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Forest plant diversity at local and landscape scales in the Cascade Mountains of southwestern Washington

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Abstract

Old-growth forests in the Pacific Northwest are known to support high levels of diversity across the varied landscapes they occupy. On 1200 plots distributed over the Cascade Mountains in southwestern Washington, climatic, physiographic, edaphic and floristic data were collected to evaluate the ecological characteristics of these coniferous forests and develop a classification framework useful in land management. The resulting abundance of data provided a unique opportunity to analyze plant diversity relationships at multiple levels and identify the environmental and biotic factors which influence diversity at local and landscape scales. Plant species richness and diversity were generally lower in communities characterized by environmental extremes (i.e., excessive or scarce moisture and severely cold high elevation) than in mesic environments at low-to-middle elevations. Evenness among plant species was greatest at higher elevations, where severe climate limited the ability of any single or group of species to dominate. Species turnover rates were also higher near the environmental extremes. High turnover rates among mountain hemlock associations were attributed to highly variable topography and local microclimates which resulted in substantial geographical isolation and species specialization among site types. Moisture appeared to have the most influence on species richness (alpha diversity) and sequential turnover rates (beta diversity) at high elevations, where available water is seasonally limited by low temperatures. Temperature had the greatest influence on overall species turnover (gamma diversity) throughout the landscape. Species richness of the landscape (epsilon diversity) was quite accurately predicted (within 7% for temperature and moisture gradients) by a computational method which uses independent measures of alpha, beta and gamma diversity. Patterns of forest plant diversity appear to be the result of environmental conditions at larger scales and the complex interactions among biological and physical variables at smaller scales, within an historical context of stochastic disturbance events. Managers wishing to restore and sustain the high diversity characteristic of these old-growth coniferous forests will need to consider the respective roles of various biophysical factors and the disturbance dynamics in these unique ecosystems. © 1998 Elsevier Science B.V.

Keywords: Old-growth; *Abies amabilis* (Dougl.) Forbes; *A. grandis* (Dougl.) Lindl.; *Pseudotsuga menziesii* (Mirb.) Franco; *Tsuga heterophylla* (Raf.) Sarg.; *T. mertensiana* (Bong.) Carr.

1. Introduction

Biological diversity has become a topic of increasing scientific and popular interest during the recent

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decade (Wilson, 1988; Wilcove, 1989; Reid and Miller, 1989; Hansen et al., 1991; McMinn, 1991). This growing interest is a result of increased scientific information, public recognition of and concern about the problem of species loss and an overall shift in societal values regarding the way in which natural resources, ecosystems, landscapes and species are viewed (Franklin, 1989; Franklin et al., 1989; Maser, 1990; Kessler, 1992). Conserving the naturally occurring diversity in a wide variety of ecosystems has become a major environmental and natural resources management issue of national and international importance (Kikkawa, 1990; Salwasser, 1991; Boyle, 1991; Angermeier and Karr, 1994; Lovejoy, 1995; Lugo, 1995; Wheeler, 1995). Numerous strategies to address the problem have been discussed (McNeely et al., 1990; Salwasser, 1990; Soule, 1991; Brussard et al., 1992; Ryan, 1992; Franklin, 1993; Scott et al., 1993; Lubchenco, 1995; Walker, 1995; Briggs, 1996), but the dangers to biodiversity remain formidable. Foremost among these threats are (1) habitat loss and fragmentation, (2) human population growth and corresponding resource extraction pressure, (3) introduction of alien species, (4) chemical pollution and improper use of biocides, (5) interruption of ecological processes such as natural fire regimes and (6) human-induced climate change, specifically global warming (Harris, 1984; Janzen, 1986; Lovejoy et al., 1986; Wilcove, 1987; Reid and Miller, 1989; Wilson, 1989; Ehrlich, 1990; Norse, 1990; Sisk et al., 1994).

Biological diversity is defined as the variety and variability among living organisms and the ecological complexes in which they occur (Office of Technology Assessment, 1987). It encompasses compositional, structural and functional diversity (Franklin, 1988) at the regional-landscape, ecosystem-community, species-population and genetic levels (Noss, 1990). As a conservation issue, it is not concerned so much with maximizing the number of species in a given area (Noss, 1990), as with the rarity, vulnerability and viability of ecosystems and species (Hunter, 1990). Biological diversity has an indispensable value to society (Huston, 1993) in that it (1) serves as a reservoir of genetic material that enhances productivity and stress tolerance of domesticated species and a source of new medicines, energy and industrial feedstock, (2) provides ecological services such as amelioration of climate, water purification, soil stabilization and flood control and (3) provides animals and natural landscapes which have an overall benefit on human health and well-being through various forms of outdoor recreation (Ledig, 1988; Riggs, 1990; Burton et al., 1992).

Numerous methods for quantifying diversity have been developed, the most basic of these being species (alpha) diversity at local levels (Pielou, 1969; Peet, 1974, 1978). Other measurements assess diversity at progressively larger scales using data derived from the alpha level (Magurran, 1988). Beta diversity expresses variation in species composition between two adjacent communities along an environmental gradient (Kimmins, 1987). Gamma diversity expresses species variation across large geographic units such as landscapes. Epsilon (regional) diversity is the total diversity of a group of areas for which gamma diversity has been computed. Measures such as pattern diversity reflect the spatial, temporal and compositional elements of diversity which explain patterns of landscape complexity (Scheiner, 1992). Dynamic concepts like the diversity spectrum (Margalef, 1994) and various methods for diversity ordering (Tothmeresz, 1995) have also been recently proposed.

Although diversity in biological communities was at one time linked to ecosystem stability (Clements and Shelford, 1939; MacArthur, 1955), it is now recognized that the relationship between diversity and stability is complex and unpredictable (Watt, 1968; May, 1974; Orians, 1975; Whittaker, 1975; Kikkawa, 1986; Pimm, 1986). Nonetheless, diversity does influence various biological functions and the manner in which ecosystems respond to disturbance (van der Maarel, 1993; Risser, 1995). Also, the structural and functional elements of diversity are related to ecological processes operating at multiple temporal and spatial scales (Franklin, 1988). Thus, biological diversity is thought to be important in overall ecosystem function (Solbrig, 1991; Baskin, 1994).

Biological diversity will be a central theme of new ecosystem management initiatives and the concept could serve as a broad framework for considering many contemporary resource management issues (Probst and Crow, 1991). Numerous efforts to incorporate biodiversity into forest management and planning are encouraging (Avers, 1992; Covington and Debano, 1993; Kangas and Kuusipalo, 1993). However, a key information component needed to develop

management plans for sustaining (or restoring) biological diversity in forest ecosystems is baseline data collected from relatively undisturbed stands. As a result of systematic timber harvest, old-growth and mature forests suitable for this purpose have become increasingly scarce.

Old-growth (and some mature) stands characteristic of the coniferous forests on the Cascade Mountains in southwestern Washington were examined to obtain baseline data concerning plant community diversity at multiple spatial scales across the landscape. Climatic, physiographic, edaphic and floristic attributes were compared with various indices of diversity measured at alpha, beta, gamma and epsilon levels to (1) identify the principal physical and biological factors which influence patterns of forest plant diversity at local and landscape scales and (2) develop baseline diversity data useful in guiding the sustainable management and ecological restoration of coniferous forest ecosystems in this and similar environments.

2. Methods and materials

2.1. Study site

This study was conducted on the Gifford Pinchot National Forest in southwestern Washington state (46°00′N, 121°45′W). The 465 000 ha study area is located in the Southern Washington Cascades Physiographic Province, bounded by Mount St. Helens on the west, Mount Rainier on the north, Mount Adams on the east and the Columbia River Gorge on the south (Franklin and Dyrness, 1973). This area is characterized by numerous ridges that are separated by steep, deeply dissected valleys. These ridges crest at elevations between 1200 and 2000 m and comprise a landscape which is dominated by volcanic peaks of ≈4000 m.

