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Comparing Ecoregional Classifications for Natural Areas Management in the Klamath Region, USA

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ABSTRACT: We compared three existing ecoregional classification schemes (Bailey, Omernik, and World Wildlife Fund) with two derived schemes (Omernik Revised and Climate Zones) to explore their effectiveness in explaining species distributions and to better understand natural resource geography in the Klamath Region, USA. We analyzed presence/absence data derived from digital distribution maps for trees, amphibians, large mammals, small mammals, migrant birds, and resident birds using three statistical analyses of classification accuracy (Analysis of Similarity, Canonical Analysis of Principal Coordinates, and Classification Strength). The classifications were roughly comparable in classification accuracy, with Omernik Revised showing the best overall performance. Trees showed the strongest fidelity to the classifications, and large mammals showed the weakest fidelity. We discuss the implications for regional biogeography and describe how intermediate resolution ecoregional classifications may be appropriate for use as natural areas management domains.

Index terms: Bailey ecoregions, Klamath Region, management domains, Omernik ecoregions, World Wildlife Fund ecoregions

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INTRODUCTION

Increasingly, natural resource management involves multipartner collaboration across landscapes and regions, often with complex arrays of administrative and ecological boundaries. Typically, the conceptual and spatial domains for natural areas management (hereafter management domains) are not clearly defined. Ideally, management domains would be grounded in biogeography, and potentially relevant to a wide array of ecological patterns, processes, and suites of species. When exploring alternate management domains for a region, natural areas managers may wish to know answers to a number of practical questions, such as: (1) Which classifications best describe ecologically significant boundaries? (2) How do such boundaries correspond to biotic distributions of different species? And (3) how do patterns of biogeography and biodiversity affect conservation and management?

Large scale classification of biotic communities has long been a goal of naturalists and biogeographers, whose works have yielded a diverse array of maps and classifications of the world's flora and fauna (Wallace 1869; Holdridge 1947; reviewed in Welsh 1994). At the same time, climatologists have been converging upon regional classifications of climate, with a number of studies focused in the western United States (Baker 1944; Mitchell 1976; Mock 1996). Formal ecoregional classifications have been developed in North America by US federal agencies (e.g., Bailey 1983, 1998; Omernik 1987, 2011), with subsequent refinement by states (Welsh 1994)

and nongovernmental entities such as the World Wildlife Fund (WWF; Ricketts et al. 1999).

The causes of variation among ecoregions include both biological and physical factors, of which climate is usually considered to be an overarching control (Bailey 1998). For plants, other abiotic factors, such as geology, have long been known to be fundamental to the distributions of species and communities (Merriam and Steineger 1890; Whittaker 1960; Walter 1973; Woodward 1987; Ohmann and Spies 1998). For other taxa, these biophysical controls have typically been less clearly understood, but a number of studies suggest these controls may be important (Root 1988; Hansen and Rotella 2002; Shine et al. 2002; Duff and Morrell 2007). Upon the coarse biophysical template, finer habitat divisions arise from vegetation structure, successional variation, interspecific competition, and a host of other biologically mediated effects (Grinnell 1917). Animals further subdivide the landscape into breeding territories, foraging and staging areas, and other functional spaces (Palik and Engstrom 1999). Consequently, ecoregional variation is best viewed as a multiscale concept containing a complex array of controls on spatial patterns.

Recent research (Wright et al. 1998; McDonald et al. 2005; Thompson et al. 2005) has demonstrated that ecoregional boundaries may not correspond closely with compositional changes in individual life forms, which may change at different rates across landscape gradients. Therefore, it may be useful to explore how differing ecological classifications fit varied species geography. For instance, highly vagile organisms (birds) may show more dispersed distributions and partition the landscape more coarsely than sessile organisms (trees) or species with limited dispersal abilities (amphibians) (McDonald et al. 2005).

Ecoregional Classifications and Natural Areas Management

In recent years, environmental management activities have evolved from single disciplines, such as fisheries or forestry,

into integrated and holistic approaches that cover many species simultaneously and span large spatial scales (Johnson et al. 1999; Vander Schaaf et al. 2004). For managers, this broader focus requires an understanding of the biodiversity and biogeography of major species assemblages in the areas they manage, as well as the ability to make sound hypotheses of ecological responses to management actions. In complex landscapes with many landowners, ecoregional classifications may be essential for developing meaningful ecological units for collaborative management (Host et al. 1996) and bioassessment (Hawkins et al. 2000).

