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A Landscape Model for Predicting Potential Natural Vegetation of the Olympic Peninsula USA Using Boundary Equations and Newly Developed Environmental Variables

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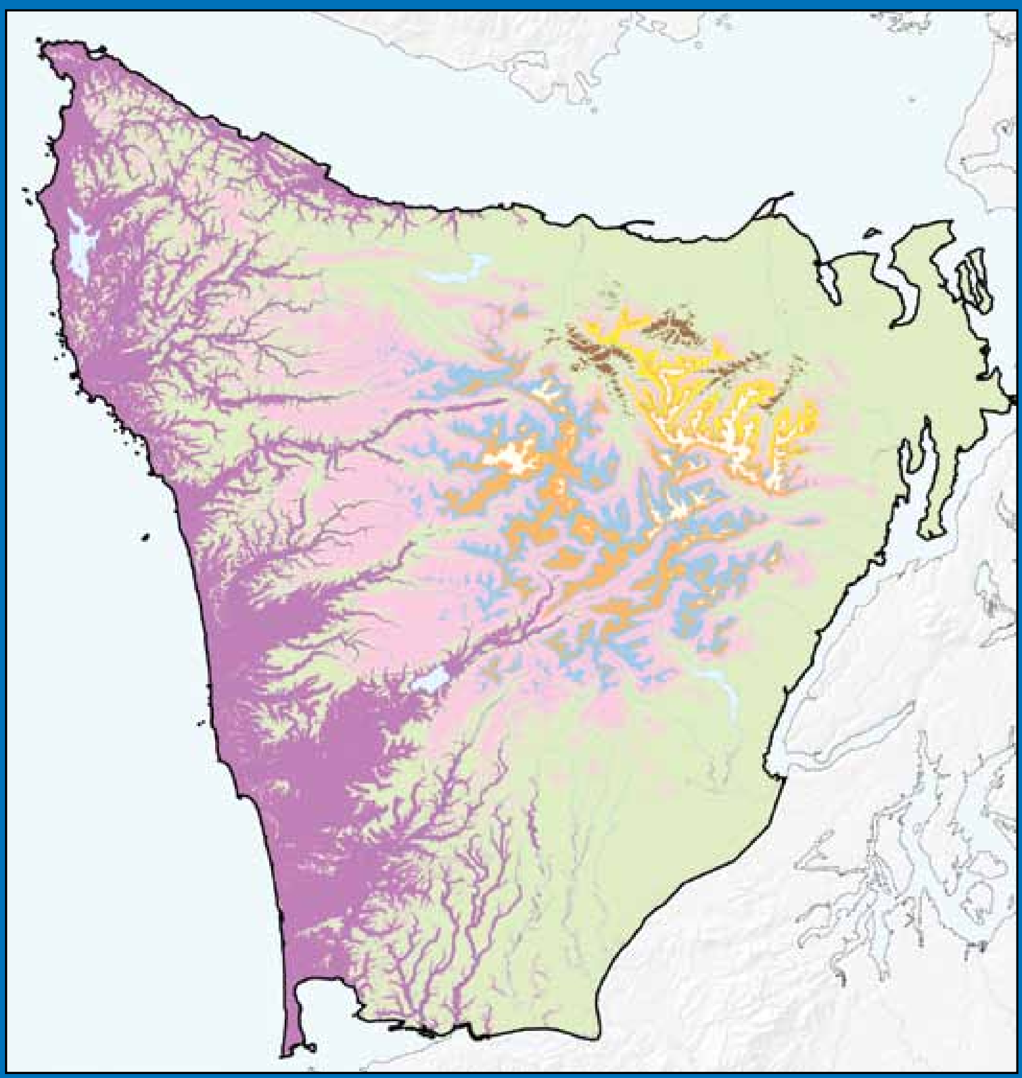

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Abstract

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A gradient-analysis-based model and grid-based map are presented that use the potential vegetation zone as the object of the model. Several new variables are presented that describe the environmental gradients of the landscape at different scales. Boundary algorithms are conceptualized, and then defined, that describe the environmental boundaries between vegetation zones on the Olympic Peninsula, Washington, USA. The model accurately predicted the vegetation zone for 76.4 percent of the 1,497 ecoplots used to build the model. Independent plot sets used to validate the model had an accuracy of 82.1 percent on national forest land, and 71.8 percent on non-national-forest land. This study demonstrated that a model based on boundary algorithms can be an alternative to regression-based models for predicting landscape vegetation patterns. Potential applications of the model and use of the environmental gradients to address ecological questions and resource management issues are presented.

Keywords: Environmental gradient model, potential natural vegetation, vegetation zone map, Olympic Peninsula USA, boundary equations, environmental gradients.

Summary

The concept of potential natural vegetation (PNV), the plant community reflecting the environmental capability of a land area, is a core concept in plant ecology and natural resource management. Rigorous, consistent, and validated potential vegetation mapping has been technically elusive, while at the same time it has remained a persistent need for land management agencies and a potentially valuable tool for stratifying and informing ecological studies. Gradients of predictive variables are sought to facilitate modeling and mapping of PNV. This paper presents a new way to model and map PNV to help meet these needs. We also present a new set of variables that describe the environmental gradients of a landscape at different scales.

A gradient-analysis-based model and grid-based map are presented that use the potential vegetation zone as the object of the model and the underlying environmental variables as the primary subject of research. Boundary algorithms were conceptualized, and then defined, that described the environmental boundaries between vegetation zones on the Olympic Peninsula, Washington, USA. These boundary equations took the form of elevation of the boundary as the dependent variable, with components of the environment representing the independent variables. This was contrasted with the traditional regression-based approaches, which focus on central tendencies of the target ecological entity.

New environmental variables developed for use in this model included "total annual precipitation at sea level," "mean annual temperature at sea level," "fog effect," and "cold air drainage effect." "Topographic moisture" and "temperature lapse rate" were newly calculated or represent new scaling for these concepts. Other more classic variables used as independent variables were "aspect" and "potential shortwave radiation."

The map produced by the study displayed the predicted pattern of eight potential vegetation zones. The model accurately predicted the vegetation zone for 76.4 percent of the 1,497 ecoplots used to build the model. An independent validation set of 155 plots showed an accuracy of 77.4 percent.

This study demonstrated that a model based on boundary algorithms can be an alternative to regression-based models. In addition, a new set of environmental variables based on first- or second-order derivatives of weather station data or new hypotheses of landscape processes were used to successfully predict landscape patterns of potential vegetation. These maps of potential vegetation and the environmental variables can provide the foundation for subsequent scientific and ecological studies and for addressing resource management questions.

Contents

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Introduction

The relationships between vegetation and environment are the core of the field of plant ecology. Understanding these relationships is the subject of most papers in the field today. Some studies use these relationships to map the distribution patterns of target organisms or communities (Ohmann and Gregory 2002, Rehfeldt et al. 2006), and others display the relationships in statistical tables or abstract space (McKenzie et al. 2003, Rehfeldt et al. 2008). Most studies are limited to using existing and easily measured or derived environmental variables.

This study used an innovative approach to predict vegetation zones (VZ) across a complex landscape, and several newly defined environmental variables are introduced. A hypothesis is presented that boundary equations can be used in lieu of more traditional regression-based algorithms (e.g., Ohmann and Gregory 2002, Rehfeldt et al. 2006). This hypothesis was tested by producing a map of the potential vegetation zones of the study area and by comparing it to an independent set of plots for validation.

Potential vegetation is the object of this study because it is more closely related to the environment, as opposed to existing vegetation, which is strongly affected by seral stage and disturbance. Potential vegetation is the reference point or context for describing successional relationships and correlations between the vegetation and environment (Henderson et al. 1992). Potential vegetation is used in science and natural resource management for stratifying land relative to the environment and by informing questions regarding succession and growth potential.

The part of the environment that directly affects individual organisms has been called the "operational environment" (Mason and Langenheim 1957) as opposed to the full range of possible or measurable environmental variables. The operational environment is currently known only in a general sense; much of its apparent or correlative effects are thought to be related to some aspects of moisture, temperature, and light.

Relative to terrestrial vegetation, moisture and temperature are highly complex forcing factors that vary in amount, phase, timing and quality in a wide array of possible combinations. These combinations of factors result in a unique environment and vegetation for nearly every place in the world. Part of the aim of plant ecology is to detect the effects of particular aspects of the moisture and temperature regimes, plus other factors including wind, light, and nutrients, while at the same time trying to uncover the complex ecological interactions, compensations, and variations over time and space.

The "operational" effects of this complex environment affect each individual organism independently (Mason and Langenheim 1957), in a corollary to the "individualistic" theory of vegetation organization (Gleason 1926). The sum of all such individual effects over time plus the effects of intra- and inter-specific interactions controls the composition of the terrestrial community. The integration of all such effects drives the structure and function of the ecosystem. Whereas the operational environment as a concept is relatively easy to identify in general terms, its parameters are poorly quantified for most species. However, the concept allows us to target for study those elements of the environment that appear to control or affect individual organisms, and by extension, communities and ecosystems.

Understanding the operational environment and resulting distributions of species and communities has many practical applications. It can contribute to the mapping of species and communities, a necessary tool in the management of natural resources, biodiversity, and the conservation of biotic communities.

Maps of the spatial patterns of units of vegetation (either existing or potential), as well as underlying environmental variables (such as different components of the moisture and temperature regimes), have a variety of uses for land management. These include analysis of biodiversity and planning for species or community protection; planning for restoration of habitats for at-risk species (such as the northern spotted owl [*Strix occidentalis caurina*] or marbled murrelet [*Brachyramphus marmoratus*]); planning for the protection of individual species, particularly those at risk; managing for beneficial or economic species; planning for timber management objectives such as yield, rotation length, or intermediate harvests; use as a benchmark or stratification for disturbance, climate change, and carbon sequestration studies and other monitoring applications; predicting the potential occurrences of wildfire and the rate of ecosystem recovery following perturbation; or describing the ecosystem departure from a sustainable range within an area. Maps of potential natural vegetation (PNV) are key to understanding patterns of existing vegetation as well as potentials for growth, species distributions, fire occurrence, and stand response to treatments. This is because of the strong link between units of PNV and the environment.

Historically, patterns of potential or existing vegetation have been depicted using intensive field surveys and hand-drawn polygon maps (Dodwell and Rixon 1902, Eyre 1980, Kuchler 1964, Pfister et al. 1977). More recent attempts use satellite images and geographic information system (GIS)-based digital data combined with weather station records to portray vegetation patterns in a pixel-based format (Cibula and Nyquist 1987, Ohmann and Gregory 2002). These digital mapping efforts use an algorithm to link environmental data to reference data of species presence (or sometimes absence), known plant community patterns, or field samples of plant community classes. This general modeling approach has its roots in the concept of "gradient modeling" (Kessell 1979) and is sometimes known as "predictive vegetation mapping" (Franklin 1995).

The purpose of this study is to build a predictive, environmentally based, spatially explicit, gradient model of PNV using boundary equations to distinguish model units. In addition, and as necessary, the purpose is to develop new predictive environmental variables that help define the operational environment.

Background, Concepts, and Definitions

Potential Natural Vegetation

Tuxen is credited with the original definition of PNV, as "…the vegetation that would become established if all successional sequences were completed without major natural or direct human disturbances under present climatic, edaphic, and topographic condition" (adapted from Tuxen [1956], as translated and cited by Mueller-Dombois and Ellenberg [1974] and Kuchler [1964]). The more modern term "climax plant community" (CPC) is synonymous with Tuxen's potential natural vegetation. However, the concepts embodied in the terms climax plant community, potential natural vegetation, association, and succession have evolved since 1956, especially regarding the link between vegetation and the environment, the nature of the climax, and the nature of vegetation itself.

The concept of the CPC (climax association sensu Daubenmire 1952, 1976; Daubenmire and Daubenmire 1968) is a theoretical classification unit representing the hypothetical end point of succession. As most plant communities (at least in the study area) are in some developmental/successional stage moving toward this hypothetical climax, such a classification of PNV (sensu Tuxen 1956) or CPC (association sensu Daubenmire 1952) is an interpretation of the potential for successional development of the site. The existing communities of any area differ inherently in terms of their successional stage **and** their environment. Projecting such existing stands forward in time to a theoretical end point implies either projecting each individual community by itself or projecting a set of communities with similar environments. In either case, the climax community type concept implies a set of similar communities with similar environments that follows a repeatable or predictable successional pathway.

A classification of the climax communities of an area (e.g., Henderson et al. 1989), without its **environmental** context, means relatively little in terms of describing the community, its successional stages, and developmental potential or potential composition. We believe the link between the environment and the CPC has been implicitly acknowledged since the time of Daubenmire and Tuxen, and that it is appropriate to formally acknowledge the link between the environment and the nature of the CPC. The nature of the climax community is a function of the genetic diversity of the flora and its various and complicated interactions with the environment. It is continually changing over time as Earth's climate and air and water circulation patterns change. Therefore, the nature of the CPC is dynamic through time. A classification or model at one point in time can only describe the potential vegetation for the climate of the time.

The concept of potential natural vegetation used here refers to the set of communities, including all successional stages that can exist within the spatial and environmental bounds set by the extent of the CPC. The bounds of the CPC are controlled by the operational environment acting on the flora. The environmental bounds of a CPC type are the same as for all successional communities that may precede it, assuming the regional climate is stable. Therefore, PNV is identified or classified by the nature of the climax or projected climax community and is determined by the environment. This is not unlike some of the concepts embodied in the terms "habitat type" and "zone" (Daubenmire 1952, Daubenmire and Daubenmire 1968).

The Plant Association and Vegetation Zone

The plant association (i.e., the CPC type as used here) has been used as the basic unit of the PNV classifications for the Western United States (e.g., Brockway et al. 1983; Daubenmire 1952; Daubenmire and Daubenmire 1968; Diaz et al. 1997; Franklin et al. 1988; Henderson et al. 1989, 1992; Lillybridge et al. 1995; Topik et al. 1986; Williams and Lillybridge 1983). However, some authors (Daubenmire and Daubenmire 1968, Pfister and Arno 1980, Pfister et al. 1977) also used the concept "habitat-type" for the land area (mapping unit) where the plant association can develop (Daubenmire 1952, Daubenmire and Daubenmire 1968). Their emphasis on the land unit where a particular plant association occurs was used to emphasize the environment of the site. Plant associations can be aggregated into broader classification units of PNV called the vegetation series.

Daubenmire's [plant] association "is a concept embodying those characters of all actual stands among which differences in species composition are attributable to historic events or chance dissemination rather than to the inherent differences in environments" (Daubenmire 1952). In this somewhat convoluted definition, Daubenmire seems to try to establish the link not only between the climax community and the environment but to establish the current stand as part of the environmental potential of the site. It is not clear, however, if considerations of the breadth of environmental conditions within the range of an association, or the effects of factor compensation were included in his concept of (climax plant) association.

Daubenmire's "habitat type" linked the climax plant community (association) to the area of land where it can occur. By identifying the area of land where a single unit of the CPC type can occur, he explicitly linked the environment of that site to the developmental potential of the vegetation. Thus by extension, he appears to acknowledge the natural range in environments from one part of the habitat type to another. Other terms have been used to denote similar relationships such as the "range site" (Hironaka 1985), "site type" (Cajander 1926), or "ecological site" (Pellant et al. 2005, Smith et al. 1995). More recently, vegetation, soil, climate, and geology have been linked in a single ecological unit called the terrestrial ecological unit inventory (Winthers et al. 2005). Daubenmire (1952) also identified a broader unit of land he called the "zone," which he defined as the area occupied or potentially occupied by a closely related group of (climax plant) associations. The National Vegetation Classification system also used the term plant association, but there it referred to existing vegetation rather than potential vegetation (Jennings et al. 2003).