The climate is humid marine and strongly influenced by weather systems originating over the Pacific Ocean (Lahey, 1979). The mountainous terrain of this landscape results in a variety of local climatic conditions. Annual precipitation is abundant, ranging from 1500 mm at lower elevations to 3600 mm on the highest mountains, where, in winter, much of this accumulates as snow (U.S. Weather Bureau, 1965). The western slopes of the Cascades receive substantially more precipitation than the drier eastern slopes, with the peak of this arriving in winter (Bailey, 1995). Except on the highest mountain peaks, temperatures are relatively mild averaging 2°C during January and 15°C in July (Lahey, 1979).

At least 90% of the surface geology in this area is comprised of andesite and basalt flows and associated breccias and tuffs (Franklin and Dyrness, 1973). Faulted and folded andesitic breccias containing interbedded andesite and basalt from the Eocene and lower Oligocene are widely distributed west of the Cascade crest. Flows of andesite and breccia from the upper Oligocene and lower Miocene occur less frequently, in scattered locations. Columbia River basalts from the middle Miocene extend into this area from the east. Pyroclastic and andesite flows of Pleistocene and recent origin are common on the slopes of Mount Rainier, Mount Adams and Mount St. Helens. Vesicular basalt lavas are widespread in the area near Mount Adams. Deposits of granodiorite, sandstone, siltstone and shale are uncommon and highly localized.

Pumice deposits of variable age, origin and thickness are common in the vicinity of volcanic peaks (Franklin and Dyrness, 1973). Volcanic ash, pumice, pyroclastic materials and other ejecta are prominent surface deposits. Alpine glacial activity during the Pleistocene resulted in episodes of erosion and deposition and the formation of lakes in several mountain valleys. The most widespread soils developed in parent materials consisting of pumice, basalt and andesite. Soils developing on deep pumice are typically Cryorthods and Haplorthods, while those on mixed pumice and basic igneous materials are Dystrandepts and Vitrandepts. These soils have poorly developed horizons and textures ranging from gravelly sandy loam to silt loam. Well developed Haplohumults, having a loam to clay loam A horizon and clay loam to silty clay B horizon, are common west of the Cascade crest. Haplorthods and Hapludalfs, with a gravelly sandy loam texture and iron rich B horizon, have developed on glacial and glaciofluvial deposits. Coarse-textured Xeropsamments are typical on alluvial materials. Haploxeralfs, with textures ranging from silt loams to loams, are common east of the Cascade crest.

Vegetation is dominated by old-growth coniferous forest interrupted infrequently by alpine meadows,

occurring at the highest elevations (Franklin, 1966; Franklin and Dyrness, 1973). These forests are characterized by an uneven-aged structure (Franklin and Spies, 1991; Spies and Franklin, 1991) and overstories contain numerous tree species including Douglas-fir (*Psuedotsuga menziesii*), western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), grand fir (*Abies grandis*), noble fir (*A. procera*), Pacific silver fir (*A. amabilis*), Alaska yellow-cedar (*Chamaecyparis nootkatensis*), mountain hemlock (*T. mertensiana*), subalpine fir (*A. lasiocarpa*), Engelmann spruce (*Picea engelmannii*), western white pine (*Pinus monticola*), western larch (*Larix occidentalis*) and lodgepole pine (*P. contorta*). The understory shrub layer is typically composed of Cascades azalea (*Rhododendron albiflorum*), Alaska huckleberry (*Vaccinium alaskaense*), big huckleberry (*V. membranaceum*), fool's huckleberry (*Menziesia ferruginea*), thimbleberry (*Rubus parviflorus*), oceanspray (*Holodiscus discolor*), creeping snowberry (*Symphoricarpos mollis*), dwarf Oregongrape (*Berberis nervosa*), salal (*Gaultheria shallon*), Devil's club (*Oplopanex horridum*), California hazel (*Corylus cornuta*) and Pacific dogwood (*Cornus nuttallii*). Beargrass (*Xerophyllum tenax*), queencup beadlily (*Clintonia uniflora*), Cascade aster (*Aster ledophyllus*), Newberry's knotweed (*Polygonum newberryi*), green fescue (*Festuca viridula*), coolwort foamflower (*Tiarela unifoliata*), starflower (*Trientalis latifolia*), western fescue (*F. occidentalis*), pinegrass (*Calamagrostis rubescens*), elk sedge (*Carex geyeri*), vanillaleaf (*Achlys triphylla*), twinflower (*Linnaea borealis*), fairybells (*Disporum hookeri*), swordfern (*Polystichum munitum*), ladyfern (*Athyrium filix-femina*), skunk-cabbage (*Lysichitum americanum*), Oregon oxalis (*Oxalis oregana*) and dogwood bunchberry (*C. canadensis*) are among the prominent herbaceous plants.

2.2. Disturbance history

The old-growth forests in this study area have developed over a period of several centuries and been influenced by a variety of disturbance agents operating at multiple temporal and spatial scales (Hemstrom, 1979; Franklin et al., 1981). Periodic outbreaks of insects and pathogens have caused localized episodes of tree mortality, while windstorms and floods have resulted in relatively small-to-moderate scale disruptions. Fire, especially during the warm and dry growing season, has been a more frequent and often large-scale disturbance (Hemstrom and Franklin, 1982; Agee, 1991). Infrequent volcanic eruptions have had localized effects, such as the early seral-tree species composition of forests near timberline on the slopes of Mount St. Helens (Franklin and Dyrness, 1973). On a millennial time scale, volcanoes have produced large-scale catastrophic disturbances, such as the 1980 eruption of Mount St. Helens which dramatically affected the northwestern and north-central portion of the study area.

Since European settlement of this region in the early 1800s, the area occupied by these old-growth forests has been progressively reduced to about 17% of its original extent (Spies and Franklin, 1988). Today, much of this area supports second growth forests that have regenerated following land-clearing, logging and wildfire (Franklin and Dyrness, 1973). These forests are relatively young, early seral stands with an even-aged structure and dominated by Douglas-fir, the preferred species of the regional timber industry. Since systematic clearcutting was projected to virtually eliminate the old-growth forests in this region by the mid-twenty-first century, an extensive analysis of the diversity present in these unique ecosystems was conducted to establish baseline data for the native forest plant species on this landscape and provide managers with information useful in guiding future ecological restoration efforts.

2.3. Study design

During the May to September field season from 1979 to 1988, ecological data were collected on 1200 sample plots distributed across the landscape, representing the full range of elevations, aspects, slopes, landforms and other environmental variables (Brockway et al., 1983; Topik et al., 1986; Topik, 1989). These circular plots were 25 m in diameter (500 m^2) and established in old-growth (and some mature) forest stands that had as little recent disturbance as possible. The plots were subjectively selected without preconceived bias to represent the floristic variation within the study area (Mueller-Dombois and Ellenberg, 1974). The primary purpose of this endeavor was to gather physiographic, edaphic, floristic and produc-

tivity information useful in developing a comprehensive ecological classification system for the forest ecosystems on this landscape. This classification system could then be used to partition the landbase into units of similar ecological characteristics that would respond in similar fashion to various forest management treatments and activities (Brockway and Topik, 1984). The abundance of environmental data developed during the course of this program provided a unique opportunity to analyze the relationship between numerous physical and biological variables and their influence upon patterns of diversity at local and landscape scales.

2.4. Measurements

At each sample location, physiographic data including elevation, aspect, slope, landform, topographic position and microtopography were recorded. A soil pit was then excavated to a depth of 1.5 m (or less when bedrock or groundwater were encountered) and a complete profile description developed including soil parent material, total soil depth, coarse fragment content, effective soil depth, rooting depth, soil horizon thickness, texture and acidity and forest floor type (Klinka et al., 1981). A list of vascular flora was prepared, including ocular estimates of the percent cover of each plant species (vertical projection of foliage). Identification and nomenclature for plant species were consistent with taxonomic authorities (Hitchcock et al., 1977). Basal area was then quantified using a thin prism at 10 points in each stand with five trees of each overstory species being measured to assess productivity. Total tree height and depth of live crown were measured using a clinometer and diameter at 1.4 m (DBH) was determined with a measuring tape. Increment cores at DBH were also collected to estimate tree age and growth rate.

