

Ecological subregions of the Interior Columbia Basin, USA

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Abstract. Land evaluations are not always conducted with adequate understanding of the relevant geologic and climatic contexts and their appropriate scales. This understanding is essential for developing representative sampling, monitoring, and conservation designs, and for pooling results of landscape analysis. To provide context for several regions of the interior northwestern United States, we conducted an ecoregion classification of the interior Columbia River Basin and vicinity ('the Basin'). We grouped land units that are influenced by the same higher order geology and landform features, and share similar areal composition of potential vegetation and climate attributes. We used the TWINSpan procedure to group 7496 watersheds of the Basin into 53 ecological subregions. We evaluated the contribution of attributes to group separation by discriminant analysis, and evaluated subregion robustness to prediction by cross-validation. Classification accuracy ranged from 80 - 97% across the subregions. All watersheds were classified to a subregion, and there were strong resemblances between members of adjacent subregions. Subregions with strong resemblances shared a similar composition of attributes, but differed in relative abundance and attribute combinations. We evaluated the geologic and climatic context of each subregion considering four levels in a nested land unit hierarchy. Most subregions nested at one of at least four scales, but some overlapped. Our results suggest that observation levels for a given ecological phenomenon need not be nested within their appropriate context levels, and across broad geographic areas context of the same phenomenon occurs at different scales.

Keywords: Hierarchy theory; Interior Columbia River Basin; Land system inventory; Land unit hierarchy; Regional assessment; Regionalization; Reference condition; Representativeness assessment.

Abbreviations: ESR = Ecological subregion; PVT = Potential vegetation type.

Introduction

The U.S. Department of Agriculture, Forest Service is responsible for managing the lands and resources of the National Forest System which includes 78 million ha distributed over 155 national forests, 20 national grass-

lands, and various other lands. Regional assessments of public lands in the western United States have documented declining biological diversity, productivity, and sustainability of terrestrial and aquatic ecosystems in the 20th century (Covington et al. 1994; Anon. 1993, 1996; Quigley & Arbelbide 1997; Hann et al. 1997, 1998; Hessburg et al. 1999a). Public land managers now face increasing social pressure to transform existing forests and rangelands to reflect conditions resulting from natural climate and disturbance regimes and patterns of biophysical environments.

In December of 1997, the U.S. Secretary of Agriculture convened a distinguished committee of scientists to review Forest Service planning and offer recommendations. As a result, the Department recommended rule changes to the National Forest Management Act of 1976 (Anon. 1999). Several broad goals shape the proposed rule which represents a landmark paradigm shift for public land management in the U.S. Chief among these is the need to promote social and economic sustainability in the context of sustainable ecosystems. Ecological and socio-economic contexts will be established with regional assessments, and a variety of regionalizations will be needed, e.g., a hydrologic regionalization will be developed that groups watersheds of a region in a manner that minimizes variation in hydrologic processes.

Regionalization in landscape evaluation

Macroclimate accounts for the largest share of environmental variation at a regional scale; weather patterns, atmospheric flows, temperature, precipitation, and solar radiation constrain the biota to that which conforms to the environmental variation of a region (Neilson 1986, 1987). Likewise, climate constrains broad patterns of disturbance and other processes that operate within the context of that environmental variability. Climatic regionalizations are based on generalized air mass boundaries (Mitchell 1976), and vegetation patchiness is correlated with the distribution of major biomes (Neilson 1986). Regional climate zones are defined by their unique climatic regime, zonal soil types, and climatic climax vegetation (Troll 1964;

Walter et al. 1975).

Regional climate zones are modified by geology and landform features (Swanson et al. 1988). Landforms, with their surface shape, geologic substrate, and relief influence variation in ecological factors such as water availability and exposure to radiant solar energy. Consequently, landform is the chief correlate of vegetation and soil patterns because landforms control the variability of factors most important in plant survival and soil development (Hack & Goodlet 1960). Ecological regionalization is a quantitative analog (Gallant et al. 1989) of climatic regionalization, and it is done at a meso-scale. Regionalizations delineate land units that contain similar ecosystems that are influenced by the same higher order climate and disturbance regimes, geology, and landforms (Bailey & Hogg 1986; Bailey et al. 1994b). Derived land units provide scale-appropriate regional context for a variety of landscape evaluations; a few are presented below.

Representativeness assessment. Representativeness assessment is landscape evaluation that characterizes the degree to which the natural¹ variability in a region, considering its climate, biota, and physical environments, is represented in a conservation area. Large heterogeneous areas with mostly unknown patterns are stratified to characterize vegetation patterns and underlying environmental gradients (e.g., see Orłóci & Stanek 1979). Gradient directed transect sampling (Gillison & Brewer 1985; Austin & Heyligers 1989) is used to characterize the distribution of patterns along environmental gradients. Results of studies using these techniques indicate that stratified sampling captures more information about rarity, diversity, and representativeness of biota and environments than standard random sampling designs (Austin & Heyligers 1989, 1991; Austin & Margules 1986).

Characterizing reference conditions. In the interior Columbia River Basin (the 'Basin', Fig. 1), 20th century management activities have transformed forest and rangeland vegetation, disturbance regime, and habitat patterns (Agee 1993; Hann et al. 1997, 1998; Hessburg et al. 1999a; Wisdom et al. 2000). To determine the importance of the detected changes in patterns, one must characterize natural variation in ecosystem states or processes to define the bounds of system behaviour that are relatively consistent over periods of similar climate regime (Millar & Woolfenden 1999). Natural variation can be described for any of a diverse set of ecosystem properties at multiple spatial and temporal

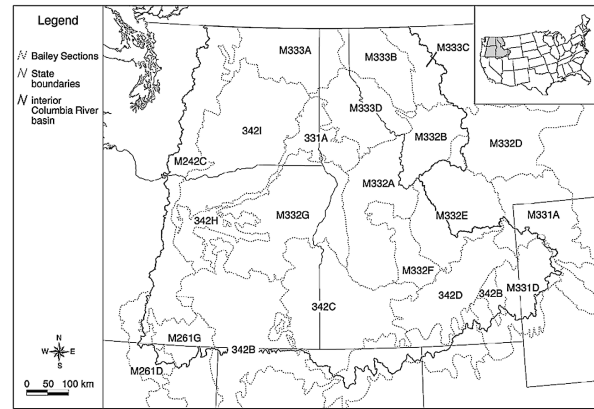


Fig. 1. Map of the interior Columbia River Basin and vicinity with Bailey's Section boundaries. Bailey's Sections are: M242C = Eastern Cascades, M261D = Southern Cascades, M261G = Modoc Plateau, 331A = Palouse Prairie, M331A = Yellowstone Highlands, M331D = Overthrust Mountains, M332A = Idaho Batholith, M332B = Bitterroot Valley, M332E = Beaverhead Mountains, M332F = Challis Volcanics, M332G = Blue Mountains, M333A = Okanogan Highlands, M333B = Flathead Valley, M333C = Northern Rockies, M333D = Bitterroot Mountains, 342B = Northwestern Basin and Range, 342C = Owyhee Uplands, 342D = Snake River Basalts, 342H = High Lava Plains, 342I = Columbia Basin (Bailey et al. 1994a).

scales (Landres et al. 1999; Morgan et al. 1994; Swanson et al. 1994). Ecological regionalization stratifies landscapes of a given geographic area into groups by their similar climatic, biogeographic and topo-edaphic conditions. Groupings can be used to estimate a variety of reference conditions (e.g. Moore et al. 1999; Hessburg et al. 1999b; Stephenson 1999).

Change detection. In the Basin assessment, we quantified change in vegetation spatial patterns (Hessburg et al. 1999a) and pooled results to broad-scale ecological reporting units (ERUs; Fig. 2), but high environmental variability masked much of the change that had occurred. We surmised that grouping landscapes to minimize environmental variation would make changes more apparent. To that end, we stratified our results by subbasins² ($\bar{x}_{\text{area}} = 425\,000$ ha; Seaber et al. 1987) and later by groupings of environmentally similar sub-watersheds³ ($\bar{x}_{\text{area}} = 10\,000$ ha; Fig. 3), and detected increasingly more changes as we minimized environmental variation of pooling strata (Hessburg et al. 1999c). Our twin goals to estimate reference conditions and

¹We use the term 'natural' when referring to conditions that are minimally altered by 20th century management activities, but may reflect patterns resulting from interactions with aboriginal peoples.

²Subbasins represent the 4th level in a US watershed hierarchy and nest within basins which comprise the 3rd level.

³Subwatersheds represent the 6th level in the US watershed hierarchy and nest within watersheds of the 5th level.