The VZ is the mapping unit of potential vegetation used in this paper. It approximates the area occupied by a vegetation series in scope and scale (as the terms are used in Daubenmire and Daubenmire 1968; Franklin and Dyrness 1973; Franklin et al. 1988; Henderson et al. 1989, 1992; Pfister et al. 1977) and is similar to the zone of Daubenmire (1952) and VZ of Franklin and Dyrness (1973). It is also similar in scope and ecological range to the "climax vegetation types" of Whittaker (1956) for the Great Smoky Mountains, and the 10 units of vegetation described and named by Whittaker and Niering (1965) for the Santa Catalina Mountains of Arizona. They variously described their 10 units of vegetation as vegetation types, zones, or coenoclines. The VZ is narrower in scope than the biotic communities of Brown et al. (1998) and Rehfeldt et al. (2006) or "potential vegetation type" of Ohmann et al. (2007).

The concept of the VZ used here is defined as "a unit of land where a single series or group of ecologically similar series predominates." The characteristic or "zonal" series

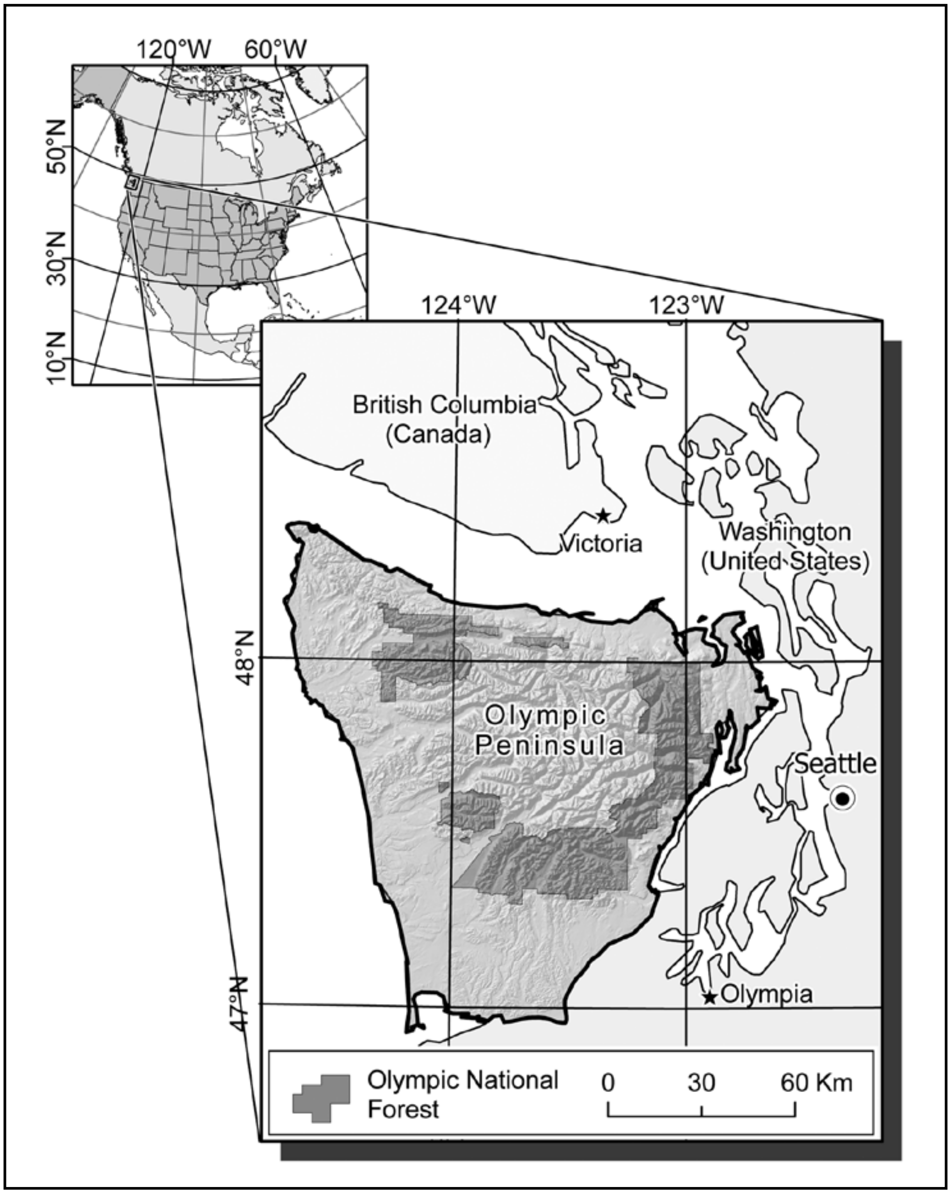

Figure 1—Location of the study area, the Olympic Peninsula, in western Washington state, USA. The area of the Olympic National Forest on the peninsula is shaded in darker gray.

(the taxonomic unit representing an aggregate of plant associations with the same climax indicator tree species) usually dominates within the broad geographic boundaries of a VZ, but azonal microsites may be occupied by vegetation of different physiognomic types and series. These sites usually represent the dry (e.g., a rock outcrop) or wet areas (e.g., a wetland) that could otherwise be seen as inclusions within the broad vegetation matrix characterized by a single series or small group of ecologically similar series. Subdivisions of the VZ are the plant association group (PAG) and the plant association (or habitat-type sensu Daubenmire).

An example of a VZ of ecologically similar but physiognomically different plant communities is the subalpine parkland zone. It is composed of tree-dominated series and several shrub- and herb-dominated series often in juxtaposition and forming a tightly integrated ecological system.

Land area above the upper limit of upright tree growth……..…………..ALPINE ZONE

Land area below alpine zone

Zonal vegetation nonforest and usually with scattered subalpine trees
or tree islands………………………SUBALPINE PARKLAND ZONE

Zonal vegetation forest (with scattered nonforest communities in very
wet or very dry habitats)

Zonal potential vegetation characterized by ≥ 10 percent cover of Sitka
spruce……………………..……...............……SITKA SPRUCE ZONE

Zonal potential vegetation characterized by ≥ 10 percent cover
mountain hemlock…………………..MOUNTAIN HEMLOCK ZONE

Zonal potential vegetation characterized by ≥ 10 percent cover
Pacific silver fir…………………………PACIFIC SILVER FIR ZONE

Zonal potential vegetation characterized by ≥ 10 percent cover western
hemlock and/or western redcedar..........WESTERN HEMLOCK ZONE

Zonal potential vegetation characterized by ≥ 10 percent cover
subalpine fir………………….……………SUBALPINE FIR ZONE

Zonal potential vegetation characterized by ≥ 10 percent cover
Douglas-fir……………………………….....DOUGLAS-FIR ZONE

Figure 2—Key to the eight potential vegetation zones on the Olympic Peninsula. This key works like a simple dichotomous key except that all the leads that would say "not as above" have been eliminated. Consider each pair of leads as in a normal dichotomous key, and read the lead as a question. If it is true, follow the lead to the right, if not, go to the next lead below it, and treat that line as a question, and so forth.

In a slightly different way, two or more very similar tree-dominated series can be aggregated into a single ecological VZ. An example of this is the western hemlock zone, which applies to areas where either the western hemlock series or the western redcedar series predominates.

There are eight VZs that occur on the Olympic Peninsula (fig. 1). These are identified in the key (fig. 2). These VZs are distinguished by the presence of key indicator tree species or certain community structural conditions related to dominant overstory species. This key is used to distinguish these eight VZs, and is based on a threshold of 10 percent cover of the indicator tree species for the potential vegetation. The basis for the 10 percent threshold is given below. Plant names for the tree species follow the taxonomy of Hitchcock and Cronquist (1973).

Gradient Analysis

The origin of gradient analysis of vegetation is from Whittaker (1956, 1967) and is based on the "individualistic" concept of Gleason (1926). Gradient analysis is the approach of relating gradients of plant populations and community characteristics to gradients of environment (Whittaker 1956: 63). It seeks to understand the structure and variation of the vegetation of a landscape in terms of gradients of environmental factors, species populations, and characteristics of communities (Whittaker 1967: 207). Gradient modeling is the mathematical process of evaluating the links between environmental gradients on a landscape and their effects on communities and organisms (Kessell 1979).

Various analysis techniques have been used in gradient analysis. Direct gradient analysis is usually applicable

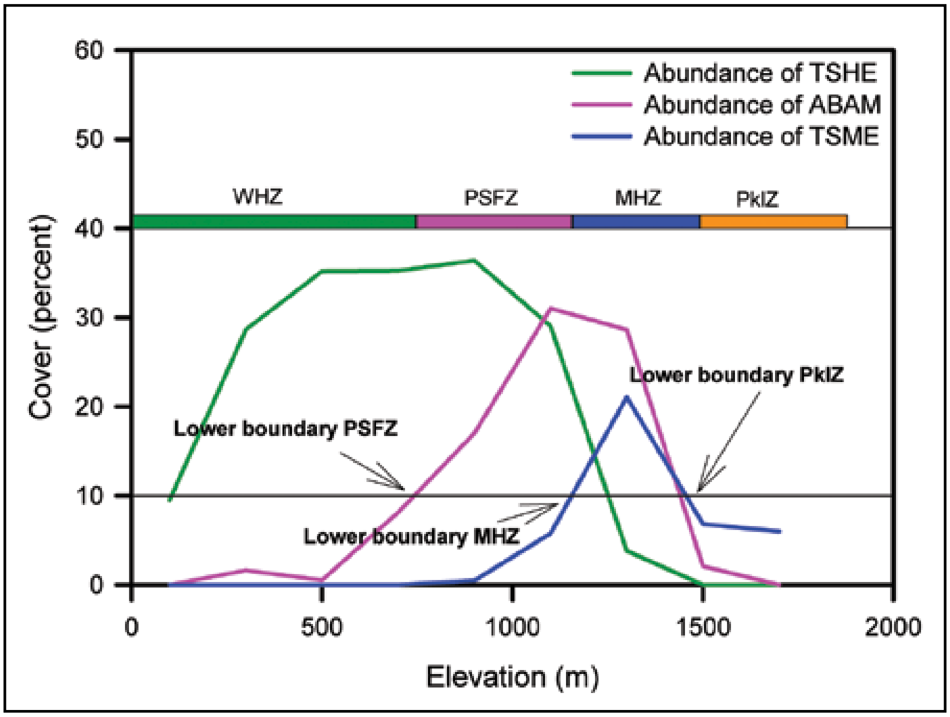

Figure 3—Distribution of key indicator tree species along the elevational gradient, with nodes separating different vegetation zones, from ecoplot data on the Olympic National Forest, Olympic Peninsula, Washington. Where "TSHE" is *Tsuga heterophylla* (western hemlock), "ABAM" is *Abies amabilis* (Pacific silver fir), "TSME" is *Tsuga mertensiana* (mountain hemlock), "WHZ" is western hemlock zone, "PSFZ" is Pacific silver fir zone, "MHZ" is mountain hemlock zone, and "PklZ" is subalpine parkland zone.

to patterns of individual species abundance along a simple or complex environmental gradient (ter Braak and Prentice 1994, Whittaker 1967). Sometimes the direct gradients are complex or geographical gradients such as "elevation" (Dymond and Johnson 2002; Lookingbill and Urban 2005; Oksanen and Minchin 2002; Whittaker 1956, 1960).

In this study, direct gradient analysis is reserved for processes that use or generate ordinations of species abundance or frequency along known or quantified environmental gradients (fig. 3). Indirect gradient analysis is used to refer to any analytical method whose objective is to uncover or elucidate an unknown environmental gradient. Factor analysis refers to those analytical techniques used to determine which factors are best correlated between a known set of environmental factors and some quality of vegetation. Ordinations may be used in direct or indirect gradient analysis (ter Braak and Prentice 1994). All four of these approaches were used in this study.

Mapping Considerations

One problem encountered while developing a pixel-based map of PNV is the resolution of scale. That is, transferring the scale of the field plots (fine) and classification (moderately fine) to a landscape (moderately coarse) via a model. Often the resolution of the types of vegetation on the ground is finer than the resolution of pixels (or polygons) used to portray them. Thus a single 90-m (0.81-ha) pixel can contain two or more fine-scale field plots of different community types or plant associations.

Maps based on pixels are restricted to representing patterns of vegetation that are groups of pixels; therefore, the spatial pattern represented is necessarily coarser than the size of the individual pixel and usually much coarser than the scale of the field plots. The size of a pixel is often a function of the technology being used and the constraints of computer hardware and software used to represent them. Quantifying map accuracy between field plots of one scale and a map of pixels of another scale is difficult, both conceptually and practically.

Another major challenge in developing a spatial model of PNV is having or developing appropriate mappable environmental variables that can be linked mathematically and conceptually to the dependent variable. Existing environmental variables have conventionally been those easily generated from weather stations or from digital elevation models (DEM) (Ohmann and Gregory 2002). Previous models have typically used aspect, slope steepness, elevation (as an independent variable), mean annual temperature (MAT), and total annual precipitation (in recent years) as quantitative variables, and slope position, soil, or geology have been used as qualitative variables.

Any mapping exercise must necessarily generalize the detail of a landscape. Some practical or thought model is usually employed to classify the mappable elements of the landscape and to link the mapping algorithm back to the land. In practice, it is difficult to account for the finer scale of all inclusions and mosaics of vegetation in a complex and variable landscape, thus resulting in a model and a representative map that is more general than the actual landscape.

Objectives

There were four objectives in this study: (1) create a map of VZs for the national forest land on the Olympic Peninsula, (2) create a map of VZs for the entire Olympic Peninsula, (3) find or develop a set of predictive and ecologically meaningful environmental variables, and (4) develop a predictive model of VZs using boundary equations and underlying environmental gradients. Development of a map of VZs of the Olympic National Forest required developing a spatially explicit model of VZs based on the available data while concurrently determining, finding, or developing the set of environmental variables to be used by the model. The model was then extrapolated to the entire Olympic Peninsula.

Study Area

The area of study is the Olympic Peninsula in Washington state, USA (fig. 1). It is bounded on the west by the Pacific Ocean, on the north by the Strait of Juan de Fuca, on the east by Hood Canal, and on the south by an approximate line running southwest from the southern tip of Hood Canal, to Grays Harbor and the Pacific Ocean. The Olympic Mountains form much of the interior of the peninsula, centered about 123° 45 min. W. long. and 47° 45 min. N. lat. At the center of the Olympic Mountains lies the Olympic National Park (380 418 ha), which is surrounded on most sides by the Olympic National Forest (254 961 ha) (fig. 1). These two federal ownerships make up the bulk of the mountainous terrain of the peninsula. The lowlands are mostly held by state and private owners, plus six Indian reservations. Total land area of the study area is 1 490 773 ha. The elevation ranges from sea level to 2427 m at Mount Olympus.

The Olympic Peninsula is known for its range of climates over a very short distance (Henderson et al. 1989, Peterson et al. 1997). Annual precipitation ranges from a total of 3353 mm at Quinault (western Olympics) to a low of 432 mm at Sequim (northeastern peninsula), a distance of only 88 km. The western Olympic Range is characterized by the wettest and most maritime climate in the conterminous United States. The dry northeast corner is the driest place in western Washington and is an unusual mix of continental and dry-maritime climates.

The Olympic Range is geologically young and immature, originating near the end of the Pliocene Epoch. It consists of a core of sedimentary rocks, which are surrounded on three sides by an outer ring of mostly marine volcanic basalts (Tabor 1975). Mountain building is ongoing and is the result of the collision of the Juan De Fuca and North American plates and erosion, mostly owing to the numerous Pleistocene ice ages. Glacially carved U-shaped valleys characterize most of the Olympic Peninsula with some “V”-shaped exceptions, especially in the south, indicating that recent glaciers were limited to the highest elevations and that water erosion has created much of the topography.