A combination of subjective and objective methods were used to develop the ecological classification from these data. Initial plot ordering tables (Volland and Connelly, 1978) were compared with detrended correspondence analysis (DECORANA) results (Gauch, 1977, 1982). A two-way indicator species analysis (TWINSPAN) was used to examine the classification value of various species and plot groups. These results served as the basis for re-ordering the subjective association groupings. The final plant associations were based on key classification criteria, including (1) distinctive flora, (2) different productive potentials, (3) distinctive management considerations and (4) ease of identification in the field (Hall, 1988).

The resulting 53 forest plant associations were then used as the basis for analyzing the alpha, beta, gamma and epsilon diversity present on this landscape. Climatic (precipitation, growing season length, temperature), physiographic (elevation, aspect, slope, topographic position), edaphic (parent material, total depth, rooting depth, horizon thickness, humus type) and floristic (percent canopy cover, tree age, tree density, basal area, quadratic mean diameter, stand density index, stand volume, volume increment) data were first evaluated to discern any relationships between the physical and biological factors and alpha diversity in the plant associations. These factors (independent variables) and diversity values (dependent variables) were analyzed using the least-squares procedure of multiple-regression analysis (Hintze, 1995).

Foliar cover data from each association were used as importance values to compute several measures of alpha diversity (Ludwig and Reynolds, 1988). Species richness (total number of species present) and evenness (the manner in which abundance is distributed among species) are the two principal components of diversity. Species richness is frequently characterized by the number of species present (N_0), abundant species (N_1), very abundant species (N_2), Margalef species richness (R_1) and Menhinick species richness (R_2). Evenness (approaching unity when all species are of equal abundance and declining toward zero when few species dominate) can be described by Pielou's evenness index (E_1), Sheldon's evenness index (E_2), Heip's evenness index (E_3), Hill's evenness index (E_4) and the modified Hill's ratio (E_5). Diversity indices combine species richness and evenness components into a single numeric value. The most commonly used indices of diversity are Shannon's diversity index (H') and Simpson's diversity index (λ).

Computed values for species richness (N_0), Shannon's diversity index (H') and evenness (modified Hill's ratio) for all plant associations were arrayed along the prominent temperature and moisture gradients of the region and summarized as estimates of the mean and variance for each forest series. Beta diversity values, the rate of species turnover (species loss and gain) between plant communities juxtaposed

along an environmental gradient, were then computed (Wilson and Shmida, 1984). Gamma diversity, also termed delta diversity (Whittaker, 1972), the species turnover rate across the geographical gradients of an entire landscape was calculated next (Cody, 1975, 1983). Finally, epsilon diversity, the regional richness of a landscape (number of species present on a landscape), was derived as a function of the interaction among the three independent measures of alpha, beta and gamma diversity (Cowling, 1990). Statistical analysis for computed diversity indices was completed using the bootstrap technique PROC MULTTEST in SAS (Efron and Tibshirani, 1993; Westfall and Young, 1993; SAS Institute, 1996). Adjusted p-values, which maintain a constant Type I error across the full range of comparisons, were used to determine significant differences among means (10 000 bootstrap iterations were used). A probability level of 0.05 was used to discern all significant differences.

3. Results

3.1. Physical and biological factors

Climatic, physiographic and edaphic variables were in general poorly related to the various indices of alpha diversity computed for these forests. Correlation coefficients infrequently exceeded 0.7 and scattergrams revealed no clearly discernible patterns. Elevation was the physical variable most consistently related to alpha diversity, but this correlation was also weak. Biological variables showed consistently high correlations (R>0.7) with all alpha diversity indices, except the Simpson index. Regression analysis indicated that stand volume and canopy cover were most often positively related to plant species richness, diversity and evenness. However, r^2 values rarely exceeded 0.5 and were typically $\leq$0.2, indicating a weak linear relationship between most biological factors and alpha diversity.

3.2. Ecological classification and environmental gradients

Given the weak overall relationship between the physical and biological variables and alpha diversity, the ecological classification system developed during phase I of this study was used to analyze plant diversity at multiple scales across the major environmental gradients of temperature and moisture. A total of 53 plant associations containing 278 total plant species were identified upon this landscape (Table 1). These 53 associations were grouped into four major forest series, designated by the dominant tree species present (mountain hemlock, Pacific silver fir, grand fir and western hemlock). Each forest-plant association is characteristic of a unique set of environmental conditions along the temperature and moisture gradients that dominate this region (Fig. 1). The temperature gradient corresponds to elevation, with average temperatures decreasing with increasing elevation, and the moisture gradient generally coincides with east-west position, the eastern slopes of the Cascades receiving much less precipitation than the western slopes.

3.3. Alpha diversity

Species richness (N_0) ranged from 19 plant species present in the Tsme-Abla2/Fevi association to 84 species in the Tsme/Phem-Vade association (Fig. 2). No clear trend related to temperature or moisture was discernible, except that the most species-poor associations seemed to occur near the extremes of temperature and moisture. The Shannon divesity index (H') ranged from 1.75 in the Tshe-Psme-Arme association to 4.06 in the Tsme/Phem-Vade association (Fig. 3). With a few exceptions, forest plant associations containing the highest diversity (>3.50) generally occurred in the moderate position (cool, mesic) along the environmental gradients. Species evenness (modified Hill ratio) ranged from 0.37 in the Tshe-Psme-Arme and Psme/Acci/Feoc associations to 0.84 in the Tsme/Phem-Vade and Tsme-Pial/Luhi associations (Fig. 4). Overall, evenness appeared to be lower in warmer and drier plant associations and higher in colder or wetter associations.

When summarized by forest series, species richness averages 52, Shannon diversity approximates 3.25 and mean species evenness is 0.64 (Table 2). The grand fir series has significantly lower richness (46.6), diversity (3.05) and evenness (0.55) than most other forest series. The 47 species observed on the typical plot are 56% of the 84 species found throughout this series. The mountain hemlock series also has low species richness (45.3), but the significantly higher evenness

Table 1
Forest plant associations of the southwestern Washington Cascades [a]