Managers and applied conservation scientists often must develop and apply standardized inventory and monitoring techniques across large and heterogeneous landscapes. For instance, the Klamath Network Inventory and Monitoring Program of the National Park Service is currently developing a long term monitoring program for six park units (three national parks, two national monuments, and one national recreation area) in the Klamath Region of northern California and southern Oregon that vary tremendously in climate, geology, plant and animal species, and a host of ecological processes (Sarr et al. 2007). An integrated and rigorous monitoring program requires a basic understanding of how important functional relationships change across landscapes and where important boundaries or semi-homogeneous regions occur. Such an understanding also would be helpful for fostering collaboration among reserves and with adjacent landowners to address issues of mutual interest.

To evaluate the utility of ecoregional classification for describing ecological patterns, processes, and suites of species, we investigated the performance of several classification schemes for the Klamath Region of North America (Figure 1). The Klamath Region is one of the most biophysically complex regions in western North America (DellaSala et al. 1999). In such heterogeneous regions, the selection of general landscape boundaries can be challenging because there are many possible factors that might be used for ecoregional classification, yet the impor-

tance of each factor will vary depending upon the life history of the organisms involved. Moreover, any classification used should ideally offer sufficient generality to be easily recognized and used by natural area managers. Thus, lessons learned from evaluating ecoregional classification schemes in this diverse region will provide examples of challenges that managers in many parts of the world may expect to confront.

Our initial survey of ecoregion classifications revealed several alternatives to compare for potential use in our region. Of these, we chose the Bailey (Bailey 1983, 1998), Omernik (Omernik 1987, 2011), and WWF (Ricketts et al. 1999) classifications. We also noted that although the existing ecoregional classifications appeared to capture a number of broad landscape boundaries across the Klamath Region as a whole, they did not adequately differentiate climate zones within the most complex part of our region, the Klamath Mountains subregion, where biodiversity is particularly high and climatic gradients are especially pronounced. Therefore, in addition to evaluating the existing ecoregional classifications, we decided to analyze available climate data to see if more refined climate zones could be identified for our study area. Our objective was to compare the three existing ecoregional classifications and two derived classification schemes for the Klamath Region using a suite of biological and physical datasets to compare their effectiveness in representing ecologically significant boundaries for our region. More specifically, we sought to better understand the biophysical and biogeographic patterns within our region by investigating the following four research questions:

1. Which ecoregional classifications best describe ecologically significant boundaries in the Klamath Region?
2. How might the ecoregional classification(s) be revised to better describe variation in the Klamath Region?
3. How do ranges of selected groups of organisms with different vagility and life history correspond to different ecoregional classifications?
4. What are the general biogeographic linkages between ecoregional units within and outside the Klamath Region?