Vegetation is highly variable on the Olympic Peninsula owing to the strong maritime/rainshadow gradient from southwest to northeast and the rugged topography (Henderson et al. 1989). The Sitka spruce zone (SSZ) occurs at low elevations mostly along the Pacific coastline, where *Picea sitchensis* (Bong.) Carr. (Sitka spruce) and *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) dominate. Elsewhere, the western hemlock zone (WHZ) occurs at lower elevations where *Pseudotsuga menziesii* (Mirbel) Franco (Douglas-fir) and western hemlock dominate. *Thuja plicata* Donn (western redcedar) may occur as an occasional species or codominant at low to mid elevations. The Pacific silver fir zone (PSFZ) occupies mid elevations, where western hemlock and *Abies amabilis* (Dougl.) Forbes (Pacific silver fir) usually codominate, along with small amounts of western redcedar and, occasionally, Douglas-fir as a long-persistent seral species. The mountain hemlock zone (MHZ) occurs at higher elevations, where Pacific silver fir and *Tsuga mertensiana* (Bong.) Carr. (mountain hemlock) codominate. *Chamaecyparis nootkatensis* (D. Don) Spach (Alaska yellow-cedar) occurs infrequently at mid to high elevations. The subalpine fir zone (SAFZ) occurs at higher elevations in the drier areas of the northeast Olympics where *Abies lasiocarpa* (Hook.) Nutt. (subalpine fir) dominates. The Douglas-fir zone (DFZ) also occurs to a limited extent in the northeast Olympics, at low to mid elevations and on southerly and drier topographic positions. Here Douglas-fir is the dominant climax species, and the environment is too dry for western hemlock or western redcedar. At upper elevations, the forest zones give way to the subalpine parkland zone (PKIZ) composed of tree islands and subalpine meadows at about 1067 m in the west and at elevations over 1524 m in the northeast part of the peninsula. Small areas of alpine zone occur at the highest elevations.

Methods and Analysis

Field Methods

Four types of field data were used to develop and validate the VZ model presented here. The first type is the "ecoplot" data collected as part of the U.S. Forest Service (USFS) Region 6 Ecology Program (Henderson et al. 1989, Henderson et al., unpublished data). Data collected on these fixed-area plots included, but were not limited to (1) location, (2) elevation, (3) direction of the sloping land (i.e., aspect), (4) steepness of the sloping land (slope), (5) topographic moisture (Henderson et al. 1989, 1992; Whittaker 1956, 1960; Whittaker and Niering 1965), (6) identity of each vascular plant species according to Hitchcock and Cronquist (1973) plus a measure of their individual cover, (7) plant association (Henderson et al. 1989), vegetation series, and vegetation zone. A total of 1,497 ecoplots were used in this study; these plots were well distributed in different watersheds and represent a wide range of ecological conditions on the Olympic National Forest. The locations of many of these plots were randomized near the center of accessible General Land Office sections (square miles) of land. This was the primary data set used to build the VZ model.

The second type of plot data used was a set of 447 check plots collected along road transects throughout the Olympic Peninsula. These plots occurred on all types of ownerships where access was available or where permission to enter was granted by the owner or administrator. Data on these plots included (1) location by Rockwell[1] "PLGR" global positioning system (GPS), (2) elevation, and (3) VZ. Other data were extracted by intersecting the GPS location (if local error was less than 10 m) with GIS grids of topographic or environmental variables. These plots were used in model building to extend the ground-truthed part of the map to areas not previously sampled, including extensive areas of private or state-owned lands.

A third type of plot data used for model building was field plots (n = 1,051) contributed by the Olympic National Park (ONP). These data are represented by three sets called "ONP-Elwha" (n = 63) (A. Woodward, U.S. Geological Survey [USGS], unpublished data), "ONP Animals" (n = 431) (K. Jenkins, USGS, unpublished data), and "Hoh/Dosewallips 1979" (n = 557) (J.A. Henderson and B.G. Smith, ONP, unpublished data). These field plots were taken using various field protocols from 1978 to 2002. Plot locations were extracted from field data, maps, or aerial photos. Vegetation zone identifications were done by National Park Service personnel or contractors and checked by the authors. The protocol used for the "Hoh/Dosewallips 1979" data set was similar to the field protocol used in the USFS ecoplots described above.

[1] The use of trade or firm names is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

A fourth set of independent plots was used to validate the final model. These plots were a subset of USFS Current Vegetation Survey (CVS) plots (n = 84) (USDA 1998) and Forest Inventory and Analysis (FIA) plots (n = 71) (Campbell et al. 2010). These systematically distributed permanent plots are maintained across federal, state, and private ownerships for the purposes of periodic national timber inventory mandated by Congress in the Forest and Rangeland Renewable Resources Planning Act (RPA) of 1974. These plots were first screened for accuracy of GPS location and then assigned to a vegetation zone. Those plots with field collected data sufficient for reliable placement into a VZ were then used as an independent validation sample to determine the accuracy of the final version of the VZ map of the Olympic Peninsula.

To summarize, the set of USFS ecoplots (n = 1,497) was used for model building and environmental variable identification. The check plots (n = 447) and ONP plots (n = 1,051) were used to extrapolate the model to non-national-forest lands. Two independent data sets were used for model validation, the CVS plots on national forest land (n = 84), and FIA plots on non-national-forest lands (n = 71). The total number of field plots used in this study was 3,150.

Analysis and Model Building

Overview of model building—

This study was done in three parts. Each part represented a different approach with different objectives. Part one set the broad environmental gradient context and identified the boundary nodes between the VZs (figs. 2 and 3). Part two was the development of the new environmental variables and adaptation of existing variables used in the model. Part three was the development of the boundary equations between adjacent pairs of VZs.

Part one consisted of extensive field survey and classification of climax community types (associations sensu Daubenmire) (Henderson et al. 1989). It also used a direct gradient analysis of the tree component of the climax vegetation to help define boundaries between VZs of the Olympic National Forest (fig. 3), and was later expanded to the Olympic Peninsula (fig. 1). In these initial stages, tree cover measured on the 1,497 ecoplots was summarized by elevation classes from sea level to the highest peaks (2126 m). This broad averaging of tree cover (fig. 3) over such a wide range of moisture and temperature gradients necessarily obscured some of the range in environmental conditions across the Olympic National Forest. Similar graphs were also done for different geographic areas, and for different precipitation and temperature regimes, here defined. Each revealed different patterns of tree cover distribution and elevation. However, for presentation, only the general form is given, as it represents the conceptual basis for determining the boundaries of the VZs.

The nodes identified along this complex gradient were used to identify the boundaries between different VZs in the study area (fig. 3). For most boundaries, potential presence of 10 percent cover of the indicator tree species at its warmer or drier boundary indicated the lower elevational boundary of the zone (Henderson et al. 1989). Exceptions to this are that vegetation physiognomy was used to distinguish between the upper forest boundary and the subalpine parkland zone, and tree form was used to distinguish between the subalpine parkland and alpine zones (fig. 2). Ten percent cover is understood to be an ecologically meaningful abundance threshold for zonal sites in the landscape. Below 10 percent cover, the distribution of indicator tree species is sporadic and they tend to occur in azonal microsites. These nodes fixed the boundary between any two vegetation zones in real space as well as in environmental hyperspace, for any given combination of model variables.

Once these nodes were established, they were used to assign VZ codes to each sample plot in the study. Because this required interpretation of the stand age and structure to determine whether at least 10 percent cover of the indicator tree species was present or potentially present in late-successional development, some knowledge of the tree species and the environments of the area was needed. For forest communities older than 300 years, the actual covers of late-successional tree species were used to represent the climax condition. Most plots were easily placed into one of the vegetation zones. A few plots were clearly transitional, and were assigned on best judgment, but some error was probably created at this time. A few plots, often because of their young age, could not be reliably assigned to a VZ, so they were omitted from further analysis. Plots with stand ages less than 10 years were not used.

Part two was the development of a set of environmental variables used to predict the VZ boundaries. Once the first variable was identified, the examination of residual errors led to the discovery of better or additional environmental variables. This was a complex process, but was initiated when the use of existing environmental variables and methods did not provide the means to adequately describe the pattern of VZs on the landscape or give the ecological understanding of the underlying causes of the distribution of vegetation. These variables included several environmental indices defined later in this paper including precipitation at sea level (PSL), mean annual temperature at sea level (MATSL), fog effect, topographic moisture (TM), and cold air drainage (CAD) effect. At that time, data sets to serve this purpose were not available at a resolution adequate for the study objectives (e.g., Daly et al. 2002, Hungerford et al. 1989).

Part three was the development of the boundary equations. We used graphical analysis of sets of plots from adjacent pairs of VZs to estimate the mathematical boundary between each such pair of VZs (fig. 4). The boundary line between the upper boundary of one VZ and the lower boundary of another was determined by the fit of an equation to achieve approximately equal numbers of errors above and below the line with a minimum of total errors.

This iterative process of analysis was repeated at each step in the uncovering of each new environmental variable. Thus part two and part three were used iteratively to evaluate and develop each variable.

These three parts culminated in a map of vegetation zones. Converting the mathematical equations to a spatial model began in the early 1980s by manually mapping the VZs in the field using topographic maps and field data. With the development of technology over subsequent years, this mapping process developed into a complex GIS computer application (the PNV Model) programmed in Arc macro language and processed in the Arc/Info Grid program (ESRI 1982–2006).

Definition and development of the model variables—

Precipitation at sea level—

Precipitation at sea level is a new variable presented here. It represents a precipitation regime for the landscape and is defined as the relative precipitation for an area with the direct effects of elevation removed, and is portrayed at the base elevation of “sea level.” Precipitation varies greatly over the Olympic Peninsula and is not the same at a given elevation, as was observed when contrasting the southwest and the northeast parts of the peninsula. However, where PSL is the same, precipitation will be the same at a particular elevation throughout that area. Precipitation at sea level values describe proportionately how much more or less precipitation can be expected across a landscape or geographical area. Thus the pattern of **total** precipitation can be described as two vectors: (1) the vertical, related to elevation and (2) the horizontal described by the pattern of PSL. It is, therefore possible to calculate actual precipitation at any point on the landscape by knowing its PSL and elevation as will be shown later.

Precipitation at sea level can be regarded as an index of relative precipitation potential, similar to how forest stand growth is often indexed by the projected height of dominant and codominant trees at a base age, i.e., the “site index.” Developing an index that allowed the spatial representation of the relationship of precipitation to a base elevation (i.e., sea level) was a breakthrough that greatly facilitated the modeling of potential vegetation over the landscape. Because the model identified elevations of the boundary between VZs, it was critical to identify areas where the relationship of precipitation to elevation remained constant. The development of PSL involved a series of successive iterations, and provided insight into both the necessity for and the utility of this variable.

The history of the development of the PSL variable began in 1982 with the initial attempt to field map the VZs. This process began with analysis to map the boundary between the western hemlock zone and the Pacific silver fir zone. These two zones were represented by the greatest amount of data and covered the greatest area across the Olympic National Forest.

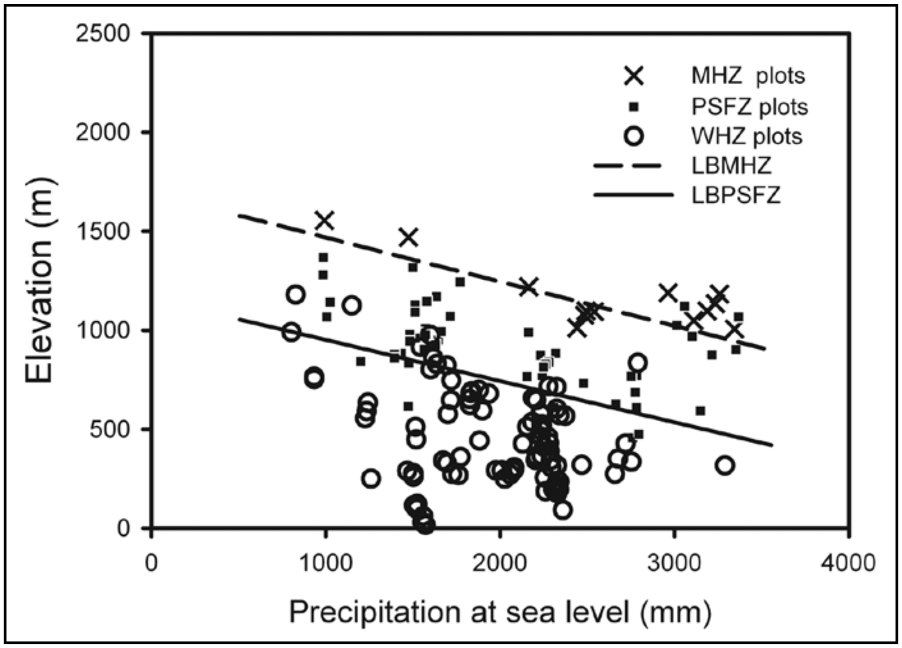

Figure 4—Vegetation zone plots displayed by elevation and precipitation at sea level, with boundary equation lines for lower boundary Pacific silver fir zone and lower boundary mountain hemlock zone. Where "MHZ" is mountain hemlock zone, "PSFZ" is Pacific silver fir zone, "WHZ" is western hemlock zone, "LBMHZ" is lower boundary mountain hemlock zone, and "LBPSFZ" is lower boundary Pacific silver fir zone.

Charts were first developed to depict the aspect/elevation patterns of the lower boundary Pacific silver fir zone (LBPSFZ) from one geographical area to another across the Olympic National Forest. For this effort, soil temperature measurements recorded on USFS ecoplots were used to estimate the magnitude of elevation effect from northerly to southerly aspects. This analysis showed a change from north to south aspect at the lower boundary of the PSFZ equivalent to a change of about 200 m elevation (Henderson et al. 1989). Also, it indicated that the greatest effect was at aspects of about 30 degrees (where the LBPSFZ was about 100 m lower) and at 210 degrees (where the LBPSFZ was about 100 m higher elevation). Initially, sample plots from a local area in the South Fork Skokomish River watershed (southeast Olympics) were plotted on a simple graph with aspect on the x axis and elevation as the y axis (fig. 5A). A sine function was fit to represent the lower boundary of the PSFZ and the upper boundary of the WHZ. A similar curve was fit to the PSFZ/MHZ boundary.

The relationship represented by the curves in this graph (fig. 5A) was applied to the South Fork Skokomish watershed by hand-drawing the lower boundary of the PSFZ on USGS topographic maps. It correlated well with the vegetation pattern observed in the field. However, when these curves were used to make a similar map for the Wynoochee watershed to the west (toward the Pacific Ocean), the relationship was weak. In this case, the predicted LBPSFZ (curves from fig. 5A) was too high in elevation to fit the data (fig. 5B). The residual errors between the predicted function and the actual elevation of the LBPSFZ were computed and the boundary curves were recalculated. Similarly, when nearby watersheds (North Fork Skokomish and Hamma Hamma) were examined to the northeast, the original function (fig. 5A) predicted a boundary that was too low compared to the data in fig. 5C. Figures 5B and 5C show the new lower boundary lines for PSFZ and MHZ that fit the data for these two geographic areas. Note the difference between the boundary curves from fig. 5A compared to the boundary curves in fig. 5B (wetter area) and fig. 5C (drier area).

