0.15938	0.33776
Y-coordinate	**0.02791**	**0.01243**	**−0.03241**	**−0.13564**	**0.05055**
Slope	**−0.78859**	0.10722	−0.37633	0.10079	0.27096
Elevation	**1.32706**	−0.14769	**−0.98454**	**−0.49874**	**−0.53297**
SLCOSASP	**−0.76474**	**−1.25287**	−0.43719	**0.68188**	**0.70791**
SLSINASP	−0.15749	0.04033	−0.17302	0.04981	0.17832
Slope curvature	0.07056	0.06723	−0.04194	0.12720	0.03332
Planform curvature	−0.01703	0.06311	−0.02197	−0.00575	−0.04694
Profile curvature	−0.11242	−0.05210	0.04142	−0.19300	−0.08571
Insolation	**−0.66149**	**−0.81450**	**−0.68230**	**0.91908**	**0.59822**
Light duration	**−0.64807**	−0.03984	0.32007	0.03434	0.19833
Wetness band	0.03804	−0.02031	0.10132	0.04865	0.14484
Wetness index	−0.15952	−0.22356	−0.06445	0.23750	0.02106

[a] See text for definition and calculation of variables.

Table 3. Weights assigned by Most Similar Neighbor routine to the first 4 eigenvectors for the 8 subseries classes determined on Priest River Experimental Forest stands, northern Idaho. Relatively large eigenvector loadings are in bold.

Subseries[a]	Eigenvector 1	2	3	4
DF/DH	−0.19268	0.17161	0.16248-NaN[b]	0.12862
CF/DH	−**0.22830**	**0.41183**	−0.21011-NaN	0.05089
CF/MH	−**0.12207**	**0.07948**	**0.28647-NaN**	**0.15658**
CH/MH	−0.15234	−**0.27329**	−0.05127-NaN	0.05783
CH/WH	−0.06551	−0.19651	−0.00535-NaN	0.07432
CH/WF	−0.01807	−0.05825	−0.13574-NaN	0.1282
CDF/DH	**0.43101**	0.12367	0.00167-NaN	−0.14036
CDF/MH	**0.46463**	−0.03229	−0.00465-NaN	0.11929

[a] Subseries definitions: CF = cool fir, CH = cedar-hemlock, CDF = cold fir, DF = Douglas-fir, DH = dry shrub, MH = moist herb, WF = wet fern, WH = wet herb. (See McDonald et al. [2000] for details.)

[b] NaN signifies a very small number.

PLFCURV and WET, are not necessarily "alike," although individual plots may be right on.

Most Similar Neighbor Classification

MSN statistics indicated a successful classification and the predicted subseries map (Figure 5) shows a good overall match with a habitat type map made from ground observation (Figure 3). In fact, the MSN subseries map (Figure 5) looks more reasonable than "truth" (Figure 3). From the point of view of genecology of host–pest interaction the MSN projection appears to be closer to the actual situation. The degree of meaningful heterogeneity depicted by the MSN map is undoubtedly an underestimate. The habitat type map contains large undifferentiated polygons, some of which may be true while others may be just heterogeneous mixes of subseries that cannot be distinguished by ground-based mapping. Other regions of the habitat type map (Figure 3) are labeled as undifferentiated ecotones.

Potential for Analysis of "Place"