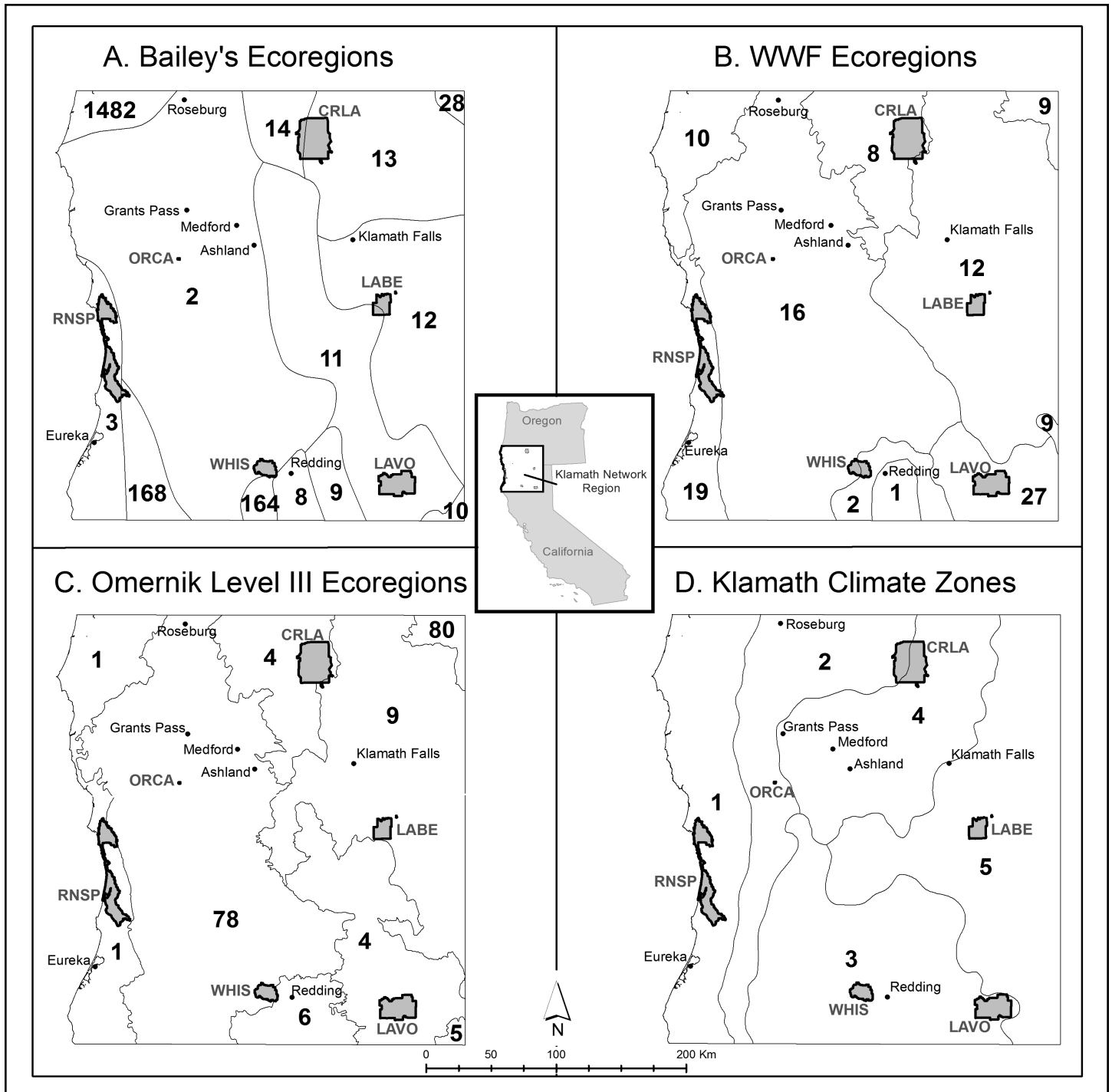


Figure 1. Klamath area and delineated ecoregions. (A) Bailey's Ecoregions, (B) World Wildlife Fund (WWF) Ecoregions, (C) Omernik Level III Ecoregions, and (D) Klamath Climate Zones. Klamath area National Park Service units are shaded (CRLA = Crater Lake National Park, LABE = Lava Beds National Monument, LAVO = Lassen Volcanic National Park, RNSP = Redwood National and State Parks, WHIS = Whiskeytown National Recreations Area, and ORCA = Oregon Caves National Monument). Numbers in bold are the original numeric codes for named ecoregions. See Appendix for ecoregion names.

METHODS

Compiling Ecoregional Classifications for the Klamath Region

We used three existing ecoregional clas-

sification systems as spatial datasets. These were: (1) *Bailey's Ecoregions and Subregions of the United States, Puerto Rico, and the U.S. Virgin Islands* (McNab and Avers 1994; <http://www.fs.fed.us/rm/ecoregions/products/map-ecoregions->

[http://www.fs.fed.us/rm/ecoregions-](http://www.fs.fed.us/rm/ecoregions/products/map-ecoregions-) united-states/; Figure 1A); (2) World Wildlife Fund's *Terrestrial Ecoregions of the World* (<http://www.worldwildlife.org/science/data/terreco.cfm>; Olson et al. 2001; Figure 1B); and (3) Omernik's *Level III Ecoregions of the Continental United*

States (Omernik 1987, 2011; http://www.epa.gov/wed/pages/ecoregions/level_iii_iv.htm; Figure 1C).