This trend was noted across the entire Olympic Peninsula. It was not known at the time which environmental factor(s) was causing the aspect/elevation shift. This did not

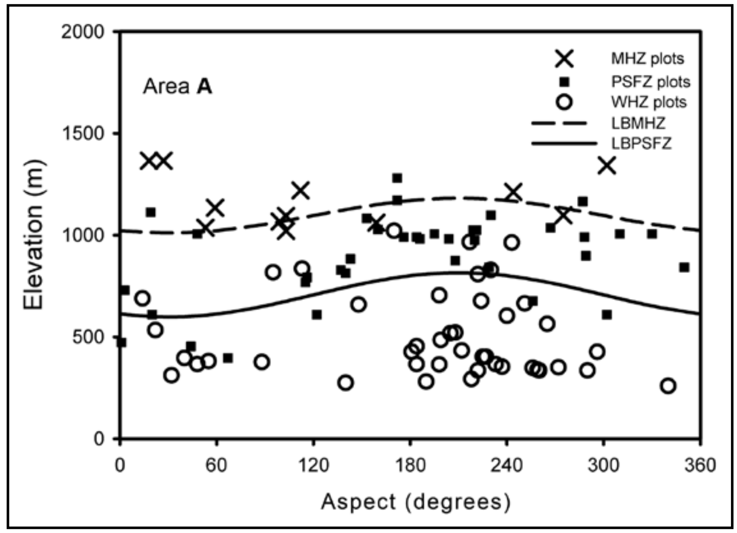

Figure 5A

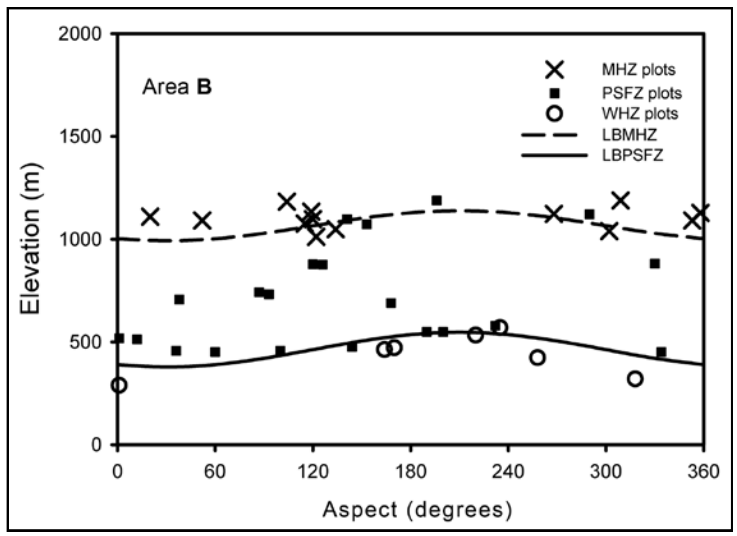

Figure 5B

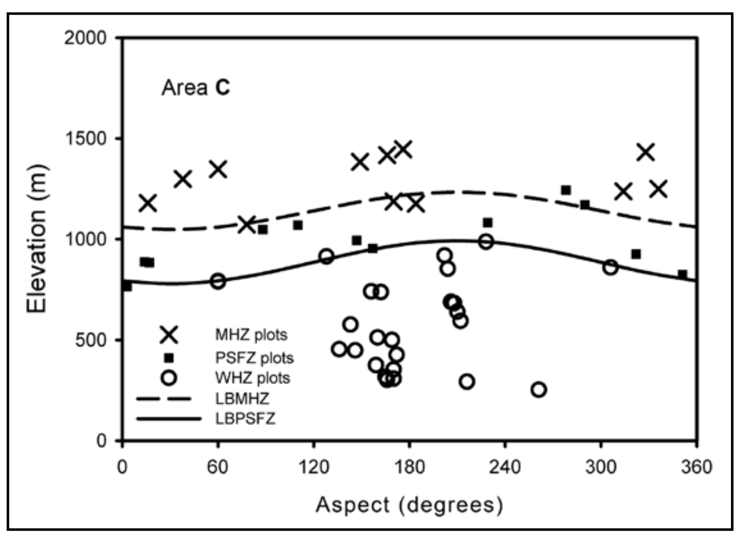

Figure 5C

Figure 5—Vegetation zone plots displayed for three small geographic areas in the southern Olympic Mountains, with boundary curves between vegetation zones. “MHZ”is mountain hemlock zone, “PSFZ” is Pacific silver fir zone, “WHZ” is western hemlock zone, “LBMHZ” is lower boundary mountain hemlock zone, and “LBPSFZ” is lower boundary Pacific silver fir zone. Area of graph 5A (South Fork Skokomish watershed) has average precipitation at sea level (PSL) of 2413 mm and mean annual temperature at sea level (MATSL) of 11.0 °C. Graph 5B is for an area west (Wynoochee watershed) of graph 5A, with average PSL 2896 mm and MATSL 10.8 °C. Graph 5C is for an area northeast (North Fork Skokomish and Hamma Hamma watersheds) of graph 5A, with average PSL 1753 mm, and MATSL 11.2 °C.

prevent the empirical and systematic field mapping of the LBPSFZ across the Olympic National Forest. This serpentine boundary line traversed the area, up and down in elevation in response to many, as yet unknown environmental factors. It was lower in areas with wetter soils, higher precipitation, north aspects, concave slopes, colder areas, or in valleys with cold air accumulations.

Areas where the LBPSFZ was located at the same arbitrary elevation were defined as "environmental zones" (Henderson et al. 1989: 40, fig. 24). These zones represented geographical areas where the environment was judged to be similar and were originally identified by codes from zero to 12 where each zone is represented by the increase in elevation of the LBPSFZ of about 80 m. These geographical areas were used to analyze the upper boundary of the PSFZ and to define curves for it. Similarly upper and lower boundary "aspect/elevation" functions were defined for each boundary in the area. This tool was used to make the first preliminary map of vegetation zones for the area (Henderson et al. 1989: 45, fig. 25).

The correlation between the "environmental zones" and the existing precipitation map for the peninsula (Henderson et al. 1989: 35, fig. 18) was obvious. However, evaluation of apparent differences along the coast and other discrepancies inland suggested that other variables were also driving these "environmental zones" besides total annual precipitation. Some evidence pointed to an interaction between precipitation and elevation, other evidence pointed to an interaction with fog or some other maritime factor.

A number of transformations of the precipitation data were attempted to fit a better function between VZ boundaries and environmental zones. The relationship was somewhat obscured, partly because of the small number of weather stations on the peninsula and their aggregation at low elevation near saltwater. It was not until a similar study was done in the North Cascade mountains of Washington that the relationship between precipitation and elevation (to be called "precipitation at sea level") was formalized.

The new variable "precipitation at sea level" (PSL) was generated by graphing the measured annual precipitation at weather stations against the elevation. At first, a single linear regression was fit to each of a number of sets of nearby weather stations across western Washington. Linear functions were used initially until it became apparent that a quadratic function would better fit the weather station data of precipitation relative to elevation. As there were few stations at higher elevations, this trend could not be established with any certainty. However, it was assumed that the rate of precipitation increase gradually decreased with elevation approaching an asymptote at the elevation of the highest ridges, and then declining slightly as air thinned with increasing altitude, as represented in equation 1. From this analysis, a single equation was generated to project the measured annual precipitation at each weather station back to an elevation equal to zero (eqn. 1):

$$TAP = PSL + (A + B \times PSL) \times ELEV + (C + D \times PSL) \times ELEV^{2} \quad (1)$$

Where
TAP = total annual precipitation (mm)
PSL = precipitation at sea level (mm)
A = 3.07916667E-02
B = 5.18339895E-04
C = - 5.17648321E-06
D = -7.19779665E-08
ELEV = elevation in meters

Although PSL was originally solved graphically with a set of curves using equation 1 with different intercept values, it can be solved directly using equation 2. Equation 1 was rewritten as follows (eqn. 2) to predict PSL for each weather station:

$$PSL = 1 / \{M+N / TAP + [1 / (P+Q \times TAP)] \times ELEV + [1 / (R+S \times TAP)] \times ELEV^{2}\} \quad (2)$$

Where
PSL = precipitation at sea level (mm)
M = 3.14066E-07
N = 0.99908387
P = -139015.01
Q = 1922.4891
R = 561677190
S = -13825146
TAP = total annual precipitation (mm)
ELEV = elevation in meters

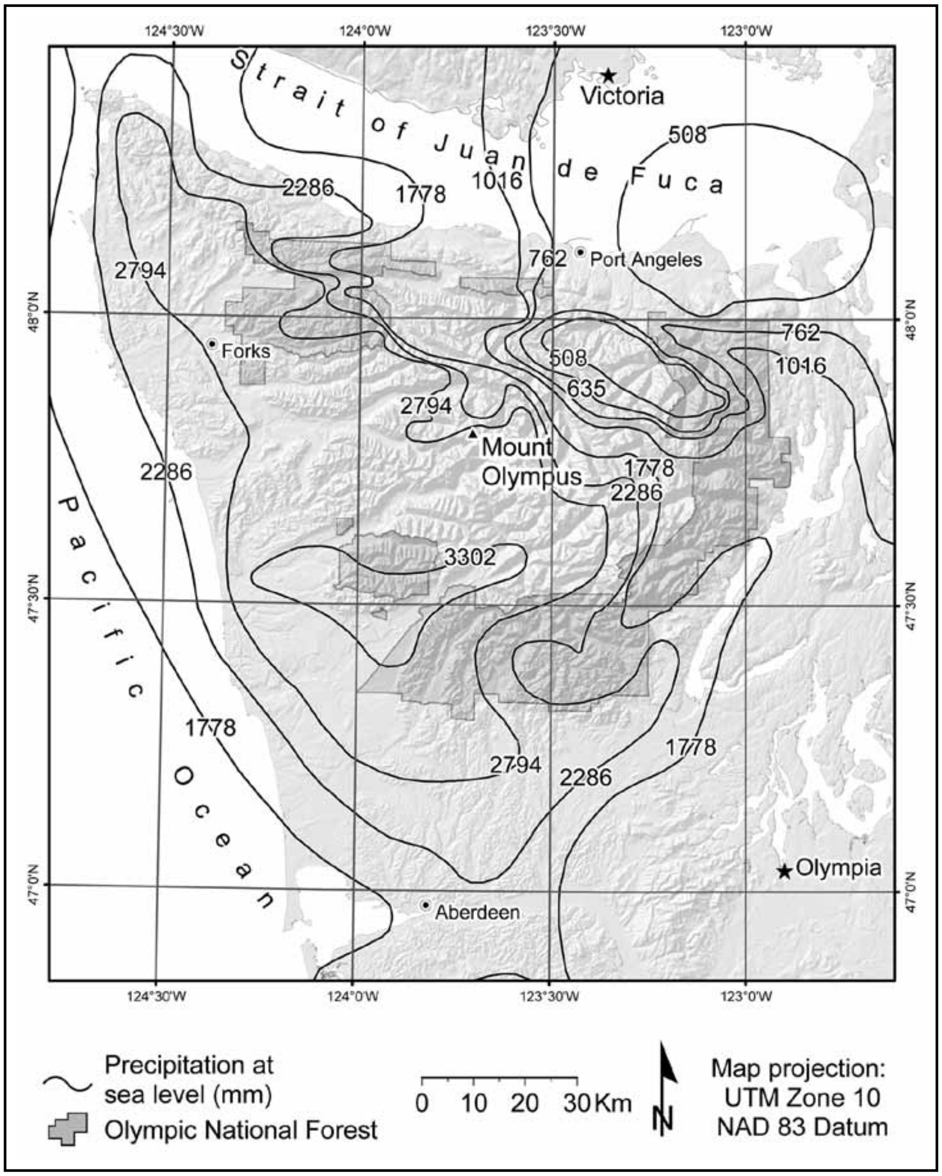

Figure 6—Precipitation at sea level (PSL) for the Olympic Peninsula. Contour lines represent PSL in millimeters. PSL values for each pixel in the study area were derived by triangulation on these curves.

These PSL values for each weather station on the Olympic Peninsula were calculated and plotted on a map and interpolated to generate an isoline map of PSL (fig. 6). Precipitation at sea level values for each pixel in the study area were derived by triangulation on these isolines. This map of PSL was later substituted for "environmental zones" and became the basis for the VZ model. However, the original pattern of environmental zones was retained as the starting point for drawing the PSL lines. Later as this analysis was extended throughout the states of Washington and Oregon, the PSL isolines were refined.

The PSL isolines were then calibrated so that the model correctly predicted the average total annual precipitation for each station to less than 1.0 percent error and the sum of deviations was zero. Later a topographic/geographic analysis was done to determine on-shore flow and rain-shadow patterns. This was used to refine the original coarse pattern of PSL lines to better reflect the effects of topography and geography on the flow of clouds, storms, fog, and rain across and around the Olympic Peninsula (fig. 6).

Once the environmental variable of PSL was developed, and the base model with elevation of the VZ boundary as the dependent variable and PSL as the independent variable was derived, the next step was to evaluate the residual errors of VZ prediction both mathematically and spatially to generate patterns of deviation. This was followed by hypothesizing and exploring possible environmental/ecological relationships in the landscape that could account for these errors. The successful development and application of the PSL concept led to the exploration of the idea that other new environmental variables related to the patterns of distribution of PNV could be developed and incorporated into the PNV Model application.

The next step in the process started by evaluating a relationship borrowed from Whittaker (1956) called "topographic moisture," and its effect on the distribution of the PSFZ and later all VZs. Eventually four new variables in addition to PSL (topographic moisture, fog effect, MATSL cold air drainage effect), plus an adaptation of potential shortwave solar radiation (Kumar et al. 1997) were evaluated and added to the model.

Topographic moisture—

This is a quantification of the "topographic moisture gradient" concept of Whittaker (1956, 1967, Whittaker and Neiring 1965). Whittaker (1967: 218) presented species data along a scale from 1 to 13 representing "mesic to xeric" conditions, but without otherwise quantifying the gradient. Whittaker noted that the units of the scale were groups determined by ordination.

Conceptually, the topographic moisture (TM) variable as used here is this: as soil water moves downslope under the influence of gravity, it tends to move faster on steeper and more convex slopes and slow down or accumulate on gentle and concave slopes. This TM index is intended to scale the relative hillslope drainage (e.g., Beven and Kirkby 1979). Therefore in areas with higher TM values, there is potentially more soil water availability (soil texture and other impediments being otherwise equal), and in areas with lower TM values, there is the topographic potential for less available water. In contrast to Whittaker's (1956, 1967) use, TM as used here does not include effects of soil texture or aspect. Also it does not take into account potential subsurface waterflow at bedrock surface or at textural discontinuities in the soil or seeps or springs, as these features are mostly unmapped in the study area.

For the present study, a scale of values from 1 to 9 was developed to represent the range of topographic moisture potentials for the landscape. The values ranged from 1 (absolute driest topographic condition) to 9 (absolute wettest topographic position, i.e., open body of water), where the value of 5.0 represents the modal topographic moisture value for the landscape. These values were assigned to sample plots in the field (ecoplots) (Henderson et al. 1989) to use in calibrating the effect of this variable on the lower boundary of the PSFZ in western Washington.

A landscape model was constructed to predict the topographic moisture value for pixels in the landscape. This algorithm used the "CURVATURE" function in the Grid Module of Arc Info Workstation (ESRI 1982–2006) plus adjustments for steepness of slope. These values were averaged to windows of 270 m and 900 m radius, to compute TM for the Olympic Peninsula. These two windows were set to reflect meso-topography at the local ridge scale and the broader scale of major ridges.