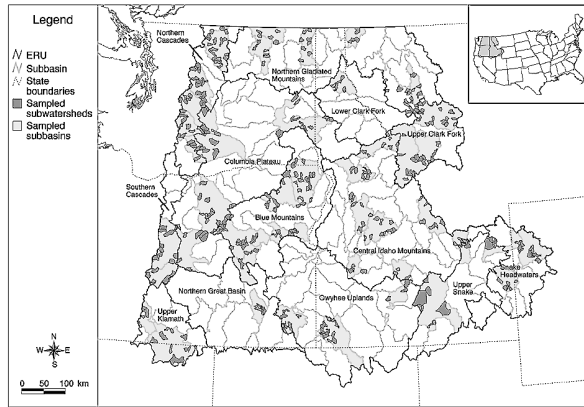


Fig. 2. Map of ecological reporting units (ERUs) and sampled subbasins and subwatersheds in the mid-scale assessment of the interior Columbia River Basin.

detect ecologically important change guided this effort.

Here, we re-examine the Basin study area to (1) group Basin subwatersheds into ecoregions based on their similar geology, landforms, climate, and potential vegetation composition; (2) evaluate the contribution of ecological attributes to group separation; (3) evaluate ecoregion robustness to prediction; and (4) evaluate hierarchical relations of subregions. Our work is based on the assumption that the environmental composition of subwatersheds can be approximated using potential vegetation and climate attributes.

Methods

Study area

The study area, an area of ca. 61 000 000 ha, included all of Washington and Oregon east of the crest of the Cascade Range, Idaho, northwestern Montana, western Wyoming, northern California, northern Utah, and northern Nevada. The following provinces were included in the study area: Northern Rocky Mountain Forest-M333, Cascade-M242, Great Plains-Palouse Dry Steppe-331, Middle Rocky Mountain-M332, Intermountain Semidesert-342, Intermountain Semidesert and Desert-341, Sierran-M261, and Southern Rocky Mountain-M331 (Bailey 1995, Fig. 1). Following, we describe broad differences in environments as an overview of study area conditions (adapted from Bailey 1995).

Landforms of the Northern Rocky Mountain Forest Province (M333) consist of glaciated high mountains separated by broad valleys. Winters can be severe with a heavy snow pack. Dry growing seasons result from westerly air masses; climatic regimes are maritime where Pacific Coast influence dominates and continental elsewhere. Precipitation averages 51-102 cm annually and

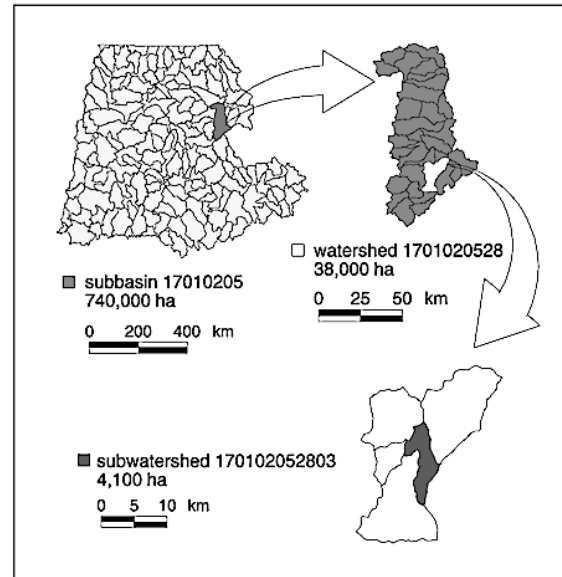


Fig. 3. Hierarchical organization of subwatersheds (6th level), watersheds (5th level), and subbasins (4th level) in the interior Columbia River Basin (see also Seaber et al. 1987).

is concentrated in fall, winter and spring.

Dominant landforms of the Cascade Province (M242) are the result of widespread volcanism. Rugged mountains of the northern Cascades have been repeatedly glaciated, and terrain is steep and dissected with narrow valley bottoms except where glaciated. A maritime climate dominates due to the close proximity of Pacific Coast air masses. Annual precipitation at the crest is 3800 mm; eastern foothills receive as little as 510 mm. Fog partially compensates for droughty summer seasons and most precipitation occurs as snow. To the east, landforms of the Great Plains-Palouse Dry Steppe Province (331) consist of rolling plains and loess-covered basalt tablelands ranging in elevation from 370-1800 m. Plains are flat or rolling and frequently dissected by valleys and canyons. Short grass prairies lie in the rain shadow of the Cascade Range in Washington, where summers are hot and dry, and precipitation reaches its maximum in the winter.

The Middle Rocky Mountains Province (M332) is comprised of the Blue Mountains, Salmon River Mountains, and the basins and ranges of southwestern Montana. Central Idaho and Salmon River Mountains developed from granitic intrusions, the highest peaks of which have been influenced by repeated glaciation. In southwestern Montana, basin and range landforms are mountains with broad alluvial plains. The Blue Mountains in the western portion of the province are comprised of uplifted basalts, and climate is influenced by maritime air flow up the Columbia River. Precipitation in montane forests occurs mostly as snow, and interior valleys are

semi-arid.

The Intermountain Semidesert Province (342) including the Columbia and Snake River plains is the largest province, spanning more than 412 000 km². Landforms consist of flat to rolling plains and tablelands. Above 762 m, plateaus are surrounded by folded and faulted lava ridges. Rich alluvial deposits are widespread in broad flood plains and at the base of the Cascade and central Idaho mountains. Dry lake beds are numerous as are dune and loess deposits. Climate of the high plateaus is cool and semi-arid. Average annual precipitation ranges from a low of 250 mm in the rangelands at the foot of the Cascades, to 51 mm farther east. Winters are long and cold, and summers are hot and dry.

Great Basin and northern Colorado Plateau physiographies form most of the Intermountain Semidesert and Desert Province (341) which enters the study area at its southern edge in Nevada. Landforms are varied with mountains rising from semi-arid shrub-covered plains. Mountains are vegetated, but conifer forests are limited to the upper elevations of high mountains, and forest composition varies by mountain range. Salt flats and playas occur in the lower elevations of basins with interior drainage. Summers are hot, and winters are moderate. Annual precipitation averages 130-490 mm, much of which accumulates as snow.

The Sierran Province (M261) is comprised of the Cascade and Coast Ranges in southern Oregon, the Klamath Mountains of southern Oregon and northern California, and the central Sierra Nevada of California. Landforms consist of precipitous mountains separated by valleys with long, steep elevation gradients. Within the study area, only alpine environments of the Klamath Mountains are glaciated, and subalpine and alpine environments are rugged. Pacific Coast air masses influence the climate; average annual precipitation ranges from 250-1780 mm with rain and snow occurring in roughly equal proportion. Dense, mixed coniferous forests occupy the montane zone (900-2100 m) where the greatest precipitation occurs. Subalpine settings receive as much as 1000-1250 mm of precipitation, with most occurring as snow.

In the Southern Rocky Mountain Province (M331), only the Snake River headlands in southeastern Idaho and western Wyoming reside within the study area. Landforms include glaciated high mountains with peaks of 4300 m or more, intermontane parks (herblands and shrublands) or depressions at intermediate elevations (< 1800 m), and semi-arid valleys at lower elevations. Climate is dry, resulting from continental air masses. Primary influences are prevailing westerly winds and the north-south orientation of major ranges. Average annual precipitation ranges from 250 mm at the lowest

elevations to 1000 mm in the high mountains where most precipitation occurs as snow. Vegetation zones are the result of elevation and latitude gradients, prevailing winds, and the degree of slope exposure.

Overall, there are 7496 subwatersheds in the Basin. Catchments the size of subwatersheds (Fig. 3) were used as sample units because studied landscapes must be large enough to avoid the problem of pattern attribute correlation with size of analysis area (Lehmkuhl & Raphael 1993; O'Neill et al. 1988; Turner 1989). Additionally, we defined landscapes using hydrologic boundaries to enable integrated terrestrial and aquatic ecosystem analysis (e.g., see Rieman et al. 1999).

Mapping ecological subregions

Classes of three ordinal and one categorical variable were assigned to a digital polygon map of all subwatersheds in a geographical information system (GIS). The ordinal variables were mean annual temperature, total annual precipitation, and averaged annual daylight incident short-wave radiative flux ('solar radiation') for the 1989 weather year (Figs. 4A, B and 5A). The categorical variable was potential vegetation group (PVG). The PVG and climate data were available in continuous 1 or 2 km raster maps, respectively.

In the broad-scale Basin assessment (Hann et al. 1997, 1998), 88 potential vegetation types (PVTs) were mapped. A PVT is a theoretical endpoint of succession in the absence of disturbance; it identifies a unique biophysical setting that supports a distinctive plant community (Arno et al. 1985; Steele & Geier-Hayes 1989; cf. Zerbe 1998 for the equivalent concept of Potential Natural Vegetation). From these 88 PVTs, Hann et al. (1997) developed 12 PVGs by clustering similar PVTs based on climate, topography, disturbance regimes, and landforms (Keane & Long 1998, Fig. 4A).