The Bailey system incorporates climate, topography, and vegetation (Bailey 1983, 1998). The Omernik system, from which the WWF system is also partly derived (Olson et al. 2001), integrates soils, land surface form, potential natural vegetation, land use, and other variables (Omernik 1987, 2011). The WWF system, along with the other classifications to a degree, also involved the subjective assessment of experts to delineate meaningful ecoregional boundaries (Olson et al. 2001). Ultimately, all ecoregional classifications involve professional judgment and qualitative determinations of ecoregional units and boundaries, usually informed by a broad array of physical and biological factors.

Developing Climate Zones for the Klamath Region

The Klamath Region is considered a transitional area between maritime, continental, temperate, and Mediterranean air masses in western North America (Mitchell 1976). In mountainous regions, identification of climate zones is often complicated by the local effects of elevation on climate (Mitchell 1976). Elevation neutral climate grids can be created to overcome the strong confounding effect of local elevation in climate by projecting all sites to sea level using spatially explicit regression equations from existing climate data (Henderson 1997). We used a gridded spatial dataset of six climatic variables that were projected to provide sea-level characteristics: (1) Mean annual temperature at sea level; (2) Total precipitation at sea level (data from Henderson 1997), or were largely elevation neutral; (3) Total precipitation days; (4) Average diurnal temperature range (average daily maximum minus average daily minimum); (5) Annual air temperature range (July average minus January average); and (6) July maximum temperature adjusted based on a spatially constant lapse rate of 7.3 degrees Celsius per 1000 meters (all data were for the period 1980–1997 from Thornton et al. 1997; DAYMET 2007). With the effect of

elevation removed, we sought to generate distinct climatic zones to identify important boundaries that might have been missed by the existing ecoregional classifications. Spatial resolution of all climate data was 1000 m.

We performed an unsupervised classification in ArcGIS Spatial Analyst (Version 9.3, ESRI 2003) to delineate climate zones. To ensure our variables were weighted equally, all six climatic variables were scaled to an 8-bit data range. We performed a migrating means clustering procedure, utilizing the IsoCluster routine, followed by maximum likelihood classification. The isoclustering routine procedure uses an ISODATA (Iterative Self-Organizing Data Analysis Techniques; Ball and Hall 1965) clustering algorithm for defining natural groupings of data points in attribute space. It is a commonly used algorithm in satellite image classification to determine classes of multiple wavebands. In this procedure, the user dictates the number of clusters, and we performed a series of analyses using different numbers of clusters to arrive at a scheme that was readily interpretable and ecologically meaningful.

A Refined Ecoregional Classification for the Klamath Region

After looking at the most recent Omernik (2011) classification, we developed a revised version for our region, which we called Omernik Revised (Figures 2–7; Appendix). This change was based on our preliminary review of climate and vegetation patterns in published literature (McLaughlin 1989), which suggested that the northern and southern portions of the Cascade Range differ in important ways. Because of climate and geographic affinity, we hypothesized that the southern portion of the Cascade Range (Figure 1C, ecoregion 4) would be more aligned biologically with the Sierra Nevada (Figure 1C, ecoregion 5), despite being geologically part of the Cascade Range. For this revision, we combined the southern Cascades ecoregion with the Sierra Nevada ecoregion, retaining the original boundaries of both.

Evaluating Biological Patterns across the Klamath Region

Species distributions

We selected four taxonomic groups for which digital range maps were available to test relationships between species distributions, ecoregions, and climate zones across the Klamath Region. The groups were: (1) Trees; (2) Amphibians; (3) Birds; and (4) Mammals. For each group, we developed presence/absence grids of 402 points using 10-minute grids derived from subsampling digital range maps obtained from NatureServe (<http://www.natureserve.org>) for amphibians, birds, and mammals, and from the US Geological Survey for trees (US Geological Survey 1999). For vertebrates, NatureServe range maps are built from scientific literature, web sites, experts, and information from local data centers. Many of the same sources used for taxonomy and nomenclature are consulted for distribution information. In turn, much of the published information is based on museum specimen records and, especially for birds, reliably documented observation records. Review of the available literature and other sources is done by NatureServe zoologists and by other experts contracted to develop this information, who supplement their literature research with personal knowledge. Such range maps are known to contain errors of commission, as real ranges are porous, especially in mountainous or otherwise complex terrain (Hurlbert and White 2005). Nonetheless, they are often the only available data in areas with sparse or inconsistent surveys, and are considered a primary resource for large-scale analyses.