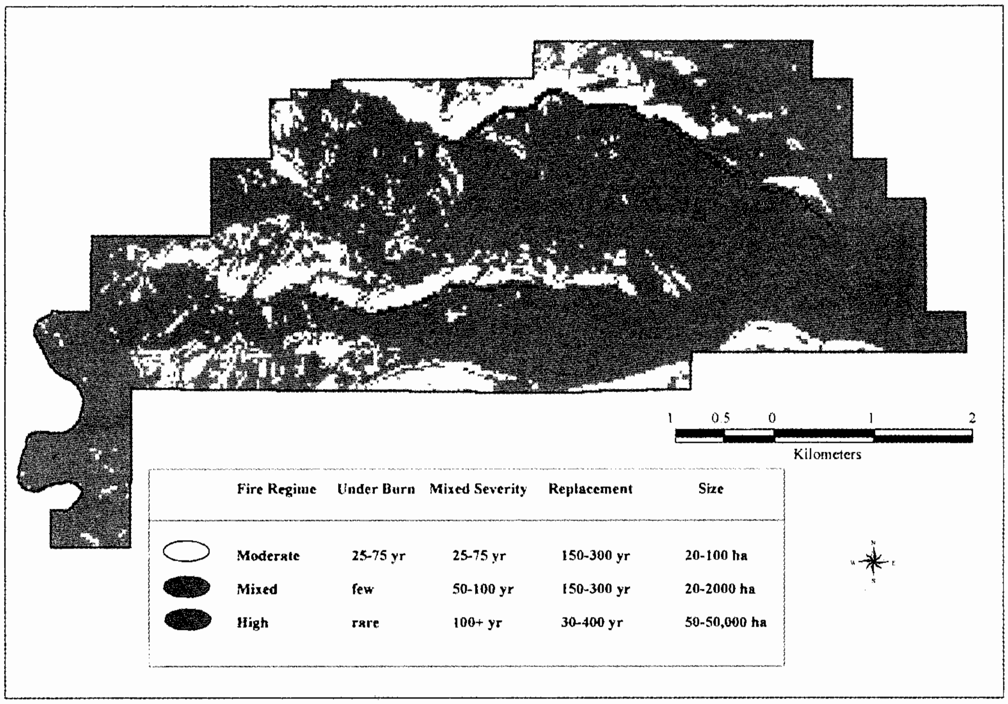
Our objective was to add a "sense of place" to plot data and the MSN imputation illustrates several important features of place. Some features are "islands of dry in a sea of wet," "wet in a sea of dry," narrow linear ecotones along ridges, and narrow linear ecotones along streams (Figure 5). There are heterogeneous regions about 100 ha in area that contain all 6 of the low-elevation subseries. After production of a validated map, "place" could be quantified by shape, size, and orientation of "ecosystems" and their ecotones. Quality and scale of DEM data will be important considerations. Two ways to improve reliability in this application of topoclimatic models are use of finer-scale DEMs and the validation of such models with landscape deployment of low-cost sensors and data loggers (Rich and Fu 2000).

Even though the MSN error matrix (Table 4) indicated 30% incorrect classification of pixels, it is evident upon inspection of the subseries map that many of the linear and island features of distribution are preserved (Figure 5). With regard to individual predictor variable interpretations, X-coordinate represented slope contour gradient, and most similar neighbor choices were weighted to plots along the E–W gradient by their X-coordinates (PREF is topographically oriented largely E–W). Many ecological processes can be highly influenced by topographic orientation. Some examples are the influence of wind on fire behavior and on pollen, spore, and insect dispersion. Elevation is an obvious topographic predictor of subseries as shown by its high R^2 (Table 1). The high R^2 of insolation (Table 1) indicates potential of this variable to be a surrogate for important biophysical parameters such as moisture and temperature that influence ecosystem productivity. High R^2 of SLPCOSASP was expected since it is a well-known integrator of site parameters correlated with productivity.

Table 4. Error matrix resulting from Most Similar Neighbor (MSN) classification of 245 subseries[a] training stands, Priest River Experimental Forest, northern Idaho. Overall accuracy of the MSN classification approach = 0.70.

Observed	Predicted DF/DH	CF/DH	CF/MH	CH/MH	CH/WH	CH/WF	CDF/DH	CDF/MH	Total
DF/DH	3	2	1	8	0	0	1	0	15
CF/DH	1	9	0	6	0	0	0	0	16
CF/MH	0	0	1	6	0	0	0	0	7
CH/MH	5	3	3	134	12	0	5	1	163
CH/WH	0	0	0	10	3	0	0	1	14
CH/WF	0	0	0	1	0	0	0	0	1
CDF/DH	0	0	0	4	0	0	8	3	15
CDF/MH	0	0	0	0	1	0	0	13	14
Total	9	14	5	169	16	0	14	18	245

[a] Subseries definitions: CDF = cold fir, CF = cool fir, CH = cedar-hemlock, DF = Douglas-fir, DH = dry shrub, MH = moist herb, WF = wet fern, WH = wet herb. (See McDonald et al. [2000] for details.)