We obtained 2-km mean annual temperature (°C), total annual precipitation (mm), and averaged annual daylight solar radiation (W/m²) raster maps for the 1989 weather year from the University of Montana (Thornton et al. 1997). Thornton et al. (1997) considered 1989 to be an average weather year. Daily meteorological observations from 500 weather stations distributed throughout the Basin were extrapolated to all map pixels using the MTCLIM and DAYMET models (Glassy & Running 1994; Hungerford et al. 1989; Running et al. 1987, Thornton et al. 1997). We classified continuous climate variables to ordinal variables to reduce the size of the matrix submitted to classification. Mean annual temperatures ranging from -10-+14 °C across the study area were arranged into four classes (Fig. 4B). Total annual precipitation data ranging from 0-10000 mm were separated into five natural logarithm classes (Fig. 4B). Solar

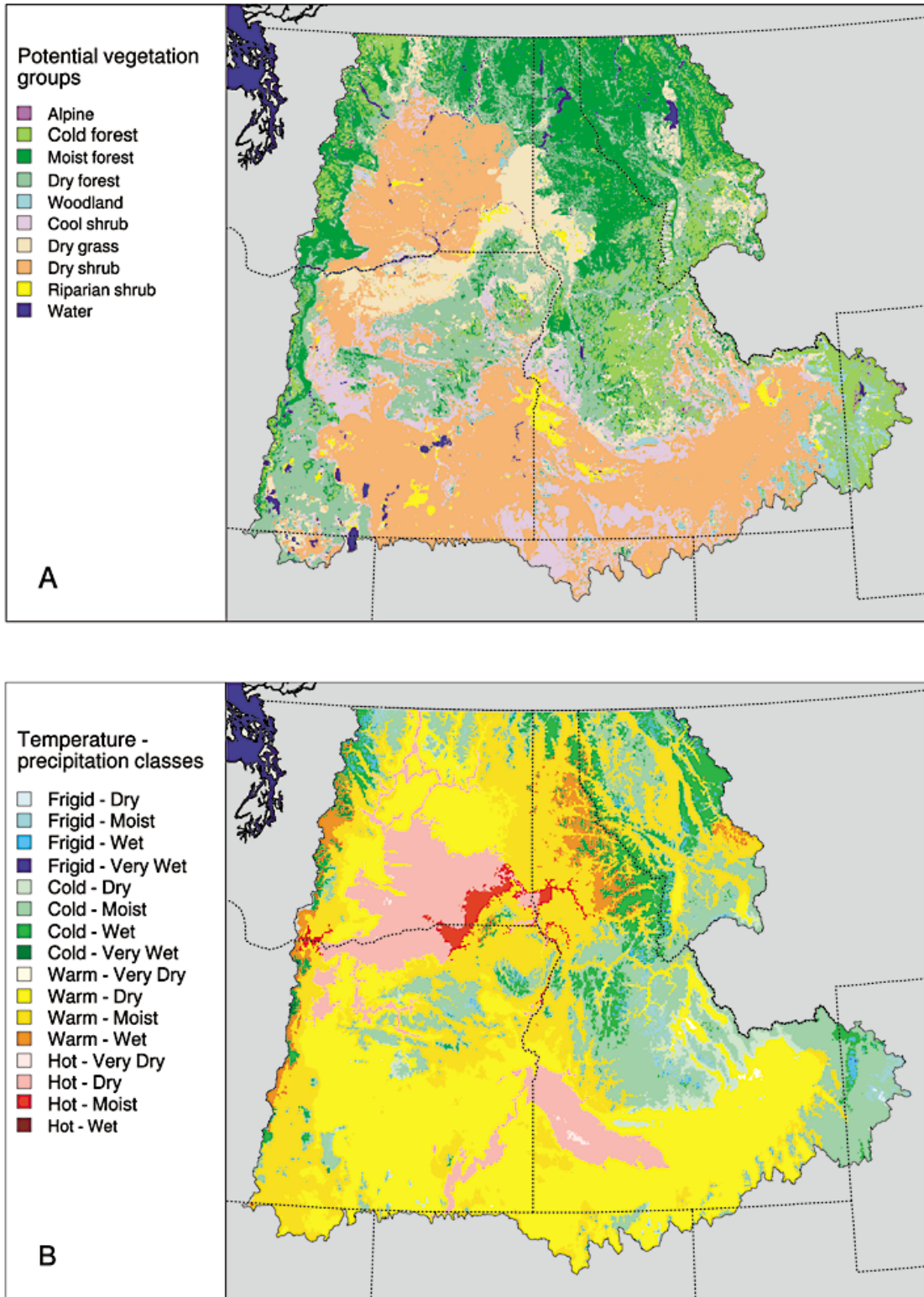


Fig. 4. Broad-scale maps of potential vegetation groups (**A**), and mean annual temperature / total annual precipitation classes (**B**) for the 1989 weather year in the interior Columbia River Basin and vicinity. Temperature classes are: Frigid = -10 - -1 °C; Cold = 0 - 4 °C; Warm = 5 - 9 °C, Hot = 10 - 14 °C. Precipitation classes are: Very dry = 0 - 150 mm/yr; Dry = 150 - 400 mm/yr; Moist = 400 - 1100 mm/yr, Wet = 1100 - 3000 mm/yr; Very Wet = 3000 - 8100 mm/yr.

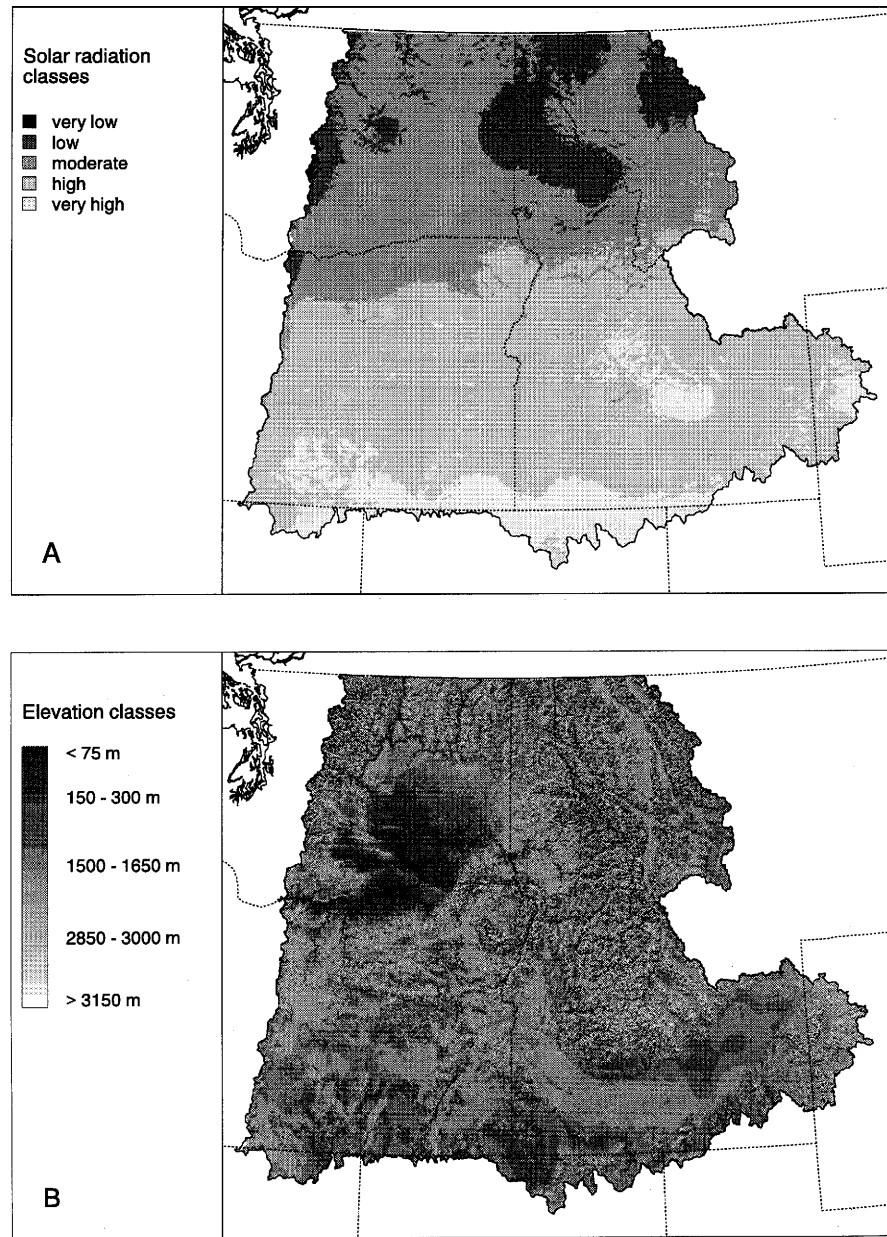


Fig. 5. Broad-scale maps of annual average daylight incident shortwave solar radiative flux (**A**) for the 1989 weather year, and elevation (**B**) in the interior Columbia River Basin and vicinity. Solar Radiation classes are: Very low = 150 - 200 W/m²; Low = 200 - 250 W/m²; Moderate = 250 - 300 W/m²; High = 300 - 350 W/m²; Very high = 350 - 400 W/m².

radiation values ranging from 0-450 W/m², were grouped into six classes (Fig. 5A). We overlaid the climate attribute, PVG, and subwatershed maps to produce a single multivariable map, and determined the area of each subwatershed in each unique class combination. Unique combinations (1440) were the complex attributes used in analysis. For example, a 1-km cell occupied by the complex attribute CF11W25, was comprised of a Cold Forest PVG, a precipitation class of 400-1100 mm, a temperature class of Warm (5-9°C), and a solar radiation class of 200-250 W/m² (Figs. 4 and 5).