Abbreviation	Scientific name	Common name
Tsme series:		
Tsme/Vasc	*Tsuga mertensiana/Vaccinium scoparium*	Mountain hemlock/Grouse huckleberry
Tsme/Vame/Xete	*Tsuga mertensiana/Vaccinium membranaceum/ Xerophyllum tenax*	Mountain hemlock/Big huckleberry/Beargrass
Tsme/Vame/Clun	*Tsuga mertensiana/Vaccinium membranaceum/ Clintonia uniflora*	Mountain hemlock/Big huckleberry/ Queencup beadlily
Tsme/Mefe	*Tsuga mertensiana/Menziesia ferruginea*	Mountain hemlock/Fool's huckleberry
Tsme/Rhal	*Tsuga mertensiana/Rhododendron albiflorum*	Mountain hemlock/Cascades azalea
Tsme/Phem-Vade	*Tsuga mertensiana/Phyllodoce empetriformis–Vaccinium diliciosum*	Mountain hemlock/Red mountain heather–Cascade blueberry
Tsme/Luhi	*Tsuga mertensiana/Luzula hitchcockii*	Mountain hemlock/Hitchcock's woodrush
Tsme-Abla2/Asle2	*Tsuga mertensiana–Abies lasiocarpa/Aster ledophyllus*	Mountain hemlock–Subalpine fir/Cascade aster
Tsme-Abla2/Pone4	*Tsuga mertensiana–Abies lasiocarpa/ Polygonum newberryi*	Mountain hemlock–Subalpine fir/ Newberry's knotweed
Tsme/Juco4	*Tsuga mertensiana/Juniperus communis*	Mountain hemlock/Mountain juniper
Tsme-Pial/Luhi	*Tsuga mertensiana–Pinus albicaulis/ Luzula hitchcockii*	Mountain hemlock–Whitebark pine/ Hitchcock's woodrush
Tsme-Abla/Fevi	*Tsuga mertensiana–Abies lasiocarpa/Festuca viridula*	Mountain hemlock–Subalpine fir/Green fescue
Abam series:		
Abam/Gash	*Abies amabilis/Gaultheria shallon*	Pacific silver fir/Salal
Abam/Bene	*Abies amabilis/Berberis nervosa*	Pacific silver fir/Dwarf Oregongrape
Abam/Vaal-Gash	*Abies amabilis/Vaccinium alaskaense–Gaultheria shallon*	Pacific silver fir/Alaska huckleberry–Salal
Abam/Vaal	*Abies amabilis/Vaccinium alaskaense*	Pacific silver fir/Alaska huckleberry
Abam/Actr-Clun	*Abies amabilis/Achlys triphylla–Clintonia uniflora*	Pacific silver fir/Vanillaleaf-Queencup beadlily
Abam/Titr	*Abies amabilis/Tiarella unifoliata*	Pacific silver fir/Coolwort foamflower
Abam/Opho	*Abies amabilis/Oplopanax horridum*	Pacific silver fir/Devil's club
Abam/Rhal	*Abies amabilis/Rhododendron albiflorum*	Pacific silver fir/Cascades azalea
Abam/Mefe	*Abies amabilis/Menziesia ferruginea*	Pacific silver fir/Fool's huckleberry
Abam/Vame/Clun	*Abies amabilis/Vaccinium membranaceum/Clintonia uniflora*	Pacific silver fir/Big huckleberry/Queencup beadlily
Abam/Vame/Xete	*Abies amabilis/Vaccinium membranaceum/Xerophyllum tenax*	Pacific silver fir/Big huckleberry/Beargrass
Abgr series:		
Abgr/Hodi	*Abies grandis/Holodiscus discolor*	Grand fir/Oceanspray
Abgr/Acci-Beaq/Trla2	*Abies grandis/Acer circinatum-Berberis aquifolium/ Trientalis latifolia*	Grand fir/Vine maple–Tall Oregongrape/Starflower
Psme/Acci/Feoc	*Pseudotsuga menziesii/Acer circinatum/Festuca occidentalis*	Douglas-fir/Vine maple/Western fescue
Abgr/Caru	*Abies grandis/Calamagrostis rubescens*	Grand fir/Pinegrass
Abgr/Cage	*Abies grandis/Carex geyeri*	Grand fir/Elk sedge
Abgr/Conu/Actr	*Abies grandis/Cornus nuttalliil/Achlys triphylla*	Grand fir/Pacific dogwood/Vanillaleaf
Abgr/Symo/Actr	*Abies grandis/Symphoricarpos mollis/Achlys triphylla*	Grand fir/Creeping snowberry/Vanillaleaf
Abgr/Bene/Actr	*Abies grandis/Berberis nervosa/Achlys triphylla*	Grand fir/Dwarf Oregongrape/Vanillaleaf
Abgr/Coco2/Actr	*Abies grandis/Corylus cornuta/Achlys triphylla*	Grand fir/California hazel/Vanillaleaf
Thpl/Actr	*Thuja plicata/Achlys triphylla*	Western redcedar/Vanillaleaf
Abgr/Vame/Libo2	*Abies grandis/Vaccinium membranaceum/Linnaea borealis*	Grand fir/Big huckleberry/Twinflower
Abgr/Vame/Clun	*Abies grandis/Vaccinium membranaceum/Clintonia uniflora*	Grand fir/Big huckleberry/Queencup beadlily
Abgr/Rupa/Diho	*Abies grandis/Rubus parviflorus/Disporum hookeri*	Grand fir/Thimbleberry/Fairybells
Tshe series:		
Tshe/Opho/Pomu	*Tsuga heterophylla/Oplopanex horridum/Polystichum munitum*	Western hemlock/Devil's club/Swordfern
Tshe/Atfi	*Tsuga heterophylla/Athyrium filix-femina*	Western hemlock/Ladyfern
Tshe/Lyam	*Tsuga heterophylla/Lysichitum americanum*	Western hemlock/Skunk-cabbage
Tshe/Vaal/Oxor	*Tsuga heterophylla/Vaccinium alaskaense/Oxalis oregana*	Western hemlock/Alaska huckleberry/Oregon oxalis

Table 1 (continued)

Abbreviation	Scientific name	Common name
Tshe/Titr	*Tsuga heterophylla/Tiarella trifoliata*	Western hemlock/Coolwort foamflower
Tshe/Pomu	*Tsuga heterophylla/Polystichum munitum*	Western hemlock/Swordfern
Tshe/Pomu-Oxor	*Tsuga heterophylla/Polystichum munitum–Oxalis oregana*	Western hemlock/Swordfern-Oregon oxalis
Tshe/Vaal/Coca	*Tsuga heterophylla/Vaccinium alaskaense/Cornus canadensis*	Western hemlock/Alaska huckleberry/ Dogwood bunchberry
Tshe/Vaal-Gash	*Tsuga heterophylla/Vaccinium alaskaense–Gaultheria shallon*	Western hemlock/Alaska huckleberry–Salal
Tshe/Bene	*Tsuga heterophylla/Berberis nervosa*	Western hemlock/Dwarf Oregongrape
Tshe/Bene-Gash	*Tsuga heterophylla/Berberis nervosa–Gaultheria shallon*	Western hemlock/Dwarf Oregongrape–Salal
Tshe/Actr	*Tsuga heterophylla/Achlys triphylla*	Western hemlock/Vanillaleaf
Tshe/Bene/Pomu	*Tsuga heterophylla/Berberis nervosa/Polystichum munitum*	Western hemlock/Dwarf Oregongrape/Swordfern
Tshe/Conu/Actr	*Tsuga heterophylla/Cornus nuttallii/Achlys triphylla*	Western hemlock/Pacific dogwood/Vanillaleaf
Tshe/Gash	*Tsuga heterophylla/Gaultheria shallon*	Western hemlock/Salal
Tshe-Psme/Hodi	*Tsuga heterophylla–Pseudotsuga menziesii/ Holodiscus discolor*	Western hemlock–Douglas-fir/Oceanspray
Tshe-Psme-Arme	*Tsuga heterophylla–Pseudotsuga menziesii–Arbutus mensiesii*	Western hemlock–Douglas–fir-Madrone

[a] Total number of associations=53. Total plant species=278.