	Fire Regime	Under Burn	Mixed Severity	Replacement	Size
○	Moderate	25-75 yr	25-75 yr	150-300 yr	20-100 ha
●	Mixed	few	50-100 yr	150-300 yr	20-2000 ha
●	High	rare	100+ yr	30-400 yr	50-50,000 ha

Fig. 6. Expected fire regimes at Priest River Experimental Forest, northern Idaho, as mapped from crosswalk table. (See McDonald et al. [2000] for details.)

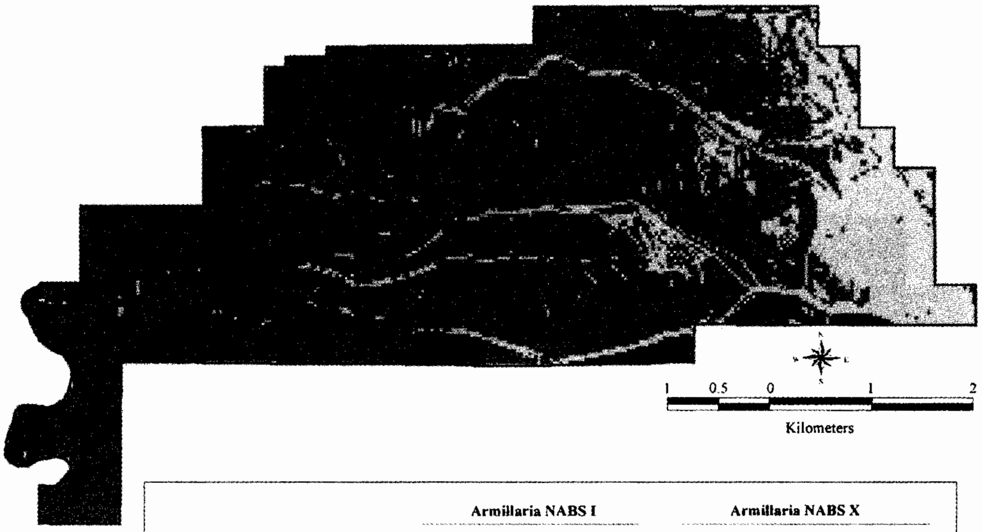
Fire Regimes

The real power of MSN-facilitated fine-scale mapping of subseries lies in the sense of place that can be attributed to data collected from individuals. For example, crosswalk tables developed from data collected throughout the northern Rocky Mountains can describe relationships among ecological regimes for such disturbances as fire and *Armillaria*-caused root rot versus subseries (McDonald et al. 2000). Such tables enabled mapping of these regimes at a specific location when combined with an MSN potential vegetation imputation (Figures 6 and 7). In this way landscape interactions among the regimes can be interpreted. The total area of PREF is 2,753 ha. Of the total, 275 ha were not forested (rock, meadows, administrative areas). Analysis of the fire regime map (Figure 6) showed that 'the PREF is dominated by the mixed-severity regime. This regime supports little underburning (McDonald et al. 2000) and it covers 82% of the forest. About 1% of the forest is in the high-severity regime that is characterized by no underburning. Essentially this entire regime was located in the east-to-west trending stream bottoms. At first glance, one would think that this regime should have little influence on the behavior of fire at PREF. When placed into the perspective of this landscape where 16% of PREF had a moderate-severity regime (Figure 6) supporting regular underburning at a 25- to 75-year return interval, the CH/WF subseries may be performing an ecological function of prime importance to the overall PREF ecosystem. Perhaps it is a barrier to ground fire moving into the upland mesic subseries. A much different dynamic is probably at play in the areas of the forest where the moderate- and mixed-severity regimes form a heterogeneous mix (Figure 6). In one heterogeneous region 100 ha in area, 6 of 6 PREF low-elevation subseries were indicated.