Delineating analysis areas

Using the TWINSpan procedure (Hill 1979) as implemented in PC-ORD (version 4.0; McCune & Mefford 1995) and the matrix of all subwatersheds (7496² cells), we found that geographic areas that were substantially different in geology, lithology, climate zones, and land surface forms were grouped when we regionalized the Basin all at once. To improve the sensitivity of our analysis, we partitioned the Basin into 20 areas using Bailey's Sections (Bailey et al. 1994a, b;

Table 1. Primary design criteria used in Bailey's land system inventory (from Bailey et al. 1994b).

Mapping level	Typical area/scale	Primary design criteria	Associated characteristics
Domain	259 000 km ² , 1 : 30 000 000	Climatic zone or group	Repeatable patterns of vegetation classes or subclasses and soil orders or suborders
Division	129 500 km ² , 1 : 15 000 000	Climatic type (Köppen 1931)	Repeatable patterns of vegetation subclasses or formations and soil suborders or great groups
Province	12 950 km ² , 1 : 3 000 000	Hammond's (1964) land surface form, plant climax formation patterns	Repeatable patterns of vegetation formations and soil great groups
Section	2 590 km ² , 1 : 1 000 000	Climax plant series patterns following Kùchler (1964)	Repeatable patterns of vegetation series and soil subgroups or great groups
Subsection	259 km ² , 1 : 500 000	Geologic (e.g., lithologic structure), physiographic (e.g., glaciated mountain slopes), and state-wide climatic zones	Repeatable patterns of vegetation series and soil subgroups
Landtype association	26 km ² , 1 : 250 000	Physiographic and geologic criteria (e.g., fluvial dissected, granitic, mountain breaklands)	Repeatable patterns of plant association groups and soil subgroups
Landtype	2.6 km ² , 1 : 63 000	Physiographic criteria (e.g., landform, shape, elevation, range, drainage, aspect, dissection characteristics)	Repeatable patterns of plant associations, soil families, and stream types
Landtype phase	0.26 km ² , 1 : 24 000	Topographic criteria (e.g., percent slope, position, aspect), plant association, soil family, stream type	Repeatable patterns of soil series, ecological sites, and fishery habitat components
Site	0.026 km ² , 1 : 15 840	Ecological site, phase of soil family, fishery habitat components (e.g., pools, riffles, glides)	

Table 1, Fig. 1). We reasoned that landscape environments were unique if only their broader biophysical contexts were different. Subsequently, an analysis area included subwatersheds of all subbasins that were partially included in a Section. Buffering in this manner enabled us to readily explore similarities among subwatersheds across Section boundaries.

TWINSPAN classification

We submitted the subwatersheds of each analysis area to TWINSPAN, a dichotomized ordination and classification procedure (Hill 1979) used in community ecology analysis. The basic idea of TWINSPAN is that samples can be characterized by 'differential species' (our complex attributes) that are prevalent on one side of a dichotomy (Hill et al. 1975). We plotted attribute abundances during data screening and exploration, and evaluated pseudospecies cut levels for five cuts across a range of values before selecting final levels. Cut levels varied by analysis area according to attribute abundances. TWINSPAN analysis was allowed to proceed until all subwatersheds of an analysis area were assigned to a subregion. TWINSPAN divisions were suspended when there were no apparent differences in attributes or attribute abundance levels when we examined group mean values of all complex attributes. Statistical confidence in group membership and separation was evaluated in later steps using discriminant analysis

and cross validation. Subregions were indicated by their unique TWINSPAN division and analysis area, and a map was generated in a GIS. This process was repeated for each of 20 analysis areas.

Tracing similar TWINSPAN analysis pedigrees

When TWINSPAN analysis was completed for each analysis area, each subwatershed had been regionalized several times as a result of generously overlapped analysis areas. To build final subregion groupings, we traced the TWINSPAN results from all analyses and determined which subwatersheds were grouped in the same manner across the greatest number of analyses. Pedigrees (similar analysis ancestries) of each of the 7 496 subwatersheds were constructed by building a matrix with subwatersheds as samples and the final TWINSPAN division number from each analysis as attributes. Using a presence-absence TWINSPAN analysis, we grouped subwatersheds by most similar TWINSPAN pedigree and mapped the result.

Relations among subregions

To construct a tree that reflected relations among the resulting 54 ecological subregions (ESRs), we conducted two related classifications. In the first, we graphed ESR similarities considering their composition of PVG, climate attributes, and Bailey's Section membership

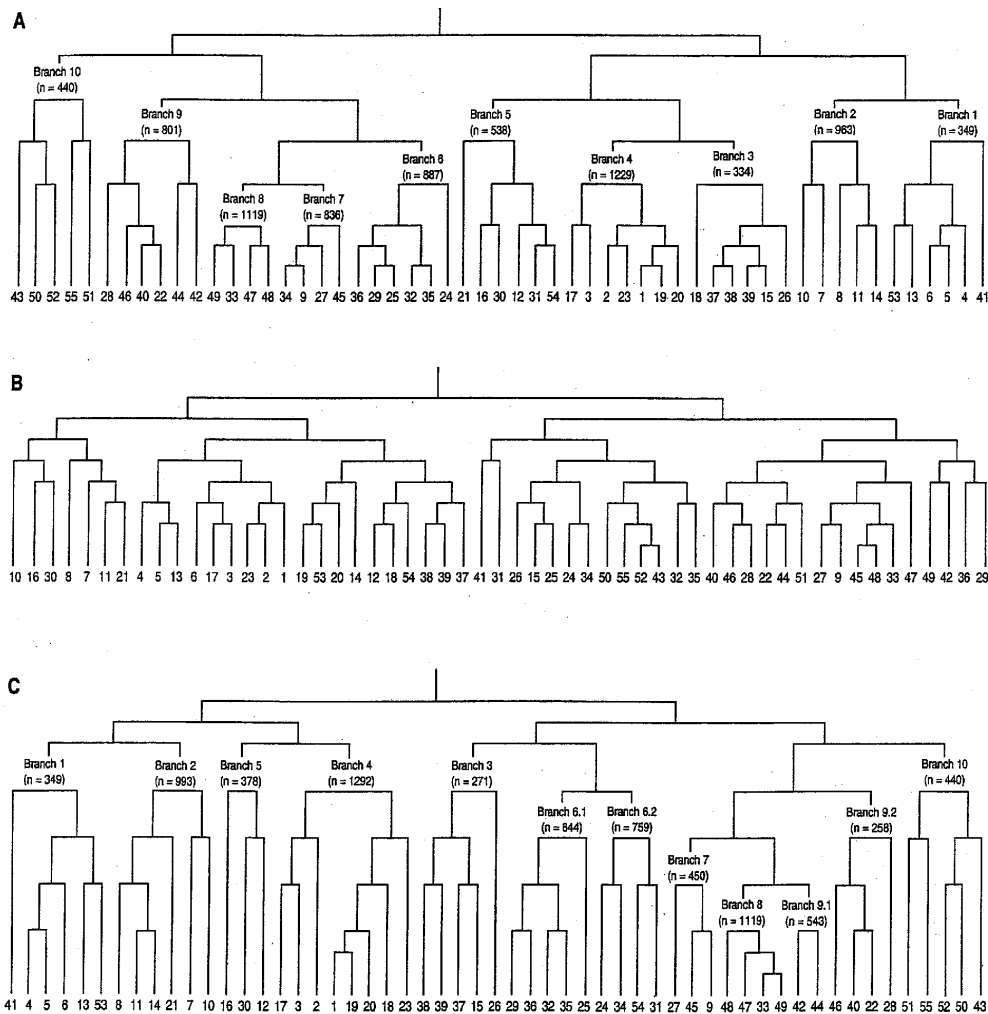


Fig. 6. Dendrograms showing relations among Basin ecological subregions: (A) using simple attributes and Bailey's Section membership; (B) using simple attributes and not considering Section membership; and (C) using complex attributes and Bailey's Section membership (compare with Table 2). Values in parentheses (A and C) are the subwatershed numbers used in discriminant analyses involving each branch.

independently ('simple attributes'). We combined the Bailey's Section, PVG, and climate attribute maps independently with the ESR map, and computed the percentage of ESR area in each attribute. We submitted this matrix to TWINSpan using ESRs as samples, and classes of each attribute as the differential species. In a second analysis, we observed similarities in composition of simple attributes among ESRs when the Bailey's Section membership variable was removed from the classification. Dendrograms resulting from either classification with simple attributes are shown in Figs. 6A and B, respectively.