Fog effect—

The nature of the vegetation along the western peninsula indicated that the vegetation appeared to be responding to a wetter environment than was represented by precipitation alone (fig. 6) (Henderson et al. 1989: 35, fig. 18). Davis (1966) had suggested a relationship between spruce forests and coastal fog effects in Maine. A new effect, resembling the fog patterns presented by Stone (1936) or Vogelmann et al. (1968) was developed to reflect this "fog" effect on vegetation. Weather satellite images and field reconnaissance further indicated that some maritime effect appeared to contribute a surrogate of precipitation or to enhance the precipitation effect in this area. Isolines of fog effect along the coast of Washington and Oregon were drawn to reflect both cloudiness and the presumed effect of fog and dew on vegetation (fig. 7). Later, through direct observations and

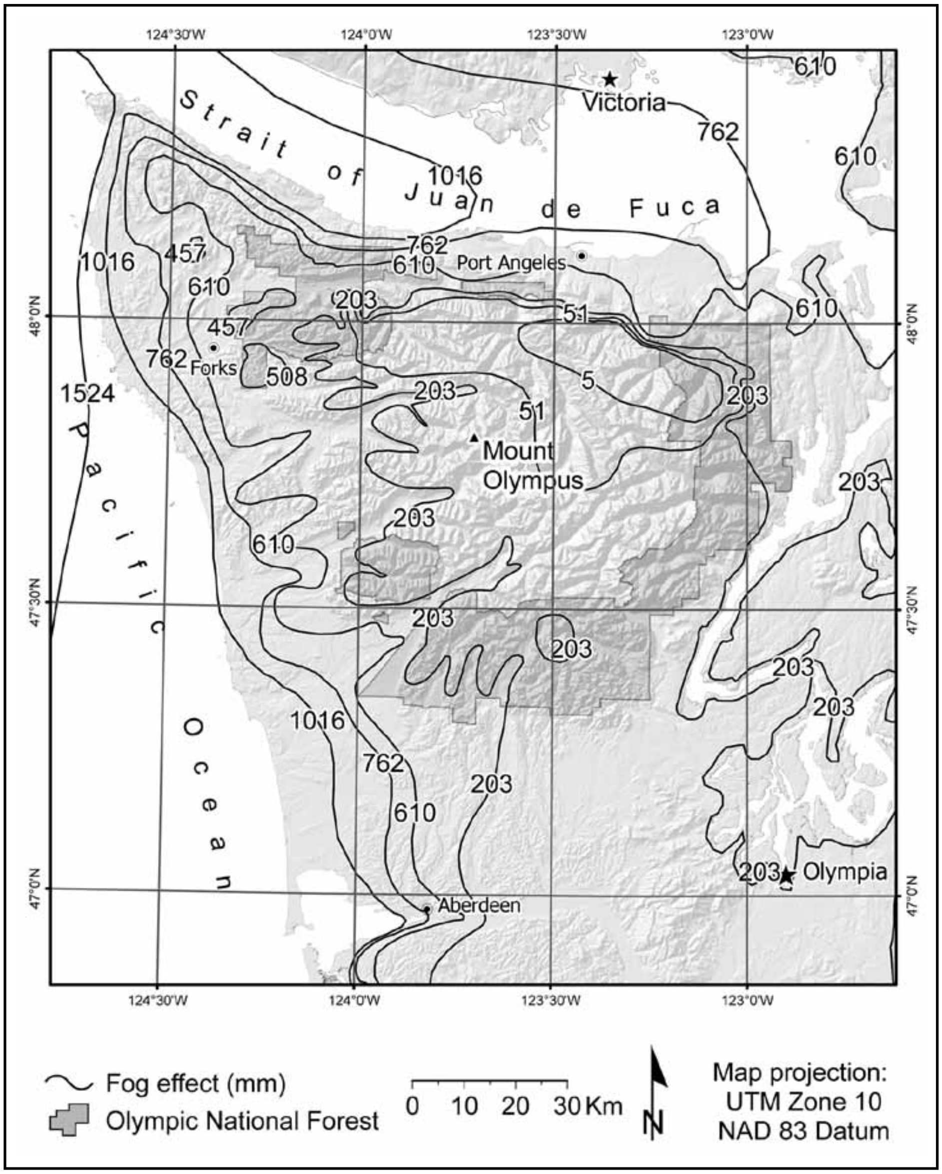

Figure 7—Fog effect for the Olympic Peninsula. Contour lines represent fog effect in millimeters equivalent of precipitation. Fog effect values for each pixel in the study area were derived by triangulation on these curves.

identification of topographic barriers, this map was refined further to reflect actual fog and low cloud penetration onto the land. This fog effect was weighted to reflect the average value of effective precipitation added to the site by fog drip; a number suggested by several studies in coastal California and Oregon. For this study we used a weighting of 508 mm of effective precipitation for one unit of fog effect. Azevedo and Morgan (1974) found up to 425 mm of summer fog drip in coastal redwood (*Sequoia sempervirens* (D. Don) Endl.) forests in an area with an undisclosed amount of summer precipitation. Oberlander (1956) measured 1524 mm of fog drip under an exposed tanoak (*Lithocarpus densiflorus* (Hook. & Arn.) Rehder), and Dawson (1998) measured 447 mm of annual fog drip in coastal redwood forests with annual precipitation of 1315 mm; fog drip amounted to 34 percent of the annual precipitation. Harr (1982) found 914 mm of fog drip in the Bull Run Watershed in the northern Oregon Cascades. Values of fog effect ranged up to 1524 mm in

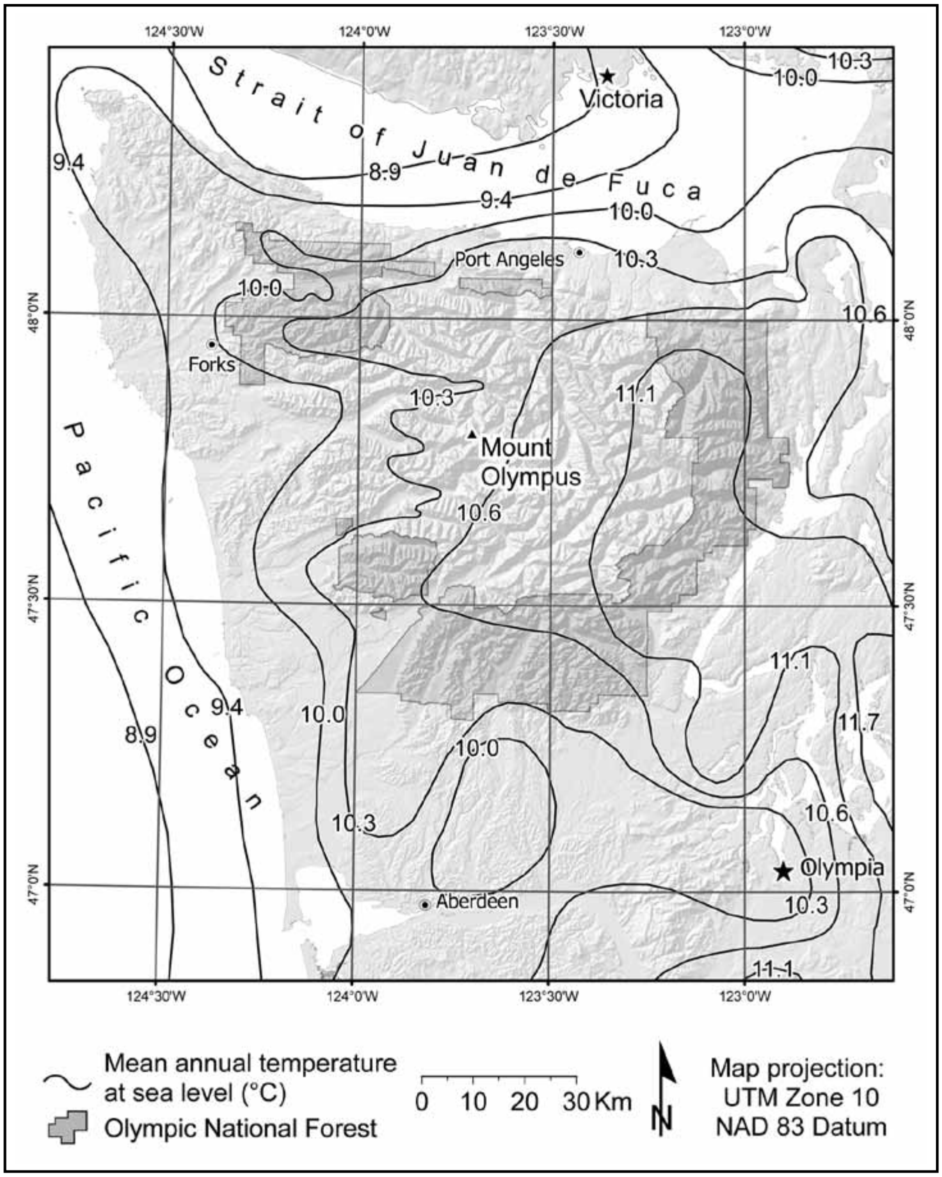

Figure 8—Mean annual temperature at sea level (MATSL) for the Olympic Peninsula. Contour lines represent MATSL in degrees C. The MATSL values for each pixel in the study area were derived by triangulation on these curves.

some areas on the Pacific Ocean side of the peninsula to less than zero in the extreme rain-shadow areas of the northeast peninsula. Although this effect was correlated with fog, the ecological effects are perceived to be more complex, involving dew, condensation on leaves, stem flow, tree drip, etc.

Mean annual temperature at sea level—
Mean annual temperature at sea level was constructed using the same approach and similar concept as for PSL. It is a new variable presented here that represents the temperature regime for a landscape, and is presented as an index of MAT at a base elevation of sea level (fig. 8). Linear regressions were done on weather station MAT and elevation using data from sets of proximal stations across northwestern Washington. The slope of these lines is the "temperature lapse rate" variable (fig. 9). The slopes of these lines were used to project the MAT of each weather station down to a base elevation of sea level. A digital data set of MATSL (fig. 8)

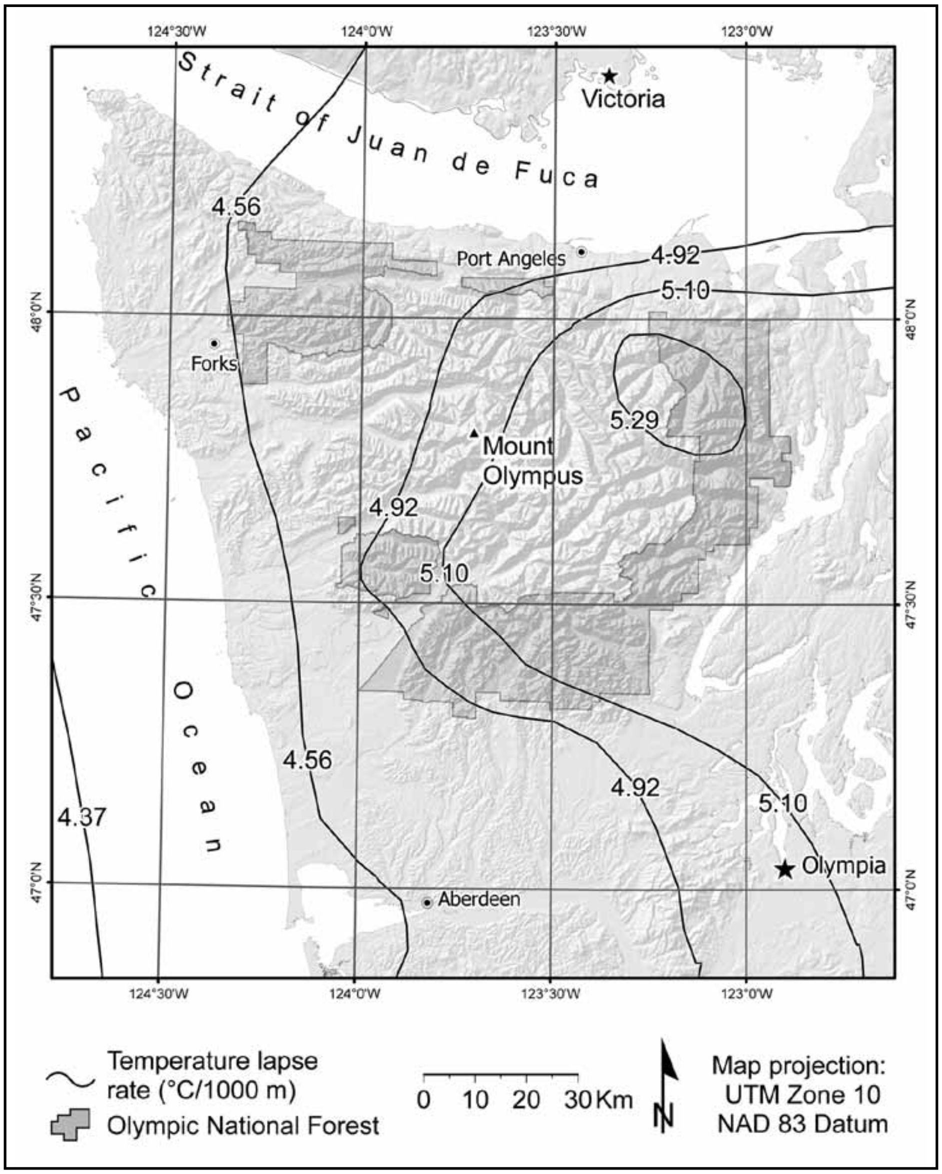

Figure 9—Temperature lapse rate for the Olympic Peninsula. Contour lines represent the rate at which temperature declines per 1000 m elevation in degrees C. Lapse rate values for each pixel in the study area were derived by triangulation on these curves.

was then generated using similar procedures as for PSL. Later the map of MATSL was calibrated using data from eight remote weather stations for the Olympic National Forest.

Cold air drainage effect—

The cold air drainage (CAD) effect model used an algorithm to calculate a MAT value for each pixel in the landscape, using MATSL, elevation, lapse rate, and aspect. The aspect effect was eventually adjusted by adding the effects of short-wave (SW) solar radiation to the model. Conceptually, cold air at night, in winter, and in still air accumulates in concave areas represented in the digital terrain model. A proxy for air density was developed using modeled MAT in a cold-air flow model. This proxy variable was called "temperature units" and was calculated as the maximum MAT for the study area plus 1.1 °C less the calculated MAT of each pixel.

ArcInfo's "FLOWACCUMULATION" function (ESRI 1982–2006) was used to identify potential cold air drainage channels across the landscape. The flow accumulation module in ArcInfo Workstation was used to determine the flow direction and flow accumulation following the natural flow patterns across a landscape. This process is described by Jenson and Domingue (1988) and Chung et al. (2006). It results in the sum of the number of pixels that are calculated to be above the target pixel and to be within its direct flow pathway as determined by relative elevation and aspect. By repeating this for each pixel in the landscape, the model calculates the "flow-accumulated" sum of pixels for each pixel in the landscape. This resulting grid contained higher values where there was greater potential for cold air accumulation. Therefore the value being accumulated through the "FLOWACCUMULATION" function was related to the density of air and the accumulation of high CAD effect values in areas in cold air drainages and cold air lakes. Thus the CAD model reflected the downward convective movement and accumulation of denser and colder air.