Armillaria *Root Rot Regimes*

At PREF 8% of the area was classified into the "*A. ostoyae* root rot" regime. This regime should support only *A. ostoyae* in a situation where the fungus would cause root rot in native and planted Douglas-fir alike. Seral species on these sites would be western larch and/or ponderosa pine. Local seed sources should be tolerant while imported sources may not be. Most of this *Armillaria* regime is situated as "islands of dry" in a "sea of wet" (Figure 7). Are these the kinds of situations where ecophysiological maladaptation may be in play? Most of the area of PREF (77%) fell into the "*Armillaria* complex" regime. In these stands, western white pine and western larch were the primary historic seral species. In addition, these stands had mixed-severity fire regimes where little underburning occurred. *Armillaria ostoyae* was an important thinning agent that selectively removed grand fir and Douglas-fir by root rot. As discussed previously, some evidence exists that NABS X may protect white pine to the point of making it appear tolerant to *A. ostoyae.* Evidence also suggests that *A. ostoyae* and NABS X may both cause butt rot in grand fir, western hemlock, and western redcedar. Stands like these represented 77% of the forested area of PREF. These are the stands at greatest risk of moving into new and more damaging fire regimes with the loss of white pine, especially if succession was allowed to move to the climax stage rather than being regenerated every 200 years or so.

The final *Armillaria* regime, "climax rot," was



	Regimes	Armillaria NABS I			Armillaria NABS X		
		Seral	2nd Seral	Climax	Seral	2nd Seral	Climax
●	A. ostoyae Root Rot	Geo Root Rot	None	Root Rot	None	None	None
●	Armillaria complex	Tolerant	Root Rot	Butt Rot	Bio Control	Butt Rot	Butt Rot
▨	Climax Rot	Tolerant	Tolerant	Both Rot	Bio Control	Epiphyte	Epiphyte

Fig. 7. Expected *Armillaria* regimes at Priest River Experimental Forest, northern Idaho, as mapped from crosswalk table. (See McDonald et al. [2000] for details.) NABS I = *A. ostoyae,* NABS X = undescribed *Armillaria* species; Geo Root Rot refers to observation that naturally regenerated trees of the seral species ponderosa pine and lodgepole pine are significantly damaged in some localities and not in others. See text for further discussion of the regimes.

present on 15% of PREF. Evidence indicates that in wet or cool and moist environments, behavior of the *Armillaria* changes once again. The map produced by the crosswalk table (Figure 7) shows a strong linear nature associated with both ridge tops and streams. Once again, microbial action can interact with fire regimes in a "place"-specific manner. Could movement toward the climax stage with its increased levels of root and butt rot activity in climax species change fuel conditions such that stream bottoms and ridge tops both lose some of their effectiveness as barriers to fire spread? Fuel and fuel ladders might accumulate because of the increased activity of *Armillaria* along ridge tops located north and northwest of areas that burn relatively more frequently (note the linear ecotone at bottom of Figure 7). This condition could significantly increase the probability of a stand-replacement fire on the adjoining north slope (Figure 7).

CONCLUSIONS

Accurate mapping of subseries can facilitate analysis of landscape interactions among fire and pests. Such maps would support ecosystem restoration, management, and research. Needed landscape perspective could be added to the design, execution, and analysis of studies directed at understanding ecosystem processes such as gene flow and adaptation in hosts and pests. To be useful, accuracy in assignment of ecosystem designation (subseries) must be high. Additional global predictor variables such as distribution of ash cap, wind exposure, cold air drainage, and soil temperature would likely improve imputation accuracy. Overall, issues of accuracy, scale, and distribution of validation plots should be given high priority in any future development of the technique presented.

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