Obviously, Bailey's Section membership alone separated several ESRs that were similar in simple attribute composition. We questioned whether better groupings may have been missed because no analysis had considered grouping subwatersheds beyond the vicinity of

neighbouring analysis areas. To address this possibility, we identified ESRs that had not been associated with each other in at least one analysis and discovered 14 combinations that had not been evaluated. Each of these were subsequently evaluated using TWINSpan with subwatersheds as samples, and the subwatershed composition of complex attributes as the differential species. In all cases but one, existing ESR groupings were corroborated. In the noted exception, an additional subregion (ESR 55, Fig. 7) was suggested by analysis and added to the map. These analyses showed that ESRs displaying highly similar composition of simple attributes were actually unique due to differences in attribute combinations.

Finally, we constructed a third tree that reflected compositional relations among ESRs. To do so, we overlaid a revised ESR map (with 55 ESRs) with the

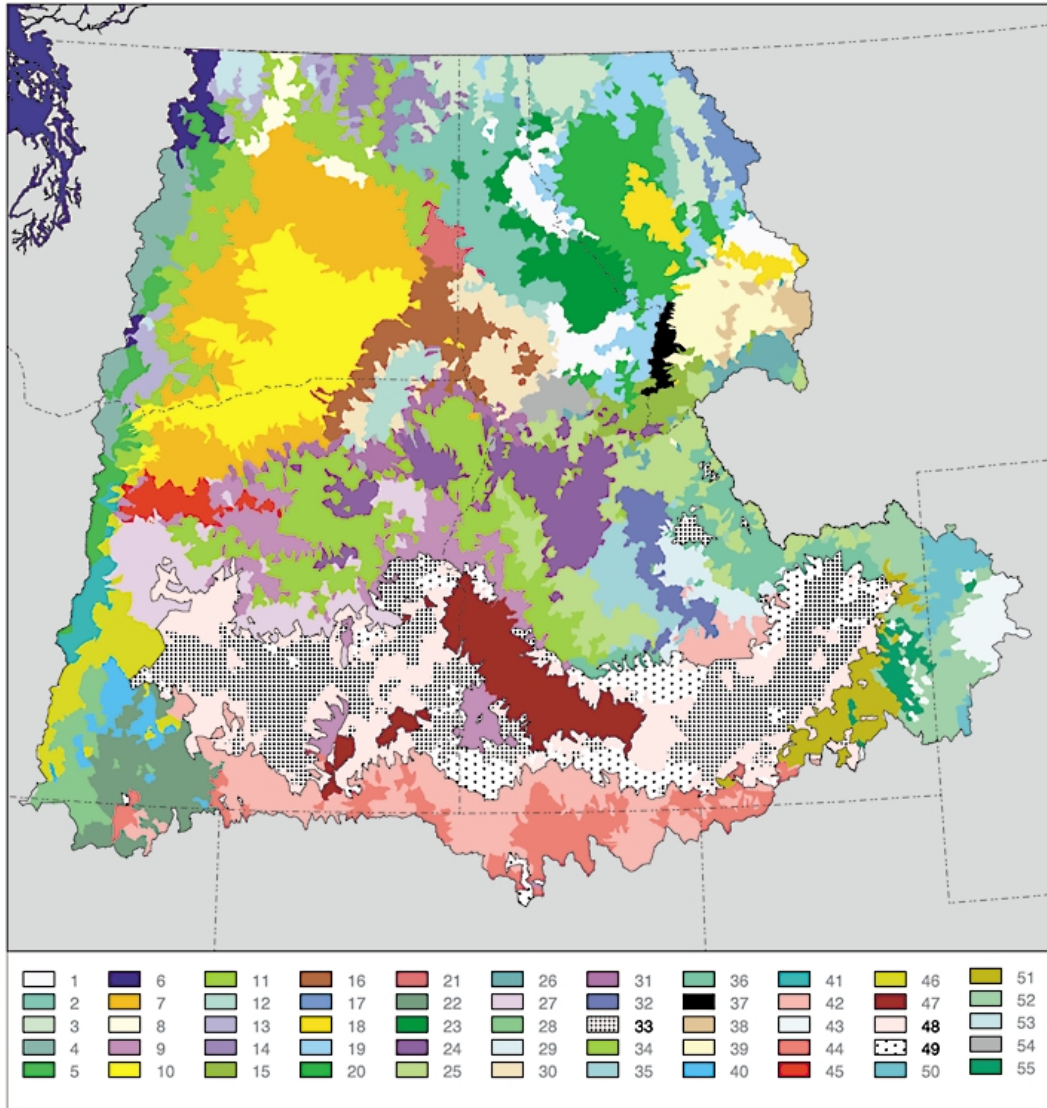


Fig. 7. Map of ecological subregions of the interior Columbia River Basin and vicinity. Subwatersheds are grouped by TWINSpan classification according to their similar composition of potential vegetation and climate attributes.

Bailey's Section, PVG, and climate attribute maps producing a single multivariable map, and determined the area of each ESR in each unique combination. Using ESRs as samples, and ESR composition of complex attributes as differential species, we submitted this new matrix to TWINSpan analysis. The resulting dendrogram is shown in Fig. 6C. Major branches of dendrograms A and C (Fig. 6) are labeled to facilitate comparison of results; branches indicate groupings that differ in simple (A) or complex (C) attribute composition. For example, in Fig. 6C ESRs within branches share similar complex attributes but differ in dominance and abundance. In either dendrogram, ESRs within a branch are most similar and would tend to be least robust to prediction. Thus, we evaluated ESRs at the branch level using discrimi-

nant analysis to determine whether regionalization produced reliable mean differences on combinations of simple or complex attributes.

Discriminant function analysis

The primary goals of discriminant analysis are to find the dimensions along which groups differ and to find classification functions to predict group membership from a set of differential species. In analysis, we ask whether group membership is associated with reliable mean differences on a combination of independent variables. If so, the combination of variables can be used to predict group membership. A significant difference between groups implies that, given a score, one can