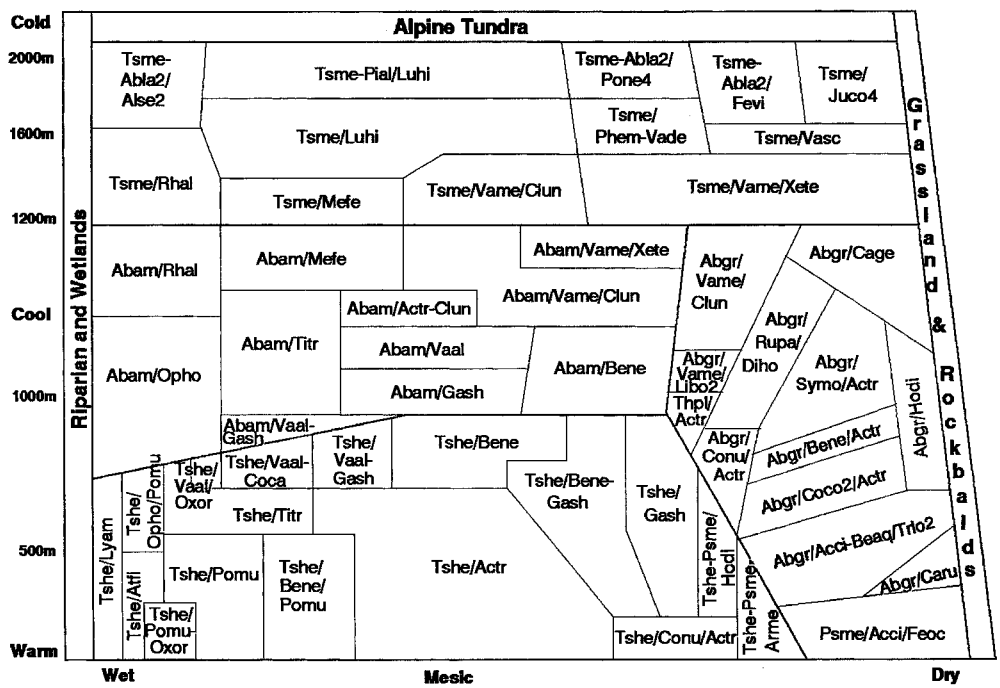

Fig. 1. Forest plant associations and environmental gradients of temperature (elevation) and moisture (wet-western-slopes-to-dry eastern-slopes).

value (0.76) results in a slightly higher diversity index (3.16). The low number of species found in the typical mountain hemlock association is not indicative of the overall species richness (175) present throughout this series. The western hemlock series has significantly greater species richness (56.6), but the low species evenness (0.57) results in a modest diversity index (3.24). The 57 species found on the typical plot are

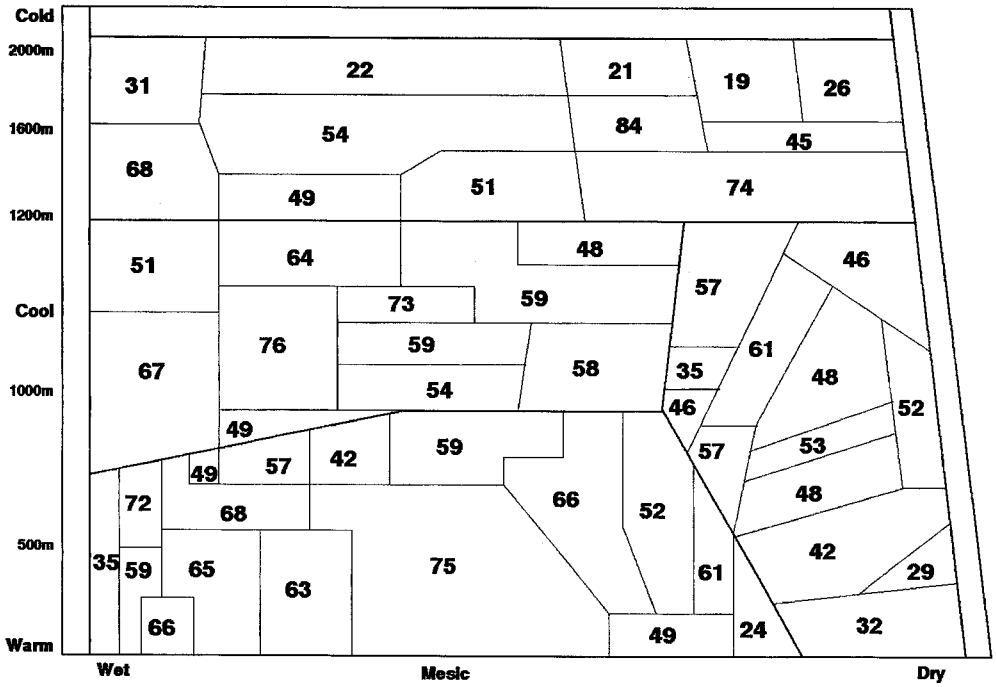

Fig. 2. Species richness (N_0) in forest plant associations arrayed along temperature and moisture gradients.

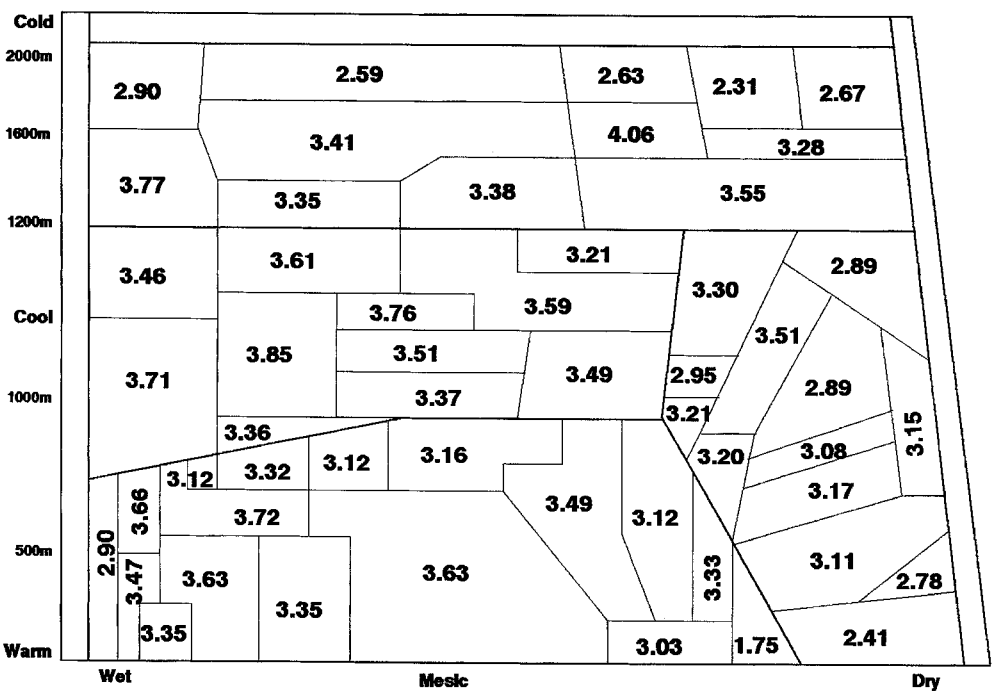

Fig. 3. Shannon diversity index (H') of forest plant associations arrayed along temperature and moisture gradients.

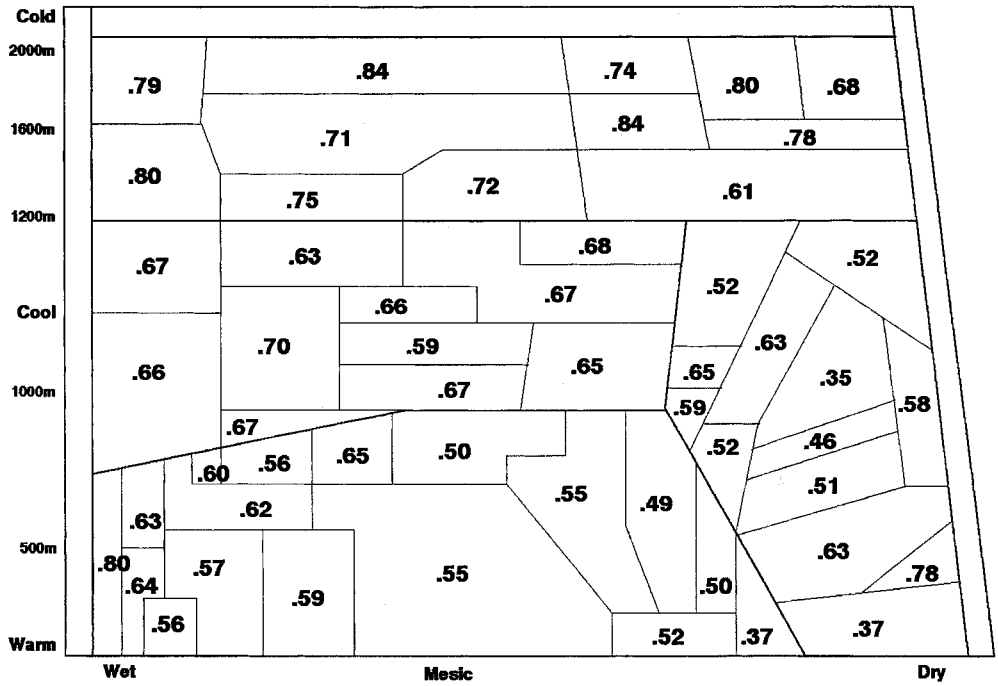

Fig. 4. Species evenness (modified Hill ratio) in forest plant associations arrayed along temperture and moisture gradients.