The flow accumulation was then modified by a diffusion function that applied a series of "FOCALMEAN" (ESRI 1982–2006) functions to "spread" the accumulated "temperature units" across increasing circles of influence dependent on the topography. The more open and flat a terrain, the more the flow accumulation is spread out among adjacent pixels. This final grid of accumulated temperature units (ATU) was then compared to the measured change in elevation of selected VZ indicator species in a sample of locations across the state of Washington. A calibration was made for the elevational change of indicator species and areas of high cold air accumulation where elevation shift owing to CAD is a function of ATU. The downward shift in VZ indicator species was calibrated to the ATU and a set of curves was developed where ATU and PSL were independent variables and elevation change expressed in meters for each VZ was the dependent variable. After repeated experiments in calibrating this function to the landscape, a final model was achieved. The output of the cold air drainage effect model was the estimated lowering of temperature in CAD accumulation areas expressed in terms of units of elevation effect on vegetation (fig. 10). A further calibration was made to calculate absolute temperature change (in degrees Celsius) relative to this predicted elevation change effect.

Shortwave solar radiation—

The effects of potential radiation load for each pixel in a landscape owing to the angle of incidence and topographic blocking of solar radiation was used to supplement the role of aspect as a variable in the model. Although aspect as a predictor was adequate for mid-slope VZs and in mountainous terrain, for areas on ridgetops, in valley bottoms, and in broad gentle terrain it did not perform well.

The solar radiation model of Kumar et al. (1997) was used to predict radiation for the area and was incorporated into the VZ model in combination with aspect. The final version of the VZ model includes a function for "aspect effect" that is:

aspect effect = $P \times f\,(\text{aspect}) + (1 - P) \times [(SW - 14930) / 3380.4]$

Where

shortwave (SW) solar radiation in watts per square meter is transformed to units of aspect by the subfunction (SW - 14930) / 3380.4 and where P and 1 - P are the proportions of the total aspect effect distributed between the variables aspect and SW. Thus a P of 0.5 would weight the direct effect of aspect equally with the transformed effect of solar radiation. This function is a complex variable that combines the effect of solar radiation and aspect by transforming solar radiation to units of aspect effect and weighting the two variables by P and 1 - P.

These environmental variables were originally added to the VZ model in the order they were developed or discovered, but the final step of model development evaluated their relative contribution. Thus variables were added to the final model in order of their effect on accuracy of VZ prediction of the field plots used to build the model.

Vegetation zone model building—

The model presented here used a different approach than other attempts to develop a landscape model of PNV. This model was based on boundary algorithms that predict the

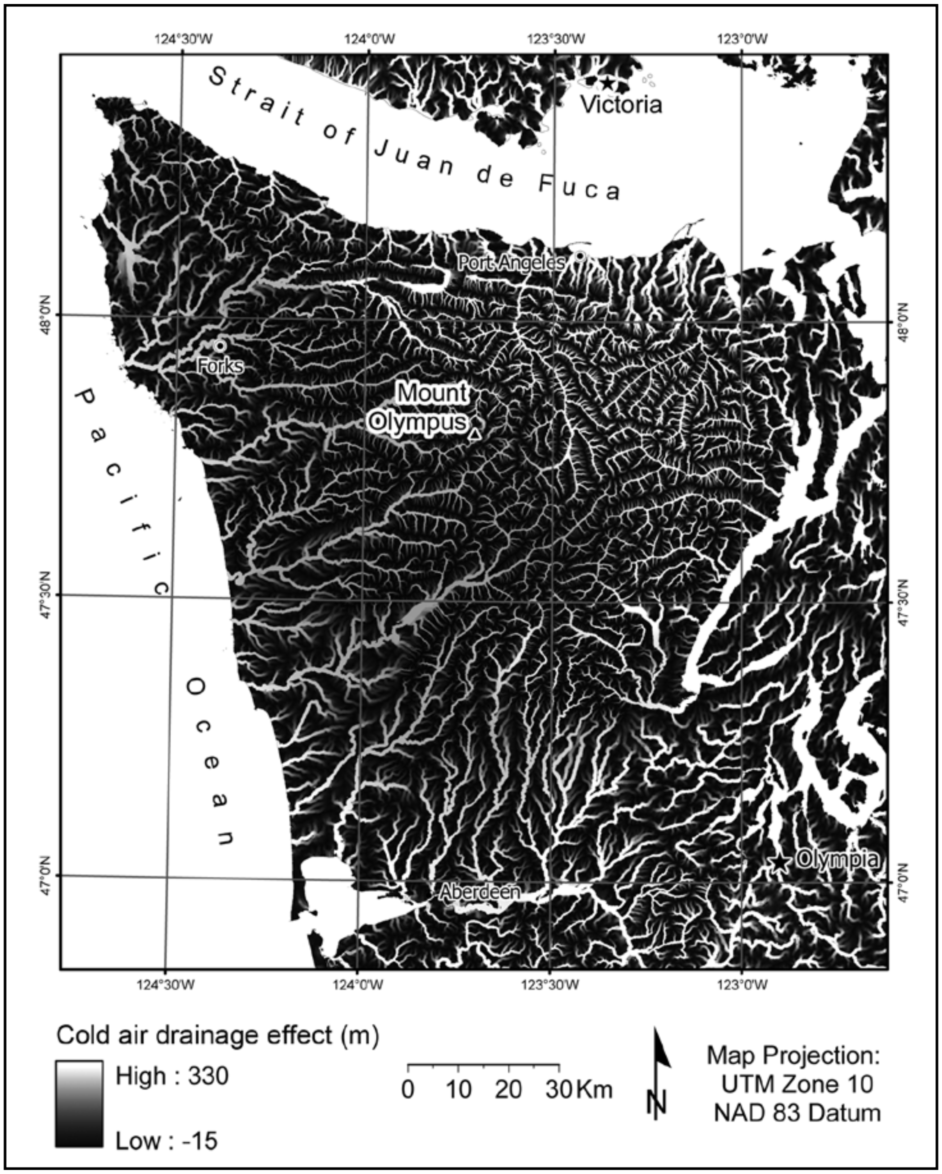

Figure 10—Cold air drainage effect for the Olympic Peninsula. The map displays the change in temperature owing to cold air drainage, expressed as the relative difference in meters of elevation.

lower and upper elevational limits of each VZ, approximating an ecological envelope approach, rather than estimating the likelihood (e.g., Ohmann et al. 2007, Robertson et al. 2001) of each pixel belonging to each potential class of PNV. The VZ model began with the lower boundary of the PSFZ equation suggested in figures 4 and 5 and is given as equation 3:

$$VZ_{elev} = A + Bx_1 + Cx_2 + Dx_3 + \ldots Nx_n \quad (3)$$

Where

VZ_{elev} = the elevation representing the node for the lower or upper elevational boundary of any VZ in the study area, A is the intercept term, B…N is the slope function coefficient or amplitude of the environmental variable $x_1 \ldots x_n$. In the case of aspect, the variable x is the transformed relationship of the sine of the aspect minus 120°. Furthermore, the dependent variable is the point in geographic space represented as elevation plus the latitude and longitude (thus the X, Y, Z coordinates) of each geographic 90-m pixel.

The boundary line between the upper boundary of one VZ and the lower boundary of another was determined by the fit of an equation to achieve a minimum of total errors, with a balance of errors above and below the boundary line. The boundary equation was typically represented by a linear or sine function; however, nonlinear or quadratic functions were permitted. In this process, sets of field plots representing pairs of adjacent vegetation zones for a small geographical area were graphed for elevation versus each environmental variable one at a time, starting with PSL. The example in figure 4 shows nine PSFZ plots below the lower boundary (LBPSFZ) line and 10 WHZ plots above for a total error of 19 out of 160 total WHZ and PSFZ plots (12 percent error). The total number of errors of 19 was the minimum value attainable by iteration; thus the errors above and below the boundary line were unequal but the minimum attainable. At the lower boundary mountain hemlock zone (LBMHZ) there were 5 MHZ plots below the upper line (fig. 4) and 3 PSFZ plots above for a total of 8 out of 72 plots (11 percent error). Thus the iteration could not find a solution of eight or fewer plots where the error plots above equaled the error plots below the boundary line.

As each variable was added to the model, a new term was added resulting in a new value for "A", "B", and an x+1 number of variables. Each new term was an iteratively fit linear or quadratic expression of the relationships of the new variable and the elevation of the intercept, or it was a complex polynomial reflecting the interaction between it and another variable.

Accuracy assessment of VZ prediction for the ecoplots was initially accomplished by comparing the output VZ model grid with the VZ call for each plot in the data set. Accuracy is calculated by comparing the predicted VZ for each plot location with the actual VZ call for each plot. This same procedure was used for the check plots and ONP plot sets when the model was expanded to the Olympic Peninsula. These spatial accuracy assessments are reported as percentage accuracy of VZ prediction for the plot data sets.

Model Validation

Two independent sets of plot data were used to validate the map output of the VZ model. These FIA and CVS plot data were used as a final and unbiased measure of the accuracy of the VZ model, as they were installed on the national systematic grid and the data collected were independent of the VZ model development. Plots were excluded from the original data sets if they did not have an accurate GPS location or could not be assigned a VZ because of stand condition, disturbance, or stand age. Of the 132 FIA plots available, 71 plots off national forest land were usable in this test, and 84 of the 140 CVS plots on the Olympic National Forest could be used for the validation of the PNV model. These 84 CVS plots plus 71 FIA plots were compared to the VZ model grid for the final spatial accuracy assessment of the model. Vegetation zone calls for the plots were compared with the mapped VZ for each plot location to determine the percentage accuracy of the VZ prediction.

Results

New Environmental Variables

Four new environmental variables were developed for this study: (1) precipitation at sea level (fig. 6), (2) fog effect (fig. 7), (3) mean annual temperature at sea level (fig. 8), and (4) cold air drainage effect (fig. 10). Precipitation at sea level is a calculation of the spatial pattern of precipitation with the effects of elevation removed. In a practical sense, it depicts the precipitation regime for the landscape. The highest PSL occurs on the windward or southwestern side of the Olympic Mountains, and becomes successively less going from southwest to northeast across the peninsula with an apparent cumulative rain-shadow effect behind each ridge. Precipitation at sea level is also less along the coast than farther inland toward the mountains. Similarly, MATSL represents the spatial pattern of MAT with the effects of elevation removed. It depicts the temperature regime for an area. The pattern of MATSL on the peninsula shows the lowest values at the northwestern corner of the peninsula and along the land/saltwater interface. It becomes warmer at greater distances from the saltwater, and reaches the highest value in the southeastern part of the peninsula farthest from major

Table 1—Accuracy assessment for model stages, variables, and plot sets

Model stage[a]	Number of variables	Number of VZ	Variable added[a]	Correct ecoplots (of 1,497 plots)	Accuracy added for ecoplots	Correct check plots (of 447 plots)	Correct ONP plots (of 1,051 plots)	Correct CVS plots (of 84 plots)	Correct FIA plots (of 71 plots)
				Percent					
1 - All as single VZ (WHZ)	0	1		53.1	53.1				
2 - Elevation	1	5	Elevation	57.6	4.5	51.5	52.8		
3 - Elev and PSL	2	8	PSL	69.6	12.0	69.7	54.6		
4 - Elev, PSL, TM	3	8	TM	71.5	1.9	73.9	58.9		
5 - Elev, PSL, TM, FOG	4	8	FOG	74.4	2.9	80.9	58.2		
6 - Final model	8	8	CAD, aspect, SW, MATSL	76.4	2.0	81.3	69.1	82.1	71.8

[a] VZ is vegetation zone, ONP is Olympic National Park, CVS is Current Vegetation Survey, FIA is Forest Inventory and Analysis, WHZ is western hemlock zone, Elev is elevation, PSL is precipitation at sea level, TM is topographic moisture, FOG is fog effect, CAD is cold air drainage effect, SW is potential shortwave solar radiation, and MATSL is mean annual temperature at sea level.

Notes: The first model stage (single VZ model) illustrates the prediction accuracy of the VZ for the ecoplots if the entire study area were mapped as the WHZ and as a single pixel. In this case, 53.1 percent of the ecoplots would have the VZ correctly identified and mapped. With expansion to the 90- by 90-m pixel resolution and the addition of elevation as a lookup variable, the accuracy of ecoplot prediction rises to 57.6 percent. By adding PSL to elevation and using the simple model Y = intercept (elev) + slope x PSL, the accuracy of prediction of the ecoplots rises to 69.6 percent. In the final model stage with seven variables plus the intercept (as elevation), the prediction accuracy for ecoplots rises to 76.4 percent and is 82.1 percent for an independent set of CVS plots on the Olympic National Forest. The average accuracy for the combined CVS and FIA validation data sets is 77.4 percent.

bodies of saltwater (i.e., Pacific Ocean and Strait of Juan de Fuca). Fog effect represents an interpretation of the combined effects of the coastal maritime environment on the growth and distribution of plants. These effects are understood to be the results of fog, tree drip, humidity, and cloudiness affecting the water relations of plants. They simulate the addition of water in the ecosystem. Cold air drainage effect was developed to help explain the downward extent of species and vegetation in corridors and basins where cold air is believed to flow and accumulate. Its effects are local, but when present, CAD effect can have a profound effect on the extension of the lower boundaries of most VZs to lower elevation. These new environmental variables are presented as hypotheses regarding their predictive ability, derivation, and conceptual validity. They are not directly measurable, nor are they direct derivatives from weather station records; therefore, they represent a degree of interpretation.

Model Building

In the stepwise addition of variables, the base model was established and then a new variable was added, one at a time, until a final model was achieved. The output of the process is summarized in table 1. The base model was the simplest version of the model possible, where the entire study area was modeled as the most common VZ identified from the field data. This was the WHZ, which was represented by 53.1 percent of the USFS ecoplots on the Olympic National Forest. Thus if the entire area was modeled as the WHZ, it would yield a model and a map with 53.1 percent accuracy for the ecoplots. Such a case might represent the resolution of a global scale map of PNV with each pixel representing an area of 2 by 3 degrees of latitude and longitude. Any model not achieving this level of accuracy was automatically rejected.

The next level of the model considered only the variable elevation, where Y_{elev} corresponded to an intercept value for each VZ boundary in a lookup table (thus $Y_{elev} = X_{elev}$). The elevation values for the boundary equation intercepts were lower boundary alpine zone (LBAlpZ) = 1835 m; lower boundary subalpine parkland zone (LBPklZ) = 1447 m; LBMHZ = 1148 m; LBPSFZ and upper boundary WHZ = 677 m. These intercept values were derived by first averaging

Table 2—Area and mean elevation of vegetation zones on the Olympic Peninsula, Washington

Vegetation zone	90-m pixels	Area	Mean elevation	Percentage of area
	Count	*Hectares*	*Meters*	*Percent*
Alpine	15,255	12,357	1,923.2	0.8
Subalpine parkland	67,304	54,518	1,513.6	3.7
Subalpine fir	17,557	14,222	1,542.9	1.0
Mountain hemlock	88,740	71,882	1,230.0	4.8
Pacific silver fir	305,348	247,341	738.3	16.6
Douglas-fir	9,247	7,490	743.6	0.5
Western hemlock	929,336	752,789	265.5	50.5
Sitka spruce	407,608	330,174	78.9	22.1
Sum/**mean**	1,840,395	1,490,773	**411.3**	100.0

the elevation for each VZ (table 2), then averaging the elevation of each adjacent pair to get the initial lower or upper boundary for each VZ, and then using the minimum total of errors and balance of errors above and below the boundary curve, as described previously. Using this approach to define the boundary between each of the five dominant VZ, the model accuracy for the ecoplots was 57.6 percent (table 1). The Sitka spruce, Douglas-fir, and subalpine fir zones were not included in this model because they did not have discrete boundary elevations; these VZs were limited to areas of high fog effect and PSL (SSZ) or to dry TMs or low PSL (DFZ and SAFZ). Thus only five of the eight VZs had any area in this model that used elevation as the sole variable.