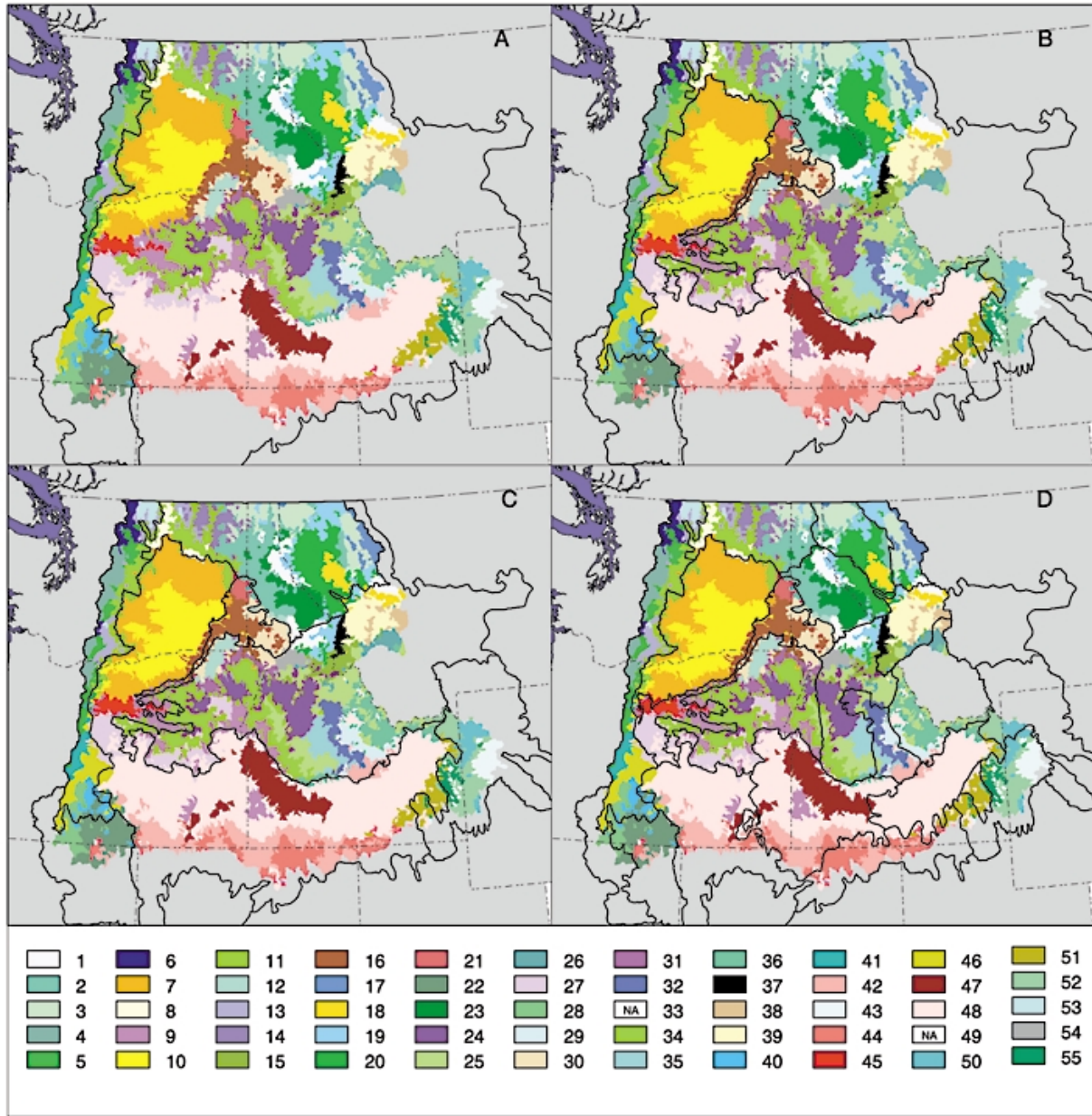


Fig. 8. Nested and overlapping relations of interior Columbia Basin ecological subregions (ESRs) with Bailey's Domains (A), Divisions (B), Provinces (C) and Sections (D) associated as environmental constraint levels in the hierarchy. Names corresponding with ESR numbers are of the form: [ESR number = Bailey's ecoregion - Dominant Precipitation class(es) - Dominant Temperature class(es) - Dominant Potential Vegetation Group(s) - Dominant Solar Radiation class(es)] 1 = M330 - Wet - Warm - MF - Mod solar; 2 = M333 - Moist - Warm - MF/DF - Low solar; 3 = M333 - Moist - Cold - MF - Low solar; 4 = M242C - Wet - Warm - MFCF - Low solar; 5 = M242C - Moist - Warm - MF/CF - Mod solar; 6 = M242C - Wet - Cold - CF - Mod/Low solar; 7 = 342I - Dry - Warm - DS - Mod solar; 8 = M333A - Dry - Warm/Hot - DG - Mod solar; 9 = 300 - Moist/Dry - Warm - DS/CS - High solar; 10 = 342I - Dry - Hot - DS/DG - Mod solar; 11 = 200/300 - Dry/Moist - Warm - MF/DF - Mod solar; 12 = M330 - Moist - Warm - DF - Mod solar; 13 = 200/300 - Moist - Warm/Cold - MF - Mod solar; 14 = M333A - Moist - Warm/Cold - MF - Mod solar; 15 = M332 - Moist/Wet - Cold - CF/DF - Mod/High solar; 16 = 330 - Moist - Hot - DG - Mod solar; 17 = M333C - Wet - Cold - MF/CF - Low solar; 18 = M330 - Moist - Warm - DF/DG - Mod solar; 19 = M330 - Wet - Cold - MF/CF - Mod solar; 20 = M330 - Moist - Cold/Warm - MF - Mod solar; 21 = 331A - Moist - Warm - DG - Low solar; 22 = 200 - Moist/Dry - Warm - DF - Very high/High solar; 23 = M333D - Wet - Warm/Cold - MF - Low solar; 24 = M332 - Moist/Wet - Cold - CF/DF/MF - High solar; 25 = M332 - Moist - Cold - DF/CF - High solar; 26 = M332 - Moist/Dry - Cold - CF - High/Mod solar; 27 = 300 - Dry - Warm - CS/DF - High solar; 28 = 200 - Moist - Warm - DF/DG - High solar; 29 = M332 - Dry - Cold - DS/CS - High solar; 30 = 300 - Moist - Warm - DG/DF - Mod solar; 31 = 300 - Moist - Warm - DF/DG - Mod solar; 32 = M332F - Moist - Cold/Frigid - CF - High/Very high solar; 34 = M332 - Moist - Warm/

predict which group it comes from. We used discriminant analysis to predict ESR membership of subwatersheds from two sets of predictors: the subwatershed composition of either simple or complex attributes. We conducted discriminant analysis at branch levels shown in dendrograms in Fig. 6 A and C, respectively.

Discriminant analysis with simple attributes. We developed discriminant functions for each labeled branch (Fig. 6A) in a forward stepping procedure. Classification accuracy ranged from 80-93% for all but branch 8, which included ESRs 33, 47, 48 and 49 (Fig. 7). In branch 8, ESRs 33 and 48 showed strong similarities among group means, i.e., subwatersheds of ESR 48 were classified to ESRs 48 and 33 with nearly equal frequency. This result was confirmed in repeated cross-validation. We used Wilk's λ (pooled ratio of error variance to effect variance plus error variance), the Lawley-Hotelling trace criterion (pooled ratio of effect variance to error variance), and Pillai's criterion (pooled effect variance) to evaluate the significance ($p < 0.001$) of each set of predictors for predicting subwatershed membership within each ESR (Tabachnick & Fidell 1996). ESRs were significantly different ($p < 0.001$) in all branches but branch 8.

Any classification in discriminant analysis is based on classification coefficients derived from samples, and they usually work too well for the sample from which they were derived. Because the coefficients are only estimates of population classification coefficients, it is desirable to know how well the coefficients generalize to a new sample of cases. Cross-validation tests the utility of coefficients on a new sample. The method of cross-validation we used involved dividing the large sample of subwatersheds within a given branch randomly into two parts, deriving classification functions on one part (learning set), and testing them on the other (test set). In cross-validation, 25% of the subwatersheds within

a branch were randomly drawn and set aside as the test set. Classification functions were derived from the remainder. Classification accuracy in cross-validation ranged from 80-87% for all but branch 8; subwatersheds of ESR 48 were classified to ESRs 48 and 33 with nearly equal frequency. Based on this evidence, we collapsed ESR 33 into 48 and derived a new discriminant function for branch 8. Accuracy of the new function by cross-validation was 89%.

Discriminant analysis with complex attributes. In the second set of discriminant analyses, the predictors were the subwatershed composition of complex attributes. We developed discriminant functions for each of 12 branches (compare A and C, Fig. 6) again using a forward stepping procedure. Classification accuracy ranged from 80-89% for all but branch 8, which included ESRs 33, 47, 48, and 49 (Fig. 7), and cross-validation accuracy ranged from 80-94% for all but branch 8. Similar to the analysis using simple attributes, subwatersheds of ESR 48 were classified to ESR 33 nearly one-third of the time. We collapsed ESR 33 into 48 and derived a new discriminant function for branch 8. Accuracy of the new function on subwatersheds of new ESR 48, and ESRs 47 and 49 by cross-validation was 87%, but ESR 49 was not robust to prediction. Based on evidence from cross-validation, we collapsed ESR 49 into 48, derived a new discriminant function for branch 8, and improved classification accuracy to 97% by cross-validation. We again used Wilk's Lambda, Hotelling's, and Pillai's criteria to evaluate the overall significance ($p < 0.001$) of each set of predictors for predicting subwatershed membership within each ESR; ESRs were significantly different ($p < 0.001$) in all branches. The final map (Fig. 8A) included 53 ESRs; ESRs 33 and 49 were collapsed into ESR 48, and each of the resulting 53 ESRs were robust to prediction.

Fig. 8 (cont.)

Cold - DF/CS - High solar; 35 = M332 - Moist - Cold - CF/DG - High/Very high solar; 36 = M332 - Dry - Cold/Warm - DS/CS - High solar; 37 = M332B - Wet - Cold - RK/CF - Mod solar; 38 = M332 - Moist - Cold - CF/DF/DG - Mod solar; 39 = M332B - Moist - Warm/Cold - DF/CF/DG - Mod solar; 40 = 200 - Moist - Warm/Cold - DF - High/Very high solar; 41 = M242C - Moist - Warm - MF/DF/CF - High solar; 42 = 300 - Dry - Warm - DS/CS - Very high solar; 43 = M331D - Moist - Cold - CF/DF/WD - Very high solar; 44 = 342 - Dry/Moist - Warm - DS/CS - Very high solar; 45 = 342H - Dry - Warm/Hot - DS/CS - High solar; 46 = M242C - Moist - Warm - DF - High solar; 47 = 342C - Dry - Hot - DS/RS - High solar; 48 = 342 - Dry - Warm - DS - High solar; 50 = M331 - Moist/Wet - Cold/Frigid - CF - High solar; 51 = 300 - Moist/Dry - Warm - DS/WD - High solar; 52 = M331 - Moist - Cold - CF/WD - High solar; 53 = M242C - Moist - Cold - CF - Mod solar; 54 = M332 - Moist - Warm - MF/DF - Mod solar; 55 = M331D - Moist - Cold - WD - High solar. Potential Vegetation Groups are: AL = Alpine; CF = Cold Forest; CS = Cool Shrub; DF = Dry Forest; DG = Dry Grass; DS = Dry Shrub; MF = Moist Forest; RS = Riparian Shrub; RW = Riparian Woodland; RK = Rock; WA = Water; WD = Woodland. Precipitation classes are: Very Dry = 0 - 150 mm/yr; Dry = 150 - 400 mm/yr; Moist = 400 - 1100 mm/yr; Wet = 1100 - 3000 mm/yr and Very Wet = 3000 - 8100 mm/yr. Temperature classes are: Frigid = -10 - -1 °C; Cold = 0 - 4 °C; Warm = 5 - 9 °C; Hot = 10 - 14 °C. Solar Radiation classes are: Very Low = 150 - 200 W/m²; Low = 200 - 250 W/m²; Moderate = 250 - 300 W/m²; High = 300 - 350 W/m²; Very High = 350 - 400 W/m². Mixed composition of attributes is indicated with a "/" and mixed attributes are listed in order of decreasing abundance.