Table 2
Summary of alpha diversity by forest series

Forest series	Species richness (N_0)	Shannon diversity index (H')	Evenness (modified Hill ratio)
Tsme	45.3 [a]	3.16 [a]	0.76 [c]
Abam	59.8 [b]	3.54 [b]	0.66 [b]
Abgr	46.6 [a]	3.05 [a]	0.55 [a]
Tshe	56.6 [b]	3.24 [a]	0.57 [a]
Mean	52.0	3.25	0.64

[a,b,c] Means in the same column followed by a different superscript (a, b or c) are significantly different at the 0.05 level.

61% of the 94 species observed throughout this series. The Pacific silver fir series has significantly higher plant species richness (59.8), evenness (0.66) and diversity (3.54) than most other forest series. The 60 species present on the typical plot are 77% of the 78 vascular plant species found throughout this series.

3.4. Species turnover rates

The rate of species loss and gain between plant communities juxtaposed along an environmental gradient (beta diversity) ranged from 0.03 between Abam/Titr and Abam/Actr-Clun associations to 0.76 between Tsme-Abla2/Alse2 and Tsme/Rhal associations (Fig. 5). The lowest turnover rates were observed between plant associations that were warm to cool and wet to mesic, and in some cases dry. Cold forest plant associations in the mountain hemlock series appeared to have the highest rates of species turnover. The rate of species turnover along geographic gradients across the landscape (gamma diversity) ranged from a low of 0.46 to a maximum of 1.00 (Fig. 6). Across the east–west moisture gradient, the turnover rate for warm

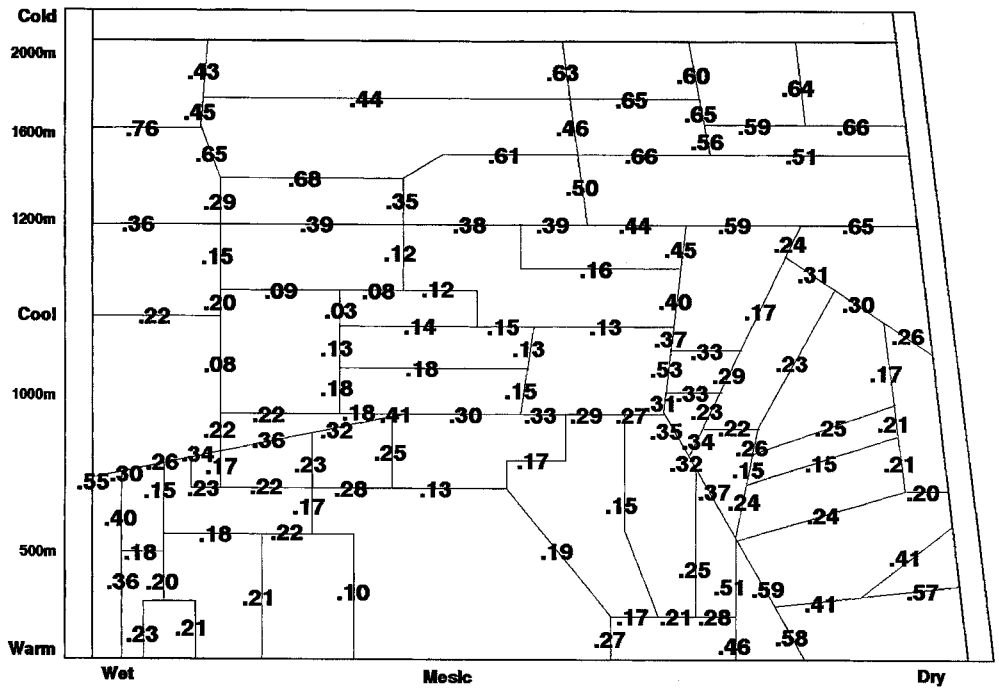

Fig. 5. Beta diversity (B_n), showing species turnover rates between adjacent forest plant associations arrayed along temperture and moisture gradients.

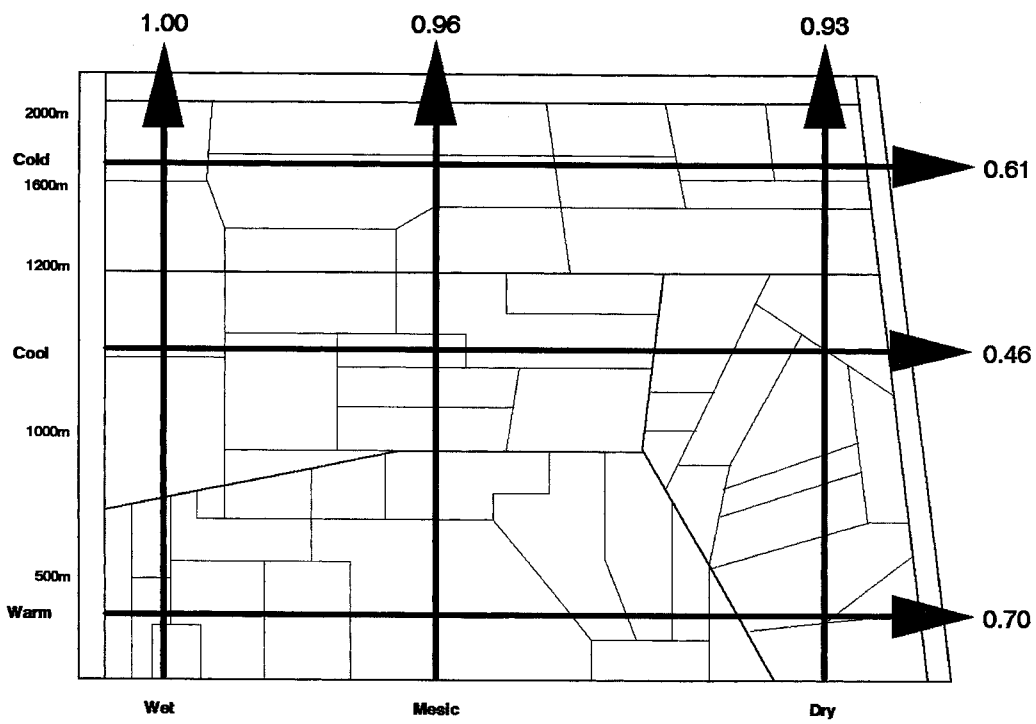

Fig. 6. Gamma diversity (B_m) among forest plant associations, showing cumulative species turnover rates across cold, cool, warm, wet, mesic and dry environmental gradients in the landscape.

plant associations was 0.70, while that for cool associations was 0.46 and for cold associations it was 0.61. Average gamma diversity along this moisture gradient was estimated at 0.59. Across the temperature (elevation) gradient, the turnover rate for wet plant associations was 1.00, with that for mesic associations being 0.96 and for dry associations 0.93. Average gamma diversity along this temperature gradient was 0.96. Mean gamma diversity across this landscape for temperature and moisture was 0.78.