Two secondary data filtration steps were performed that resulted in splitting the taxonomic groups: (1) we separated birds into migratory breeders (which leave the region during winter) and year-round residents that breed and winter in our region, on the premise that the migratory breeding and year-round residents may respond to the factors underlying ecoregional boundaries differently; and (2) we separated mammals into “large” and “small” based on functional species groupings, on the principle

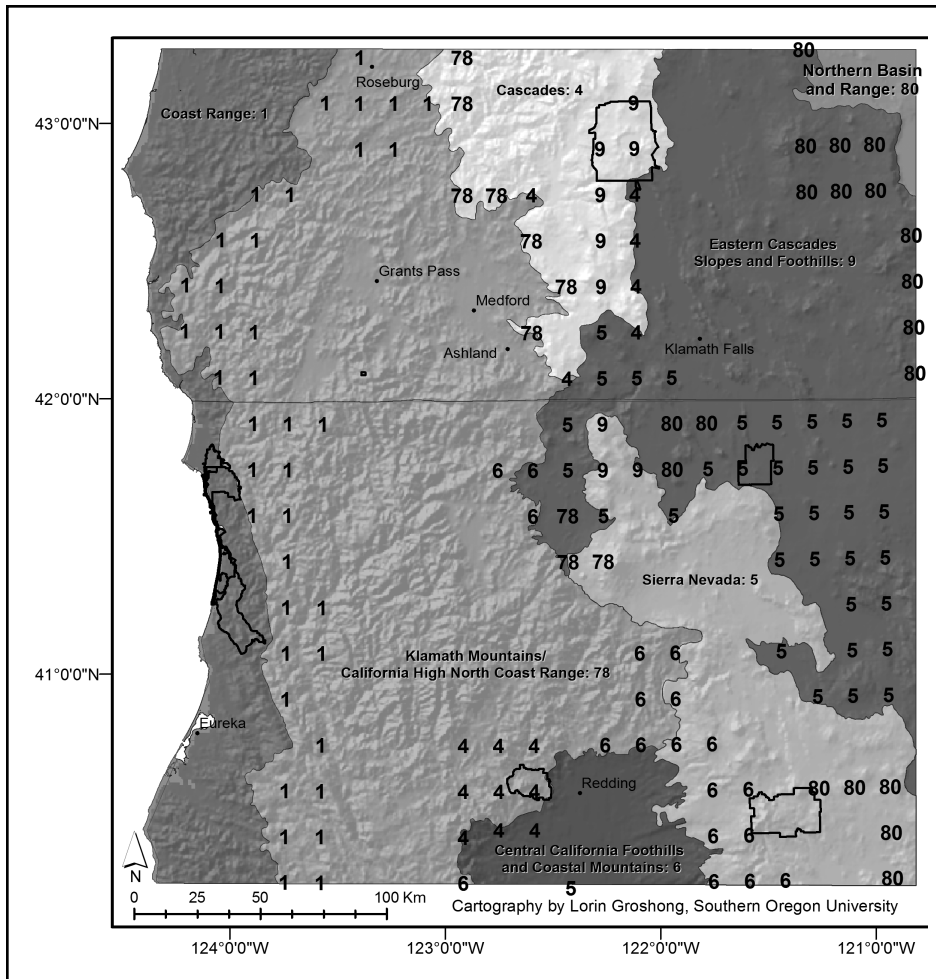


Figure 2. Map of Omernik Revised ecoregions showing misclassified plots based on *amphibian* assemblages. Large bold numbers indicate a misclassified plot, and the number indicates the erroneous ecoregion assignment based on the discriminant analysis function of Canonical Analysis of Principal Coordinates (CAP). The actual ecoregion numbers follow the ecoregion names (e.g., Klamath Mountains / California High North Coast Range: 78).

that small mammals, with typically smaller home ranges and less migration, may show more fidelity with ecoregions than larger mammals with greater vagility and larger home ranges. These steps resulted in six separate taxa groups being analyzed.