Subsequent levels of the model were built with a stepwise addition of variables. The next level of the model added the variable PSL. This yielded a model for eight VZs with 69.6 percent accuracy when the model was compared to the ecoplots used to build the model, an improvement of 12 percent over the elevation-only model (table 1). Furthermore, this model included all eight VZs. This large jump in accuracy indicated that besides the effect of elevation in controlling the intercept values of the boundary equation model, PSL added the greatest contribution to the model predictability. The next model with PSL and TM as independent variables yielded an accuracy of 71.5 percent. The next model added fog effect. This model with only PSL, TM, and fog effect as independent variables had an accuracy of 74.4 percent for the ecoplots, only 2 percent lower than the full model, indicating that most of the ecological information beyond elevation was contained in just these three independent variables. Finally, CAD effect, aspect, MATSL, and shortwave solar radiation were added to the model. In this final model, these four latter variables added a combined increase of 2 percent in model accuracy for a total accuracy of 76.4 percent for the ecoplots used to build the model (table 1).

The single most important independent variable in this model was PSL. This simple model Y_{elev} = A + B × (*PSL*), correctly predicted the VZ for 69.6 percent of the ecoplots (table 1). The importance of this variable can be seen in the relationships shown between PSL, aspect, and elevation and the lower boundary of the PSFZ (fig. 11). The lower boundary of the PSFZ changes about 200 m in elevation for each class of PSL. Across the widest range of environments from the driest area of the peninsula to the wettest, this amounts to a total of about 1000 m of elevation difference for the lower boundary of the PSFZ, all other factors held constant.

Boundary Equations

The VZ model presented here used boundary equations to determine the elevation for each VZ boundary for each pixel in the study area. The general form of the final model algorithm is given as equation 3, where elevation of the VZ boundary is the dependent variable. Table 3 presents the specific equations and coefficients for each VZ boundary on the Olympic Peninsula. As an example, the following (eqn.

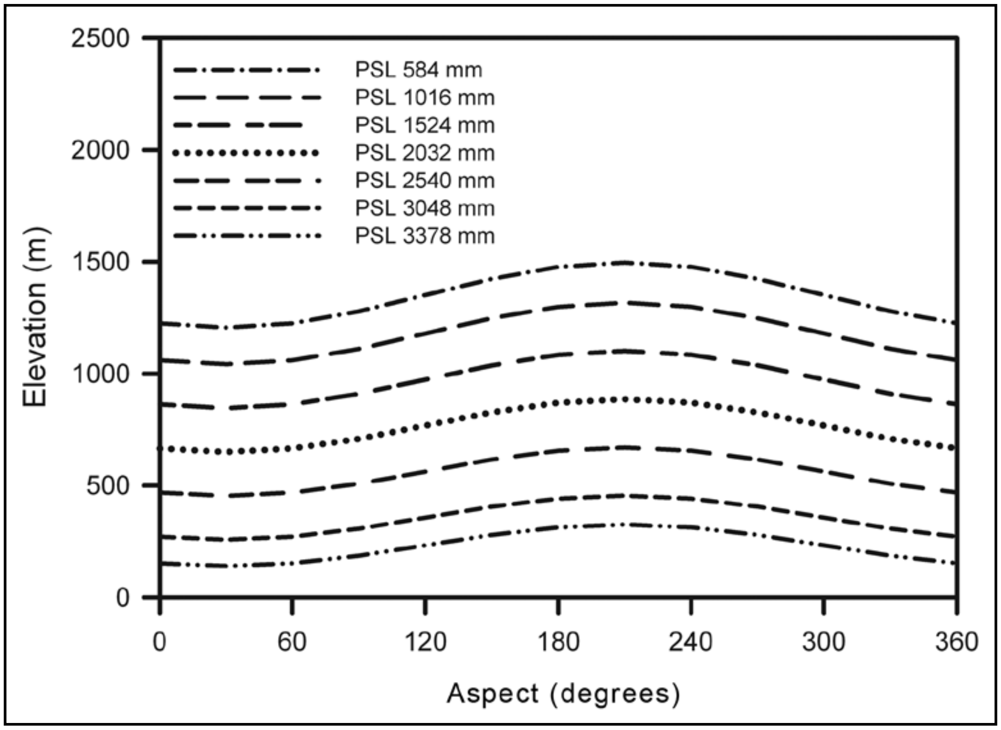

Figure 11—Elevation of the lower boundary of the Pacific silver fir zone by aspect, for seven classes of precipitation at sea level (PSL). The five middle classes each represent 508 mm of PSL, and the highest and lowest classes are represented by the actual mean PSL for the class.

4) is the specific model algorithm for the lower boundary of the PSFZ, from equation 3 and table 3 E5:

$$LBPSFZ_{elev} = A + B \times (PSL + FOG) + C \times TM + D \times MATSL + G \times FOG + H \times CAD + \{P \times [E + F \times (PSL + FOG)] \times SIN(ASPECT - 120) + [(1 - P) \times E \times (SW - 14930) / 3380.4]\} \quad (4)$$

Where

A = 1750; B = -0.300; C = -76.2; D = 10.97; E = 97.5; F = -0.0132; G = -0.180; H = -0.800, and P = 1.0; and where $LBPSFZ_{elev}$ is the elevation in meters of the lower boundary of the PSFZ for any particular 90-m pixel in the study area; the corresponding values for each environmental variable for the pixel: where (*PSL* + *FOG*) is precipitation at sea level in millimeters of precipitation plus fog effect in millimeters of water equivalent for the contribution of fog effect; *TM* is the topographic moisture for the same pixel; *MATSL* is the mean annual temperature at sea level in degrees C for the same pixel; CAD is the cold air drainage effect in meters of elevation change; and SIN (*ASPECT*-120) is the transformation of aspect to set the maximum aspect effect at 210 degrees and at 30 degrees; and *SW* is the shortwave solar radiation in watts per square meter, for each 90-m pixel in the landscape calculated using the model application of Kumar et al. (1997). The values 14930 and 3380.4 are used to calibrate the solar radiation values to relative values of the same scale as the sine of the aspect.

Map of Potential Vegetation Zones for the Olympic Peninsula

The principal output of the model was a spatial grid (map) of the eight VZs of the Olympic Peninsula (fig. 12). The model algorithm used to generate this grid computed the boundary elevations for each VZ in the study area by executing each of the equations (e.g., table 3) for each of the 1,840,395 90-m pixels in the study area. It then compared the calculated minimum and maximum elevation of each VZ with the elevation of the pixel and selected the VZ whose upper and lower boundary bracketed the elevation of the pixel. The result was a VZ grid (map) with a 76.4 percent accuracy

Table 3—Final model coefficients and equations for vegetation zone (VZ) boundary equations for the Olympic Peninsula, Washington

		Model coefficients								
VZ boundary name	**Eqn**[a]	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**P**
Lower boundary alpine zone	**E1**	1834	-0.024	-1.52	1.65	6.10				0.3
Lower boundary subalpine parkland zone	**E1**	2847	-0.540	-6.10	10.97	18.3				0.3
Upper boundary subalpine fir zone	**E1**	1911	-0.372	-16.8	5.49	18.3				0.5
Lower boundary subalpine fir zone	**E1**	1402	0.168	-13.7	0.0	-42.7				0.5
Upper boundary mountain hemlock zone	**E4**	1908	-9.144	-616257	541.93	-274		2.440		0.5
Lower boundary mountain hemlock zone	**E2**	1677	-0.216	-22.9	8.78	19.8		-0.060	-0.250	0.3
Lower boundary Pacific silver fir zone	**E5**	1750	-0.300	-76.2	10.97	97.5	-0.0132	-0.180	-0.800	1.0
Upper boundary Douglas-fir zone	**E3**	1954	-1.032	-91.4	173.74					0.3
Lower boundary Douglas-fir zone	**E2**	-1440	0.960	-106.7	-17.56	-183		0.240	2.100	0.3
Upper boundary Sitka spruce zone	**E2**	-647	0.204	45.7	-29.63	-10.7		2.640	1.000	0.5

[a] Equation number. Equations follow the form as given in equation 3 in text, where the dependent variable (the left side of the equation) is in units of elevation. Each different equation represents the lower and/or upper boundary for one or more vegetation zones.

E1: $Y_{elev} = A + B \times (PSL + FOG) + C \times TM + D \times MATSL + \{P \times E \times \mathrm{SIN}(ASPECT - 120) + [(1 - P) \times E \times (SW - 14930) / 3380.4]\}$

E2: $Y_{elev} = A + B \times (PSL + FOG) + C \times TM + D \times MATSL + G \times FOG + H \times CAD + \{P \times E \times \mathrm{SIN}(ASPECT - 120) + [(1 - P) \times E \times (SW - 14930) / 3380.4]\}$

E3: $Y_{elev} = A + B \times (PSL + FOG) + C \times TM + \{P \times D \times \mathrm{SIN}(ASPECT - 120) + [(1 - P) \times D \times (SW - 14930) / 3380.4]\}$

E4: $Y_{elev} = A + B \times TM + (C + D \times TM^3) / (PSL + FOG) + \{(P \times E + G \times TM^2) \times \mathrm{SIN}(ASPECT - 120) + [(1 - P) \times E \times (SW - 14930) / 3380.4]\}$

E5: $Y_{elev} = A + B \times (PSL + FOG) + C \times TM + D \times MATSL + G \times FOG + H \times CAD + \{P \times [E + F \times (PSL + FOG)] \times \mathrm{SIN}(ASPECT - 120) + [(1 - P) \times E \times (SW - 14930) / 3380.4]\}$

where capital letters refer to coefficients given in above table, and variables identified as:
PSL + *FOG* = precipitation at sea level plus fog effect (mm); *TM* = topographic moisture; *MATSL* = mean annual temperature at sea level (°C); *FOG* = fog effect (mm); *CAD* = cold air drainage effect (m); *SW* = potential shortwave solar radiation (watts per square meter); coefficient "P" is proportion of "aspect" effect ("E") attributed to aspect and "1 - P" is proportion of "aspect" effect ("E") attributed to potential shortwave solar radiation.

compared to the USFS ecoplots used to build the model (table 1). The predicted VZ accuracy of the check plots used to expand plot coverage off the national forest was 81.3 percent. Accuracy of the combined plot sets from Olympic National Park was 69.1 percent (table 1). The final assessment was a comparison with independent plot sets from the USFS FIA/CVS program. These 84 CVS plots (national forest land) were correctly predicted 82.1 percent of the time, and the 71 FIA plots (non-national-forest land) were correctly predicted 71.8 percent of the time (table 1).

The most abundant VZ was the western hemlock zone covering 752 789 ha, or about 50.5 percent, well-distributed throughout the study area. The Sitka spruce zone was second most common with 330 174 ha or about 22 percent of the area. It is abundant in the far western Olympic Peninsula. The least common VZs were the alpine zone and the Douglas-fir zone, each with less than 1 percent of the study

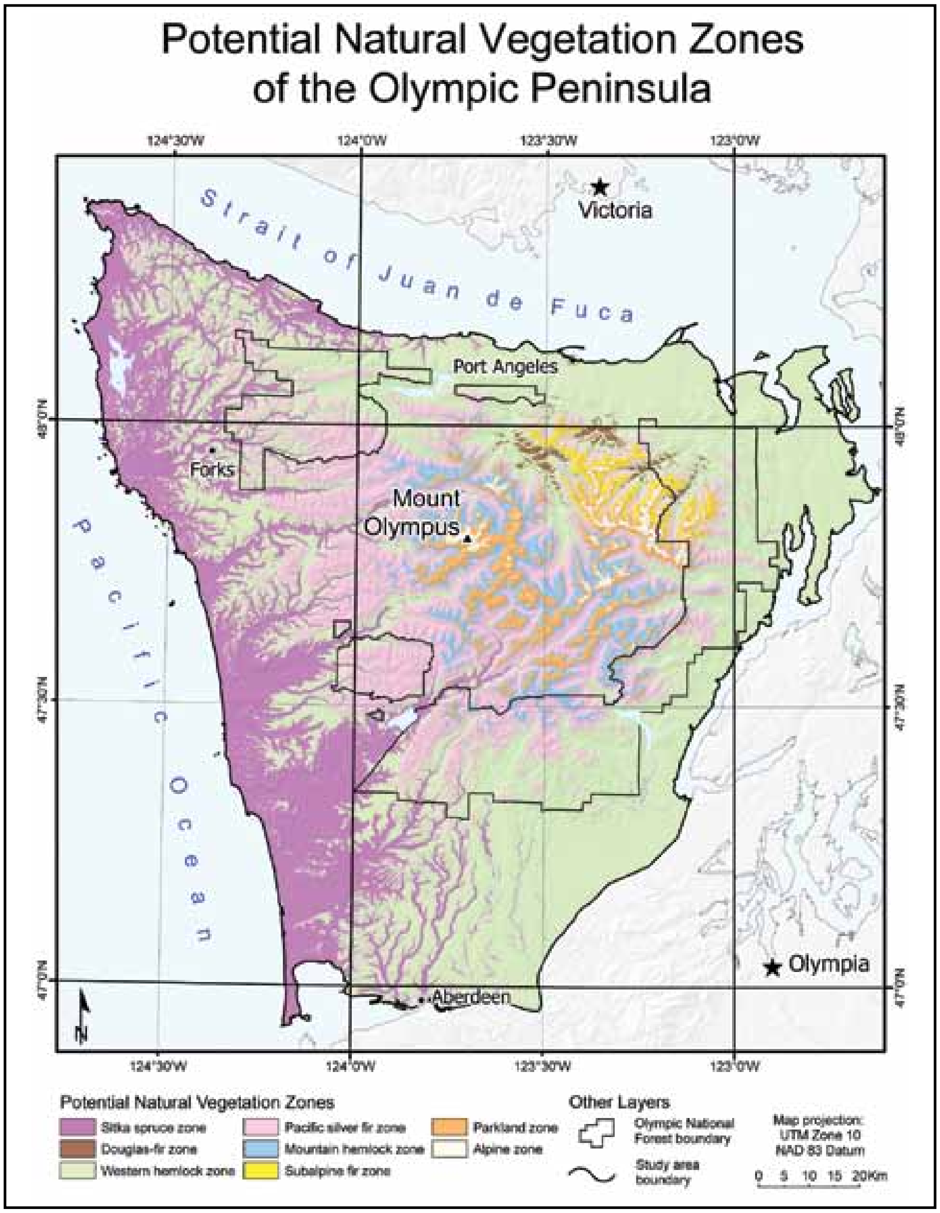

Figure 12—Potential natural vegetation zones of the Olympic Peninsula. The map is the output of the model algorithms for the eight potential vegetation zones on the peninsula.

area (table 2). The alpine zone is mostly snow and rock in the central and western peninsula, but is represented by often well-developed alpine vegetation in the northeastern peninsula. The DFZ is mostly restricted to the dry north-eastern peninsula, and is usually restricted to south aspects on low topographic moisture sites. The PSFZ occurs mainly in the central peninsula, at mid elevations and in areas with persistent winter snowpack. It is the third most common VZ on the peninsula. The MHZ occurs above the PSFZ for most of the peninsula, and below the subalpine parkland zone. The SAFZ is mostly restricted to the dry northeast part of the peninsula, replacing the PSFZ or the MHZ there. The subalpine parkland zone occupies the tops of most higher elevation ridges but occurs below the alpine zone. It is usually a mosaic of tree islands and shrub or herb meadows, marked at its lower limit by closed or nearly closed forest and at its upper boundary by krummholz, where tree species occur as shrubs.