3.5. Diversity along environmental gradients

Across the temperature gradient, alpha diversity (N_0 averaging 50) did not differ significantly among wet, mesic and dry forest plant associations (Table 3). While the lowest rate of sequential species turnover (0.29) was observed along the transect for mesic plant associations, overall beta diversity (0.41) was not significantly different among the wet, mesic and dry associations. The similarity in gamma diversity values (among the wet, mesic and dry plant associations) and the high overall species turnover rate (0.96) along the entire length of the gradient is indicative of the profound influence that temperature (elevation) has upon diversity in these forest plant communities. Across the moisture gradient, alpha diversity was significantly lower among the cold plant associations (N_0=24) than among cool (N_0=60) and warm (N_0=52) plant associations (Table 4). Beta diversity for the warm plant associations (0.30) was significantly greater than that of the cool plant associations (0.18), while the rate of sequential species turnover among the cold plant associations was highest of all (0.58). Modest gamma diversity values (averaging 0.59) for cold, cool and warm plant associations along the entire gradient indicated the moderate overall effect that moisture has on diversity in these plant communities. While temperature and moisture have similar effects upon overall alpha and beta diversity, temperature has significantly greater influence on gamma diversity across all plant associations in these forests (Table 5).

Table 3
Diversity along the temperature gradient from warm low elevation to cold high elevation conditions

Association group	Alpha (N_0)	Beta (B_n)	Gamma (B_m)
Dry plant associations	43 [a]	0.47 [a]	0.93
Mesic plant associations	56 [a]	0.29 [a]	0.96
Wet plant associations	50 [a]	0.47 [a]	1.00
Thermal gradient means	50	0.41	0.96

[a,b,c]Means in the same column followed by a different superscript are significantly different at the 0.05 level.

Table 4
Diversity along the moisture gradient from wet western slope to dry eastern slope conditions

Association group	Alpha (N_0)	Beta (B_n)	Gamma (B_m)
Cold plant associations	24 [a]	0.58 [c]	0.61
Cool plant associations	60 [b]	0.18 [a]	0.46
Warm plant associations	52 [b]	0.30 [b]	0.70
Moisture gradient means	45	0.35	0.59

[a,b,c] Means in the same column followed by a different superscript are significantly different at the 0.05 level.

Table 5
Overall diversity relationship to temperature and moisture gradients

Gradient	Alpha (N_0)	Beta (B_n)	Gamma (B_m)
Moisture	45 [a]	0.35 [a]	0.59 [a]
Temperature	50 [a]	0.41 [a]	0.96 [b]

[a,b] Means in the same column followed by a different superscript are significantly different at the 0.05 level.

3.6. Epsilon diversity

Species richness of this landscape (S_r) was predicted as a function of the three independent measures of alpha, beta and gamma diversity (Table 6). Mean alpha diversity was 52.3. Beta diversity (B_n) along the temperature gradient was 2.42, along the moisture gradient was 2.00 and the mean along both gradients was 2.21. Gamma diversity (B_m) along the temperature gradient was 0.96, along the moisture gradient was 0.59 and the mean along both gradients was 0.78. Thus, S_r along the temperature gradient was calculated as 350.6, a 26% overestimate relative to the 278 plant species observed. The S_r along the moisture gradient was computed to be 249.5, a 10% underestimate of the actual number of species present. However, the combined S_r for both gradients resulted in an estimate of

Table 6
Influence of temperature and moisture on estimates of landscape richness (S_r), epsilon diversity (E)

Forest series	Alpha diversity (N_0)	Beta diversity (B_n+1)	Gamma diversity (B_m+1)	Predicted Spp. # (S_r)	Observed Spp. # (E)	P/O Spp. # (S_r/E)
Temperature gradient:						
Tsme	45.3	1.62	—	73.4	175	0.42
Abam	59.8	1.15	—	68.8	78	0.88
Abgr	46.6	1.28	—	59.6	84	0.71
Tshe	56.6	1.21	—	68.5	94	0.73
all series	52.1	5.26	—	274.0	278	0.99
landscape	52.3	3.42	1.96	350.6	278	1.26
Moisture gradient:						
Tsme	45.3	1.52	—	68.9	175	0.39
Abam	59.8	1.15	—	68.8	78	0.88
Abgr	46.6	1.24	—	57.8	84	0.69
Tshe	56.6	1.24	—	70.2	94	0.74
all series	52.1	5.15	—	268.3	278	0.97
landscape	52.3	3.00	1.59	249.5	278	0.90
Temperature and moisture gradients:						
Tsme	45.3	1.57	—	71.1	175	0.41
Abam	59.8	1.15	—	68.8	78	0.88
Abgr	46.6	1.27	—	59.2	84	0.70
Tshe	56.6	1.23	—	69.6	94	0.74
all series	52.1	5.22	—	272.0	278	0.98
landscape	52.3	3.21	1.78	298.8	278	1.07

298.8, a mere 7% overestimate relative to the number of plant species actually observed.

4. Discussion

4.1. Alpha diversity

The poor overall correlation between plot-level biophysical data and the indices of alpha diversity indicate that this relationship is probably nonlinear and highly complex. However, when the data for plant associations are arrayed along the major environmental gradients of temperature and moisture, several interesting trends emerge. Plant species richness and diversity were lower in associations which characterize environmental extremes such as warm and wet (Tshe/Lyam association), warm and dry (Tshe-Psme-Arme, Psme/Acci/Feoc and Abgr/Caru associations) and cold conditions (Tsme-Abla2/Alse2, Tsme-Pial/Luhi, Tsme-Abla2/Pone4, Tsme-Abla2/Fevi and Tsme/Juco4 associations). Resource availability (excessive or scarce moisture) and geographic isolation at higher elevations probably account for this result. This finding contrasts with that reported for the central Rocky Mountains, where higher species diversity was observed near the environmental extremes than on sites of moderate elevation and moisture regime (Peet, 1978). Evenness among plant species was higher at cold, wet and dry environmental extremes and lower in warm, mesic environments where fewer species dominate over a broader range of sites.

When plant associations were aggregated into forest series, the varied diversity attributes of mountain hemlock, Pacific silver fir, western hemlock and grand fir dominated communities became apparent. Mountain hemlock forests typically have fewer species (45) than lower elevation forests, even though they contained the highest overall number of vascular plant species (175). This lower diversity is thought to be a product of limited site resources (water here is frozen for several months each year), highly varied topography and microclimate (which results in a wide variety

of site types) and geographic isolation (limiting the pool of available species on any specific site). Very high evenness here (0.76) is a result of the severe, cold climate at high elevation which prevents any single or small group of species from gaining dominance. Pacific silver fir forests typically have high species richness (60) and the highest diversity (3.54), with the lowest overall number of vascular plants (78). This high diversity is the product of a moderate climate that is cool and moist, with abundant site resources and reasonable contiguity among various site types. The high level of evenness here (0.66) is the result of a relatively large number of species which repeatedly co-occur on a wide variety of sites, with little dominance by any single species or group. Western hemlock forests typically have high species richness (57), moderate diversity (3.24) and the second greatest overall number of vascular plants (94). This moderately high diversity is the product of a mild climate that is warm and moist, with abundant site resources and high contiguity among various site types. Low evenness here (0.57) is the result of a relatively small number of species which repeatedly occur upon and dominate a variety of sites. Grand fir forests typically have fewer species (47) than most western slope plant communities, the lowest mean diversity (3.16) and the second lowest overall number of vascular plants (84). This low diversity is largely the product of a dry climate where moisture is often limited by drought during the growing season. Low evenness here (0.55) results from a relatively small number of species which repeatedly occur on and dominate various site types.

Patterns of diversity in the forests of the Pacific Northwest are a product of climatological, geological and ecological processes which span several time scales (Whitlock, 1992). Vegetation development was strongly influenced by large-scale controls of climate, with drought during the early Holocene favoring establishment of xeric species. Subsequent moderation of climate during the past 6 000 years led to wider establishment of mesic and hydric plant species and a substantial increase in species richness. Over shorter time scales and on finer landscape scales, plant species distribution was further influenced by local variations in environmental conditions.