Results

Table 2 shows the potential vegetation and climate attribute composition of mapped ESRs. The variable that minimized variation most among subregions was solar radiation. For example, ESRs in branches 1-5 display solar radiation values that are predominantly in the Low (200-250 W/m²) and Moderate (250-300 W/m²) classes, while those in branches 6.1-10 display values predominantly in the High (300-350 W/m²) and Very high (350-400 W/m²) classes. The next most important variable was Bailey's Section membership. ESRs either fell within a single Section (overlapping all neighbouring Sections on their common borders), or were distributed across the area of two or more neighbouring Sections (Fig. 6C, Table 3). For example, ESRs in branch 1 (ESRs 4, 5, 6, 13, 41, 53) lay primarily within the Eastern Cascades Section (M242C), but those in branch 2 overlapped the neighbouring Eastern Cascades, Okanogan Highlands (M333A), and Columbia Basin (341I) Sections. Substantive differences in potential vegetation and climate attribute composition were important in separating subregions within the same branch. In branch 1, ESRs 41 and 5 share similar composition of Cold, Dry, and Moist Forest PVGs, similar area in the Moist (400-1100 mm/yr) and Wet (1100-3000 mm/yr) precipitation classes, similar area in Cold (0-4°C) and Warm (5-9 °C) temperature classes, but differ in area in the Low, Moderate, and High solar radiation classes. 95% of the area of ESR 41 falls within the High solar radiation class, and 92% of the area of ESR 5 falls within the Low and Moderate solar radiation classes (Table 2).

Fig. 6B compares ESR simple attribute composition when Bailey's Section membership is excluded from the classifications. This comparison is useful when considering landscapes that share similar climate and potential vegetation attributes, but are widely separated geographically or by geoclimatic context. For example, in Figs. 6B and 6C we note that ESRs 29 and 36 are closely related, and similarly ESRs 32 and 35 are closely related to each other. But when Bailey's Section membership is considered along with the areal composition of either simple or complex attributes (Fig. 6A or 6C), ESRs 29, 36, 32, and 35 are all closely related. When Bailey's Section membership is ignored (Fig. 6B), the relationship is more distant, going back to the second level in the dendrogram. Since broad-scale geoclimatic context accounts for most of the environmental variation at a regional scale, we considered it appropriate to partition analysis by Bailey's Sections. Our methods allowed us to evaluate the suitability of Section-based analysis, both as to scale and

boundaries (see Discussion below).

Land system inventory classifications have been developed at continental, regional, state, and landscape scales. In most cases, map units result from subjectively drawn boundaries, 'often derived by consensus and with unclear choice and weighting of data' (Host et al. 1996). We avoided much of that subjectivity by assigning subregion membership by analysis pedigree, but could not avoid a measure of subjectivity because we could not create a single common scale for all variables. It is important to note that it may not ever be advantageous to create a single scale for variables used in a classification such as this. It is more appropriate to independently scale each variable that will be entered into a classification to determine the particular scale that best contributes toward explaining pattern in the data. As a result, variables were not weighted equally in these classifications.

From the outset, we intended to produce a final map that exploited the resolution of the data without over-exploitation, and consisted of subregions each of which were robust to prediction. To do so, it was necessary to allow TWINSPAN to group subwatersheds not only by their composition of complex attributes, but also by differences in attribute dominance and abundance, where composition was similar. This meant that we might initially produce a map with more subregions than could be explained by differences in the spatial pattern and resolution of the data. To correct for this possibility, we undertook cross-validation. We found that TWINSPAN classifications in rangelands of the Northern Great Basin, Owyhee Uplands, and Upper Snake River had separated subwatersheds into groups that were too finely resolved when considering differences in the pattern and resolution of the data.

During cross-validation, ESRs 33 and 49 were collapsed back into ESR 48, with only ESRs 48 and 47 remaining in branch 8. Classification with TWINSPAN initially separated ESRs 33, 49, and 48 from each other based on differences in abundance levels of similar complex attributes. Cross-validation revealed that these differences were not robust to prediction and that the map should be simplified. The remaining ESRs 48 and 47 were robust to prediction in repeated cross-validation trials, and they differed not only in composition of complex attributes, but also in abundance levels of attributes held in common. Table 2 shows that 21% of the area of ESR 47 is comprised of the riparian shrub (RS) potential vegetation group, 85% of the area falls in the Hot (H, 10-14°C) and 15% of the area falls in the Warm (W, 5-9 °C) mean annual temperature class. These values are in contrast with ESR 48 which displays 3%, 95%, and 4% area distribution in these potential vegetation and temperature classes, respectively.

Table 2. Simple potential vegetation and climate attribute composition of ecological subregions of the interior Columbia River Basin and vicinity, USA. Values are the percentage of subregion area. For ESR branch number, see Fig. 6C.

ESR	Branch No.	Potential Vegetation Groups ¹										Precipitation				Temperature				Solar Radiation													
		AL	CF	CS	DF	DG	DS	MF	RK	RS	WA	WD	VD	D	M	W	VW	F	C	W	H	VL	L	M	H	VH							
41	1		24	1	26	1	1	42					4						12	88					5	95							
4	1	2	21	1	7	1		67				1	1						26	71	3	7	67	26									
5	1		24		22		1	49					3					1	58	39	2	1	31	65	3	19	73	8					
6	1	3	48	1	3	4	1	40										13	87		18	70	12		48	52							
13	1		11		16	2	1	70					1					11	87	2	1	34	61	4		7	93						
53	1		73	1	4			22										98	2		14	80	6		7	93							
8	2		1	1	29	50	10	6					3						95	5		2	71	27		21	79						
11	2		4	3	33	6	16	36				1	1						59	40	1		7	87	6	23	77						
14	2				19	1		79					1						2	98		1	39	60		9	91						
21	2				7	84	3	2								4			4	96				100		100							
7	2			6	3	15	73	1					1						96	4				77	23	7	92	1					
10	2			4	2	20	70				2	2							96	4				2	98		100						
38	3		31	11	21	22		10			2		2						98	2				83	17		98	2					
39	3		29	1	41	16		11			1								8	91	2			49	50		96	4					
37	3		28		12	4		17	37			1							13	25	62		13	60	27		90	10					
15	3		40		35	1		19	3										1	68	31	1	5	76	19		51	49					
26	3		40	6	18	9		22	3				1						25	72	3		11	67	22		49	51					
17	4		34		1			65											5	94	1		5	92	3		95	5					
3	4		7		10			82				1							62	38		1	62	37		77	23						
2	4				30	6		57			7								87	13			6	94		83	17						
1	4		13		7			80											36	64			23	77		19	81						
19	4		26		10			64											35	64		5	80	16		7	92	1					
20	4		5		19	2		74				1							82	18		1	52	47		6	94						
18	4		11	3	38	28		19					1						98	2			10	89		1	99	1					
23	4		3		5			92											29	71			39	61		93	7						
16	5				4	80	7				7								16	84					48	52	6	94					
30	5			1	39	46		8			6								99	1				91	8		3	97					
12	5		4	2	53	6		31											1	83	16			14	85	1	2	98					
29	6.1		8	28	16	7	33	1	2				5						73	26	1	6	71	23					71	29			
36	6.1		9	22	13	16	28	5	2				5						68	32			62	37					99	1			
32	6.1	2	53	10	23	8	1	2											17	79	4	24	71	4					54	45			
35	6.1	1	56	2	15	16		8				1							4	95	2	4	96						55	45			
25	6.1		32	4	38	8	1	14				1	2						10	89	1	2	78	20			4	94	2				
24	6.2	1	40	1	34	4		19											1	65	34		4	83	14			2	97	2			
34	6.2		3	12	61	12	4	8					1						7	92	1		29	70	1		2	98	1				
54	6.2		6		25	5		62				1								98	2			44	56			81	19				
31	6.2		1	8	53	29	5	3											8	92	1		13	84	2		66	34					
27	7		3	38	31	5	13	7					3							86	14			4	95	1			99	1			
45	7			38	5	2	53					1	1							90	10				55	44		7	93				
9	7			33	26	6	33	1				1	1							49	51			12	83	5		1	98				
48	8			11	1	1	82					3	1	2						96	4			1	95	4			95	5			
47	8			10		1	67					21		1	2					97	1			15	85				100				
42	9.1			29	1	1	66					1	1	1						95	5			10	89	1			8	92			
44	9.1	1		30	2	3	59	1					1	3						64	36			12	88			7	93				
46	9.2		8	5	49	2	12	18				1	4							24	70	5		13	87			98	2				
40	9.2		3	5	78	1	3	10												4	91	6	2	39	60			60	40				
22	9.2			10	57	10	12	1				3	6	1						41	58			5	95			44	56				
28	9.2			2	62	18	7	1				2	8	1						1	99			1	99			97	3				
51	10		5	4	5	4	57								24					43	57			28	72			95	5				
55	10		22		22	10	3						6		37					7	92			73	27			86	14				
52	10		47	1	22	5	2								22					1	94	5		96	4			94	6				
50	10	3	72		11		3						4	6						56	44		12	86	1			94	6				
43	10	2	57		21	3	1					2		14						5	94			27	69	4		32	68				

¹Potential vegetation groups are: AL = Alpine; CF = Cold forest; CS = Cool shrubland; DF = Dry forest; DG = Dry grassland; DS = Dry shrubland; MF = Moist forest; RK = Rock; RS = Riparian shrub; WA = Water; WD = Woodland. Precipitation classes are: VD = 0-150 mm/yr; D = 150-400 mm/yr; M = 400-1100 mm/yr; W = 1100-3000 mm/yr; and VW = 3000-8100 mm/yr. Temperature classes are: F = -10--1 °C; C = 0-4 °C; W = 5-9 °C; H = 10-14 °C. Solar radiation classes are: VL = 150-200 W/m²; L = 200-250 W/m²; M = 250-300 W/m²; H = 300-350 W/m²; VH = 350-400 W/m².