Discussion

The development of a landscape vegetation model based on boundary equations represents a unique approach, as far as the authors know. Four of the model variables are original (PSL [fig. 6], fog effect [fig. 7], MATSL [fig. 8] and CAD effect [fig. 10]). In addition, this calculation of temperature lapse rate (fig. 9) and the scaling of topographic moisture were also new. The VZ map of the Olympic Peninsula (fig. 12) is the finest scale and most accurate map of this type, to date, for the Pacific Northwest.

The original purpose of this project was to develop a reliable and accurate map of the PNV of the Olympic National Forest through a combination of field reconnaissance and landscape modeling. It began in 1982 drawing on experience from two earlier landscape-modeling projects in Olympic National Park (Cibula and Nyquist 1987) and in Utah (Davis 1980). At that time, computer technology did not allow the full expression of the envisioned model.

Without sufficient computer resources at the time, but with a model in mind, the alternative was to test the model using hand computations and apply the results to topographic maps. Similarity or nearest-neighbor approaches did not lend themselves to this field-based approach. However, a boundary equation approach did, although nothing was found in the literature or from knowledgeable sources to support it. Existing variables were scant and consisted of slope, aspect, elevation, and an early precipitation map. Weather stations on the Olympic Peninsula were few and were located mostly at low elevations near saltwater. None of these variables provided sufficient information to do a reliable map of vegetation zones for this area. Thus a new approach was initiated to test a method to distinguish between different types of vegetation, and to develop new variables that might have better predictability and better represent the operational environment of these plant communities. A similar search for variables more explanatory of the operational environment was also advocated by Lookingbill and Urban (2005).

We pursued a better identification of the variables that compose the operational environment. At the same time, we also strove for a better quantification of the mathematical relationships between highly correlative environmental factors and plant distribution and abundance. That we came up with the precipitation regime being most correlated with vegetation distribution patterns should not be surprising. What is more informative, however, is how we were able to build a predictive model with a broad landscape variable (PSL), filter that factor out and then analyze the "errors." The subsequent patterns that emerged revealed more about the factors driving the vegetation distribution. This led us to evaluate the residual pattern at each step, and then begin a search for a variable or effect that could be quantified. We believe this process provided better insights to the operational environment than we would have been able to derive by starting with a set of "existing" variables and performing a statistical analysis, weighting each variable similarly, and looking for a statistical pattern of correlation.

This model used boundary algorithms to predict the environmental limits of the eight VZs modeled in the study area. The use of "boundary" in this context refers to an ecological node that is used to distinguish between the eight VZs in this study. It does not refer to vegetation boundaries in the sense of physical ecotones (Carter et al. 1994, Choesin and Boerner 2002), ecological edges (Fortin 1994), vegetation boundaries (Glavac et al. 1992), or discontinuities along ecological edges (Ludwig and Cornelius 1987). Rather it refers explicitly to algorithm-defined boundaries between units of PNV. Such boundary equations are used to identify points on the ground and in ecological hyperspace that represent these nodes. In addition, the development and use of the boundary equations (table 3) provides a new opportunity to examine the relationships between environmental variables across geographic and ecological space, the interaction of environmental variables and vegetation, as well as changes over time relative to climate change.

Associations between the different VZ boundaries and individual environmental variables and their interactions revealed patterns that help to understand the ecological links between vegetation and the landscape. One aspect of vegetation and its relationship to the environment that is often overlooked in similar studies is that the relative importance of different variables changes with different units (i.e., VZs) of the vegetation continuum and in context with other variables (table 3). Observations from these data showed PSL was strongly correlated with the distribution of these eight VZs except for the alpine zone, which was most strongly correlated with elevation (i.e., temperature). The SSZ was most correlated with the fog effect, and somewhat with MATSL and aspect. The DFZ was defined by both an upper and lower boundary equation and was also strongly affected by aspect, TM, and MATSL at both boundaries, and by a negative CAD effect (i.e., the DFZ avoided areas with high CAD effect). The PSFZ was strongly affected by TM, CAD, and fog effect as well as PSL. It was also one of only two VZs that showed a strong aspect effect, plus it showed a strong interactive term between aspect and PSL.

Modeling the boundaries of VZs where the zone is continuous around the 360-degree aspect cone is done with continuous variables where the upper boundary of one VZ is the lower boundary of another. However, when the VZ is at the tail of its ecological distribution, it may only occur on the drier, southwesterly aspects if at the northerly or wet end of its range; conversely, it may only occur on the coolest northerly aspect or highest TM at its southerly, warm or dry end of its range. In these cases, the boundaries of the VZ are described by both a lower and an upper VZ equation. Mathematically the wedge formed by the lower and upper boundary curve intrudes into the space otherwise occupied by another more geographically zonal VZ. This was true for the Sitka spruce zone, Douglas-fir zone, and the subalpine fir zone in the study area.

Precipitation at sea level was the most predictive variable in this model, indicating the importance of this index of the precipitation regime in determining the distribution patterns of the VZs in the Olympic Peninsula. The lower boundary of the PSFZ (upper boundary of the WHZ) varies from the southwest Olympics, where it is lowest, to northeast, where it is absent on some aspects and TMs. Across this geographical and topographical gradient, the elevation of the lower boundary increases with decreasing PSL (fig. 11) and fog effect and increasing MATSL, and shifts upward approximately 100 m on southwesterly aspects. The breadth of the PSFZ changes from wetter to drier areas. This is shown when comparing figure 5B (an area of high PSL) to figure 5C (an area of relatively low PSL). The upper boundary of the PSFZ shifts across this PSL gradient, but at a lower rate than the lower boundary, resulting in a contraction of the width of the zone from wetter to drier areas, approaching the extinction point at about 742 mm PSL, where the PSFZ is restricted to high TM.

This model confirms the relationship most often found in other studies, that some measure of moisture availability or potential moisture loss (Barton 1994, Bridge and Johnson 2000, Gagnon and Bradfield 1987, Rehfeldt et al. 2006) is the variable that is most strongly associated with the distribution of species and communities across the landscape. This should cause modelers of global temperature change to reconsider the relative effects of temperature versus precipitation in causing major distribution shifts or extinction of plant species in the future.

One might expect that the upward shift of VZ boundaries would be proportional to the temperature lapse rate for an area, but that was not found. The actual rate of shift upward in elevation is usually less than the temperature lapse rate for the area. The explanation appears to be the strong correlation between the environmental variables and geography, and the complex interactions between temperature and moisture with elevation, each compensating for the other in as yet unknown terms.

The two new variables of PSL and MATSL can be regarded as descriptors of the precipitation regime and the temperature regime, respectively. As such, they are broad-scale variables that interact with the finer scale site variables, such as aspect, TM, and CAD effect. As broad-scale variables, they are best associated with broad patterns of vegetation. These are patterns that would be seen from a distance or at a small mapping scale. Within this broad context there is considerable variation owing to a different set of factors that affect micro- or meso-scale variations in light, heat, soil moisture, or nutrients. Using the variables PSL and MATSL early in the model-building process is not only statistically logical but ecologically logical. The effects of microsite variables are easier to understand when viewed in the context of the broad-scale factors such as

PSL and MATSL. Using PSL and MATSL as indices of the precipitation regime and the temperature regime also helps with logical consistency. Both variables portray the broad precipitation or temperature regime with the effects of elevation removed. As elevation is the dependent variable in this spatial model, it is hard to justify using variables such as total annual precipitation or mean annual temperature as independent variables, because both are strongly correlated with elevation. Having elevation also strongly represented in one or more of the independent variables is circular logic. In addition, maps of total annual precipitation and mean annual temperature are also models with their own set of errors, especially in an area with so few weather stations and such extreme topography.

One way to visualize the effects of PSL over a landscape is to imagine several different areas with the same PSL. As an example, the PSL 2286 mm isoline (fig. 6) represents an area where the pattern of vegetation is similar for the same combination of elevation, aspect, TM, and CAD effect. But this pattern is distinctly different in drier or wetter PSL areas. Likewise, the MATSL variable represents a temperature regime across the landscape, where for a given value of MATSL, the pattern of vegetation relative to the site variables is relatively consistent. A number of hypothetical cone-shaped mountains scattered throughout the area of PSL 2286 mm and MATSL 10.5 °C would have similar patterns of VZs from bottom to top. Likewise a set of mountains in the area of PSL 1143 mm and MATSL 10.5 °C would have similar species and patterns of vegetation, but the vegetation distribution for the mountain in PSL 2286 mm would be distinctly different from those in PSL 1143 mm.

Model validation for the eight VZs of the 1.5-million-ha study area using independent plot data was 77.4 percent. This was the average of the prediction accuracy of the CVS and FIA independent plot sets (table 1). Too few studies in the literature use an independent and statistically unbiased validation sample to test model accuracy (Reynolds and Chung 1986).

No directly comparable published studies were found. However, for a model of current species and structural attributes at a 25-m resolution, Ohmann and Gregory (2002) reported a predictive accuracy of 45 percent for a reserved set of 25 percent of the original plots. Rehfeldt et al. (2006) compared a model assignment of plots to a preexisting polygon map of 25 biotic communities (Brown et al. 1998) in the Western United States. They achieved a classification **error** of 19 percent when comparing precisely located plots to a polygon map of unknown accuracy and geographic registration. Lookingbill and Urban (2005) compared two different sets of environmental variables: one a "proxy model" and another with more plant-relevant variables, but with a non-randomly located validation sample (n = 11) to four forest community types in western Oregon. They found 73 percent accuracy for the "plant-relevant" variables but only 18 percent for the proxy model variables.

This model is easily verified in the field by having map in hand. In addition, by knowing the PSL, MATSL, aspect, and TM, one can predict with relative confidence the VZ for any particular site on the landscape. For the roughly one out of five times the model will not correctly identify the field-identified VZ (table 2), one can usually deduce one of four possible sources of the error. First, the site is very near the boundary of the VZ in question, and the coarseness of the independent variables or the influence of other micro-site variables may explain the difference; two, the community might be in an early successional stage or disturbed condition, and it might not be possible to identify the VZ in the field; three, the site is affected by a variable not recognized in the model, possibly owing to lack of GIS data, such as a spring, seep, wind-affected redistribution of precipitation, or an unusual or unmapped soil or geological element; or fourth, the location of the site is not known with the same precision as the GIS-based map. Many of the plots used in developing the model were installed before the widespread use of GPS and therefore their locations are known with less precision than later plots. This locational error is believed to account for about half of the statistical "error" of the model. The qualitative assignment of VZ to plots, especially those done "after the fact," may be another source of error. When the model does not correctly identify the apparent VZ in the field and the location of the site is known with a high degree of precision, it is more interesting than when it does, as it encourages the pursuit of new ecological information or definition of a new environmental variable.

This modeling approach was developed for the broad-scale classification of PNV, i.e., the VZ. However it is believed to be equally applicable to finer scale vegetation units (i.e., plant association groups [PAG] and plant association). In addition, the concepts behind the model presented here could also be used to describe
the patterns of distribution of PNV as a noncategorical variable. As such, PNV can also be understood in terms of a scale or gradient of potential vegetation conditions that are not encumbered by artificial classes. Within each VZ described here by ecological-mathematical boundaries, there is continuous vegetational compositional change associated with more or less continuous environmental variation. This gradient approach is as much a part of the concept of potential vegetation as the typal-classification approach. Each has different uses and values in understanding the nature of vegetation or the application of concepts or stratifications to natural resource management.

The described patterns of potential VZs provide a broad vegetational stratification for addressing ecological or management questions, as the VZ and the broad classes of PSL and MATSL provide a gauge of relative ecological similarity. This stratification can provide context for comparing results of successional studies. The concept of succession describes the natural and inevitable changes that occur in plant communities over time. These changes are strongly affected by the starting condition and the environment of the site and are driven by competition for space and resources. When studying the effects of succession on community biomass, growth, diversity, or function, the factor most important in controlling these effects is the environment. The environment is strongly reflected in the potential vegetation for a site. Thus, knowing the PNV for any stand or community being studied helps in stratifying the study and in interpreting the results.

Maps of potential vegetation and environmental variables can provide the foundation for scientific and ecological studies and for addressing resource management questions. Potential VZs or finer levels of classification of PNV can be used to stratify studies of silvicultural treatment, stand growth response to disturbance, carbon sequestration, and fire resistance or probability. It is the opinion of the authors that too few silviculture studies of thinning, weeding, or regeneration inform the users regarding where the results of a study are applicable. A thinning study of a Douglas-fir stand in the grand fir zone in the southern Willamette Valley can hardly be applicable to a similarly aged Douglas-fir stand in the moist western hemlock zone in northern Puget Sound; yet, such applications have been made, with unfortunate consequences. Stand growth studies are often stratified by site index, yet knowing the VZ, plant association group, or plant association can inform the user regarding potential stockability differences or regeneration potential not associated with site index alone. Recent and unpublished stand growth/carbon sequestration studies show that some previously unrecognized stand growth patterns can be stratified by units of PNV. Fire history studies of western Washington show that historical fire patterns are strongly associated with current patterns of PNV. The VZ and PSL data have been used to stratify the peninsula into three fire occurrence zones: the wet, western part having little evidence of historical fire; the dry northeast part characterized by relatively young forests with recurrent forest fires over the last 300 years; and the middle area, where many forests date from either about 1300, 1500, or 1700 a.d. The model of potential vegetation presented here represents the current climate. However, by varying PSL or MATSL one can use the PNV model to predict how PNV could change in the future owing to climate change or how it might have been different in the past. The PNV model has also been used to predict and validate the potential habitat and range for over 10 plant and animal species, including species considered rare and at risk (Lesher 2005).

This study was a quest for a new conceptual model for understanding how vegetation is distributed across a landscape. This model included developing and validating the concept of boundary equations, development of several new environmental variables, and production of a high-resolution grid of potential VZs. This grid map and these variables permit new perspectives on the patterns of vegetation and their links to the environment, plus possible uses for studying the consequences of climate change, plant community monitoring, and ecological analysis. This project has been extended across the rest of Washington and Oregon, where the breadth of major environmental variables provides the opportunity for exploring nonlinear relationships and factor interactions across a regional landscape.

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Acronyms

ATU	Accumulated temperature units
CAD	Cold air drainage
CPC	Climax plant community
CVS	Current Vegetation Survey (USFS)
DEM	Digital elevation model
DFZ	Douglas-fir zone
ELEV	Elevation
FIA	Forest Inventory and Analysis (USFS)
GIS	Geographic information system
GPS	Global positioning system
LBMHZ	Lower boundary mountain hemlock zone
LBPklZ	Lower boundary subalpine parkland zone
LBPSFZ	Lower boundary Pacific silver fir zone
MAT	Mean annual temperature
MATSL	Mean annual temperature at sea level
MHZ	Mountain hemlock zone
ONP	Olympic National Park
PNV	Potential natural vegetation
PSFZ	Pacific silver fir zone
PSL	Precipitation at sea level
SAFZ	Subalpine fir zone
SIN	Sine function
SSZ	Sitka spruce zone
SW	Potential shortwave solar radiation
TAP	Total annual precipitation
TM	Topographic moisture
VZ	(Potential) vegetation zone
WHZ	Western hemlock zone

English Equivalents

When you know:	Multiply by:	To find:
Millimeters (mm)	0.0394	Inches
Centimeters (cm)	0.394	Inches
Meters (m)	3.28	Feet
Kilometers (km)	0.621	Miles
Hectares (ha)	2.47	Acres
Square meters (m^2)	10.76	Square feet
Square kilometers (km^2)	0.386	Square miles
Degrees Celsius (°C)	1.8C + 32	Degrees Fahrenheit
Watts per square meter	0.0929	Watts per square foot

The vegetation zone model and environmental variables presented here are available as maps in grid format at a 90-m pixel resolution. They can be downloaded from the Ecoshare Web site—http://ecoshare.info/.

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