Plant species adapted to frequent disturbance prospered during periods of rapid environmental change (Whitlock, 1992). Disturbance is recognized as an important factor in maintaining species diversity by preventing competitive dominance of one or a few species, with maximum diversity resulting from disturbances of intermediate size, frequency and intensity (Roberts and Gilliam, 1995). Fire is the most influential natural disturbance shaping the composition and structure of northwestern forests (Hemstrom and Franklin, 1982; Cwynar, 1987; Morrison and Swanson, 1990), having the most prominent effect on drier plant communities east of the Cascade crest where summer drought is common (del Moral and Fleming, 1979).

Species diversity is reported to be highest in early successional forests just prior to canopy closure and again upon attaining old-growth condition. Mechanisms, thought as responsible for peak alpha diversity in old-growth forests of the Pacific Northwest, include (1) the presence of favorable levels of site resources, especially light and moisture, (2) increased spatial (vertical and horizontal) heterogeneity of resources and environments, and (3) long time intervals without intense fire (Spies, 1991; Halpern and Spies, 1995). The presence of 278 vascular plant species in 53 associations on this landscape is testimony to the high diversity of these old-growth forests. However, several limitations of the study design must be noted in interpreting these findings. Sampling was conducted only in forests, excluding the flora of meadow communities which are a component of this landscape. Only vascular plants were sampled, thus the rich flora of lichens, mosses and other plant groups were not included. Very few rare plants were recorded, therefore the species list is not exhaustive. And the nature of the sampling protocol limited the amount of possible spatial analysis.

4.2. *Turnover rates*

Beta diversity among mountain hemlock associations was quite high, with sequential turnover rates generally exceeding 0.50 and approaching 0.80. This may be attributed to high variation in local microclimates and topography which results in a substantial amount of geographical isolation among sites. Close examination of the Tsme series reveals that it is composed of two distinct tiers of plant associations: those at the highest elevations (>1600 m) bordering

alpine meadows and those at somewhat lower elevations (≤1600 m) bordering the Abam and Abgr series. In the higher tier, are lower diversity forests which occupy the most climatically severe and geographically isolated sites. In the lower tier, are forests of substantially higher alpha diversity and lower beta diversity, indicating a slightly milder microclimate and somewhat greater contiguity among site types.

Beta diversity among Pacific silver fir associations is quite low, with sequential turnover rates always <0.25 and frequently <0.15. These low rates are likely the result of relatively uniform microclimate, low site heterogeneity and high contiguity among site types. Beta diversity among western hemlock associations and sequential turnover rates among grand fir associations are relatively moderate, typically <0.35. However, higher beta diversity values were observed near wet or dry associations. These turnover rates appear to be indicative of intermediate conditions in terms of microclimate, site heterogeneity and site type contiguity.

Along the moisture gradient, significantly fewer species were present in plant associations at high elevation (24) than at middle (60) or low (52) elevations. A significantly higher sequential turnover rate also occurred in plant associations at high elevation (0.58) than in those at low (0.30) and middle (0.18) elevations. Overall species turnover rates were lowest among middle elevation (0.46) associations, gamma diversity being greatest among the low (0.70) and high (0.61) elevation associations. Moisture appears to have the greatest influence on species numbers and sequential turnover rates at high elevation where available water is seasonally limited by low temperatures. Moisture conditions at middle elevations seem to provide an 'optimum' environment, which supports the highest number of species per site and lowest rates of sequential turnover. Along the temperature gradient, sequential turnover rates ranged from 0.29 for mesic plant associations to 0.47 for the wet and dry associations. However, these beta diversity values were not significantly different. The high rates of overall species turnover (0.93–1.00) indicate that temperature has a major influence upon gamma diversity.

Overall plant species turnover rates at the landscape scale were influenced significantly more by temperature than moisture. This is likely a result of the mountainous terrain with seasonally severe and variable climate. At the stand level, temperature and moisture have nearly equal influence upon species numbers and turnover rates, because of relatively small environmental differences within associations and between adjacent associations. Temperature appears to be a more important determinant of environmental severity because of its high degree of control over biologically mediated processes (e.g. the physiological Q_{10}) and influence upon the availability of site resources. Although moisture is abundant as precipitation at high elevations, low seasonal temperatures limit biologically available moisture, water being held as snow and ice for many months during the year.

These findings are broadly in agreement with results from studies of forests in British Columbia (Rey Benayas, 1995), California (Richerson and Lum, 1980), Washington (del Moral and Fleming, 1979) and Colorado (Peet, 1978), which also identified climatic and topographic variables as important influences upon diversity. Few empirical or theoretical insights concerning the control of turnover rates have been put forth, despite their importance in determining species richness upon a landscape (Cowling, 1990). Displacement and divergence associated with the arrival of additional species along habitat gradients (Whittaker, 1977) and habitat diversity as the ultimate determinant of beta diversity (Shmida and Wilson, 1985) are among the suggested mechanisms.

4.3. Landscape richness

Richness of the landscape occupied by old-growth coniferous forests in the southwestern Washington Cascades can be attributed to high overall species turnover among plant communities having moderate-to-high species richness. The broad range of environmental conditions present across this landscape, notably wide variations in temperature with elevation, moisture with east–west position and the degree of geographic isolation especially at high elevation, appeared to account for these high turnover rates. The pronounced affinity of many plant species for certain environmental conditions characteristic of specific site types also contributed to high turnover and species diversity.

By sampling broadly over the study area and incorporating estimates of alpha, beta and gamma diversity, nearly 100% of the species present in this landscape could be accounted for in the epsilon diversity computation. Any species unaccounted for are probably very rare plants or members of meadow and wetland communities interspersed throughout the landscape. The method used appears to be a quite accurate way of predicting landscape richness from analysis of independent diversity components. Indeed, estimates here using both temperature and moisture gradients were within 7% of landscape richness, while those elsewhere relying upon a single soil fertility gradient resulted in a 31% underestimation (Cowling, 1990).

4.4. Determinants of diversity

Diversity is thought to be regulated by environmental factors operating over multiple temporal and spatial scales and, at local scales, is strongly influenced by species richness in surrounding regions (Peet, 1978; Shmida and Wilson, 1985; Caley and Schluter, 1997). Climate and topography appear to have broad effects on diversity across the landscape, while edaphic and biological factors seem to influence diversity more at the site level (del Moral and Fleming, 1979; Richerson and Lum, 1980; Pausas, 1994; Rey Benayas, 1995). Climatic and edaphic conditions are typically less severe at lower elevations and sites at higher elevations seem to be more heterogeneous and less contiguous. High overall plant species richness (175) and turnover rates among mountain hemlock associations are indicative of a relatively severe environment that encourages site specialization and impedes plant species migration among sites.

Perhaps of equal or greater importance than environmental factors in determining the patterns of diversity are the historical development and successional sequences of these old-growth forests (Spies, 1991; Whitlock, 1992). Although the diversity of overstory and understory plants increases gradually over time, cycles of periodic disturbance substantially affect the competitive relationships among species and resulting patterns of diversity (Loucks, 1970; Whittaker, 1977; Halpern and Spies, 1995; Roberts and Gilliam, 1995). Indeed, the diversity in these forests is also a product of historical shifts in climate, periodic volcanic activity, past fire regimes, landslides, windstorms and outbreaks of insects and pathogens.

While the pattern of plant diversity may be broadly related to numerous environmental factors, it is likely the result of complex interactions at multiple scales among physical and biological factors within an historical context of stochastic disturbance events. Theoretically, diversity values could be expected to stabilize as these forests approach steady-state, but fluctuations resulting from disturbance events in the short-term and long-term will likely maintain these communities in a relatively continuous state of disequilibrium. Thus, management efforts which seek to restore and sustain the high diversity levels, characteristic of these old-growth coniferous forests, will need to consider the respective roles of climatic, topographic, edaphic and floristic variables and disturbance dynamics in these unique ecosystems.

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