Table 3. Nested and overlapping relations of interior Columbia basin ecological subregions with Bailey's Domains, Divisions, Provinces and Sections associated as constraint levels in the hierarchy. Values are the percentage of subregion area.

Subregion	Domain ^a															Hierarchical Relations								
	200					300																		
	Division ^b					M330																		
	M240			M260		330		M330												340				
	M242		M261	331	M331		M332					M333								342				
Section ^d																								
	M242C	M261D	M261G	331A	M331A	M331D	M332A	M332B	M332E	M332F	M332G	M333A	M333B	M333C	M333D	342B	342C	342D	342H	342I	Domain	Division	Province	Section
4	100																				N	N	N	N
5	94																				N	N	N	N
6	100																				N	N	N	N
7	1			3								1									N	N	N	N
8	2											93									N	N	N	N
10					2																N	N	N	N
14												100									N	N	N	N
21				86								3			1						N	N	N	N
32								12			88										N	N	N	N
37								7		93											N	N	N	N
39										96		3									N	N	N	N
41	93																				N	N	N	N
43					4	96															N	N	N	N
45												2									N	N	N	N
46	77	4	2														14				N	N	N	N
47																6	91		2		N	N	N	N
53	92											8									N	N	N	N
55						93										7					N	N	N	N
17													6	93							N	N	N	O
23												3	6								N	N	N	O
2				4								44	17	1	34						N	N	N	O
3												30	37	33							N	N	N	O
15							52	47			1										N	N	N	O
24							52				11	36									N	N	N	O
25							60	4	23	7	5										N	N	N	O
26							16	48		35											N	N	N	O
29									47	50											N	N	N	O
34				1			14				79							1	1		N	N	N	O
35							67		1	33										6	N	N	N	O
36							7		75	3											N	N	N	O
38								73		26											N	N	N	O
42			2							2	8						48	37	4		N	N	N	O
44			5														72	22	1		N	N	N	O
48																	31	32	29	2	N	N	N	O
50					34	1					2	3							5		N	N	N	O
52					25	61					7								6		N	N	N	O
54				3			75				21										N	N	N	O
1							25	12				2	8	7	45						N	N	O	O
12				4							82										N	N	O	O
18								37													N	N	O	O
19							25	5				4	58	3	2						N	N	O	O
20							8	4					47	8	34						N	N	O	O
9							2				48										N	N	O	O
16						73					13						7	19		22	N	O	O	O
22		10	7	75																15	N	O	O	O
27		8									51									37	N	O	O	O
28		35	20	45																	N	O	O	O
30					61		1				30				8						N	O	O	O
31					14		2				81										N	O	O	O
40		73	1	21																	N	O	O	O
51						1	30										5				N	O	O	O
11		32										44					53		16		N	O	O	O
13		67										33									O	O	O	O

^a Domains: 200 = Humid Temperate, 300 = Dry.

^b Divisions: M240 = Marine Regime-Mountains, M260 = Mediterranean Regime-Mountains, 330 = Temperate Steppe, M330 = Temperate Steppe Regime-Mountains, 340 = Temperate Desert.

^c Provinces: M242 = Cascade Mixed Forest / Coniferous Forest / Alpine Meadow, M261 = Sierran Steppe / Mixed Forest / Coniferous Forest / Alpine Meadow, 331 = Great Plains / Palouse Dry Steppe, M331 = Southern Rocky Mountain Steppe / Open Woodland / Coniferous Forest / Alpine Meadow, M332 = Middle Rocky Mountain Steppe / Coniferous Forest / Alpine Meadow, M333 = Northern Rocky Mountain Forest / Steppe / Coniferous Forest / Alpine Meadow, 342 = Intermountain Semi-Desert.

^d Sections: M242C = Eastern Cascades, M261D = Southern Cascades, M261G = Modoc Plateau, 331A = Palouse Prairie, M331A = Yellowstone Highlands, M331D = Overthrust Mountains, M332A = Idaho Batholith, M332B = Bitterroot Valley, M332E = Beaverhead Mountains, M332F = Challis Volcanics, M332G = Blue Mountains, M333A = Okanogan Highlands, M333B = Flathead Valley, M333C = Northern Rockies, M333D = Bitterroot Mountains, 342B = Northwestern Basin and Range, 342C = Owyhee Uplands, 342D = Snake River Basalts, 342H = High Lava Plains, 342I = Columbia Basin.

Discussion

Hierarchical considerations

The scales at which a landscape exhibits patchiness are important for understanding ecological processes and pattern-process interactions. At the scale of the Basin, we mapped and validated ESR robustness to prediction. Table 3 and Fig. 8 display the hierarchical relations of ESRs when they are associated with Bailey's Domains, Divisions, Provinces, and Sections as context. Approximately one-third (34%) of the ESRs nest at the Section level, more than two-thirds (70%) of the ESRs nest at the Province level, 79% at the Division level, and 96% at the Domain level. Two ESRs, 11 and 13, do not nest at any level (Fig. 8).

Bailey (1983, 1995) and Bailey et al. (1994b) building on the work of Zonneveld (1979), Küchler & Zonneveld (1988), Pojar et al. (1987), Rowe (1980), Miller (1978), and others, present a rationale and method for mapping a nested system of land units for use in a land system inventory (*sensu* Wertz & Arnold 1972). Indeed, much of the theoretical discussion of hierarchical systems has centered around nested hierarchies (Allen & Starr 1982; O'Neill et al. 1986, 1991; Urban et al. 1987). Such focus simplified theory development and explication, but did little to improve understanding of overlapping or independent hierarchies which may be more common than is generally assumed. Undoubtedly, regionalizations will shed more light on the nature of specific hierarchies as they are implemented.

We developed ESRs to stratify landscapes according to their similar composition of ecological attributes. ESRs partition environmental variation; e.g., within an ESR, variation in a vegetation spatial patterns is significantly less than variation among ESRs for the same attributes. Our work suggests that although most ESRs nest at some level, ecological subregions may be either nested or overlapping with respect to their environmental constraint level, and the constraint level may occur at one of at least four scales. Here it is important to note that two ESRs (ESRs 11 and 13) overlapped their constraint level even at the scale of the Domain (Fig. 8). Domains (Bailey 1995) roughly correspond with broad climatic zones at a continental map scale of about 1:30 000 000. It therefore seems inappropriate to assume that levels of a land system inventory are necessarily nested. Neither is it appropriate to assume that the environmental constraint level associated with an ecological phenomenon at some observation level occurs at the same scale in a land unit hierarchy across broad regional landscapes. These points are especially relevant when designing bioregional assessments, stud-

ies to characterize specific scale-dependent phenomena, and studies to explain the biological and physical context of those phenomena.

The influence of gradient

In Fig. 8C, we observe that the ESR map is coarse-grained in the desert and semidesert areas of the Intermountain Semidesert Province (Sections 342B, C, D, H, and I, Fig. 1), and fine to moderate-grained elsewhere. Within this Province, three ESRs, 7, 10, and 48, comprise 26.1% of the Basin area, including 1580 of 7496 total subwatersheds (21.1%). The average area of ESRs within the Intermountain Semidesert Province is more than three and one-half times that of ESRs elsewhere in the Basin; 3 032 183 ha vs. 860 837 ha, respectively. Broad-scale maps of potential vegetation, mean annual temperature, total annual precipitation, averaged annual daylight solar radiation, and elevation (Figs. 4 and 5) reflect gradual environmental gradients in rangelands of the Intermountain Semidesert Province, especially in the Columbia Basin, Northwest Basin and Range, Owyhee Uplands, and Snake River Basalts Sections (Fig. 1), and relatively steep gradients elsewhere. Due to the significant difference in gradients of rangelands versus montane forest environments, it is apparent that it is necessary to use more finely resolved climate, potential vegetation, elevation, and perhaps other data to stratify rangeland landscapes, in essence, a regionalization down-scale from work reported here.

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