Data Analysis

For the species distribution presence/absence datasets, we used three methods to evaluate the adequacy of the ecoregional and climate classifications: (1) Analysis of Similarity *R* values, (2) Canonical Analysis of Principal Coordinates misclassification, and (3) Classification Strength. These three measures provide a broad-based analysis of ecoregion congruence with biological pattern. The strengths and weakness of

each approach are detailed below.

Analysis of Similarity

Analysis of similarity (ANOSIM) is a permutational test of a priori groups based on community assemblage data (Clarke and Green 1988). Similarities between plots (here, we used Bray-Curtis distance similarities, where a value of 1 indicates 100% similarity and 0 indicates no similarity) are used to calculate average rank similarities *between* ecoregions and *within* ecoregions. A test statistic (*R*) comparing the observed difference in the *between* and *within* rank similarities is computed (see Clarke and Warwick (2001) for details). An *R* value of 1 indicates plots are more similar *within* ecoregions than to any plots

from different ecoregions. If, on average, the similarities *between* ecoregions and *within* ecoregions are the same, the *R* value will be approximately zero. In this regard, the *R* statistic is a measure of ecoregion classification success, with high values indicating stronger classification and low values indicating weaker classification. A permutation of the ecoregion allocation can be used to test the significance of the classification, but this is separate from the effect size, *R*. Statistical significance of the ANOSIM permutation is sensitive to even weak grouping effects, so that comparisons of significance level in assessing ecoregion classification is limited (e.g., when all grouping schemes are significant).

We conducted ANOSIM analyses for each taxonomic group for each ecoregion classification scheme, so that for each taxonomic group we could identify which ecoregion provided the strongest classification. ANOSIM analyses were performed in Primer (version 6.1.12, Primer-E Ltd., Plymouth, UK).

Canonical Analysis of Principal Coordinates

We used Canonical Analysis of Principal Coordinates (CAP) to assess the relative merits of each ecoregional classification scheme (ecoregions and climate zone) across the six taxonomic groups. CAP is an ordination technique that maximizes a priori group differences (e.g., ecoregion groups) in a multivariate data cloud of sites in species space. In this sense, CAP is a constrained ordination based on the ecoregion classification, which attempts to produce axes that best separate the a priori groups (Anderson et al. 2008).

The CAP ordination then can be used as a discriminant-type analysis, in an iterative process, as follows: (1) the entire ordination is performed, but one plot is left out; (2) the left-out plot is then added to the ordination, and assigned to the region with the closest centroid; and (3) the original a priori class is then compared to the newly assigned class and, where there are discrepancies, the corrected class is recorded. This process is iterated so that eventually every plot has

Classification Strength

Classification strength (CS) is a simple metric developed by Van Sickle and Hughes (2000) in assessing the best ecoregional classification of aquatic vertebrates in Oregon. A resemblance matrix of site similarities is created based on Bray-Curtis similarity measures (Van Sickle and Hughes 2000). CS is then the weighted mean of the *within* class similarities (W) minus the mean of all *between* class similarities (B). This metric is a function of within-class homogeneity and between-class separation, with high values indicating strong classification success. For all taxonomic groups and ecoregion classification schemes, we calculated CS with MEANSIM6 software (version 6.0, available at http://www.epa.gov/wed/pages/models/dendro/mean_similarity_analysis.htm). Values close to 0 indicate weak classification and values close to 1 indicate strong classification.

RESULTS

A Climate Zone Classification for the Klamath Region

After classifying climate grids at multiple levels of resolution, we found a classification of five climate zones provided a readily interpretable and ecological sensible classification, with minimal scatter across boundaries (Figure 1D). These zones broadly corresponded to: (1) a Coastal zone; (2) a Western Klamath zone; (3) a Californian zone; (4) an Eastern Klamath/Cascades zone; and (5) a Great Basin zone.

Evaluating Ecoregional and Climate Classifications

Based on average ANOSIM *R* values for all six taxa groups, the Omernik Revised classification had the strongest average grouping strength ($R = 0.61$) (Table 1). The Climate Zones had the weakest average *R* value (0.50). For individual taxa, the Climate Zones and WWF had the strongest grouping strength for Breeding Birds, while the Climate Zones had the strongest grouping strength for Resident Birds. Amphibians had the strongest

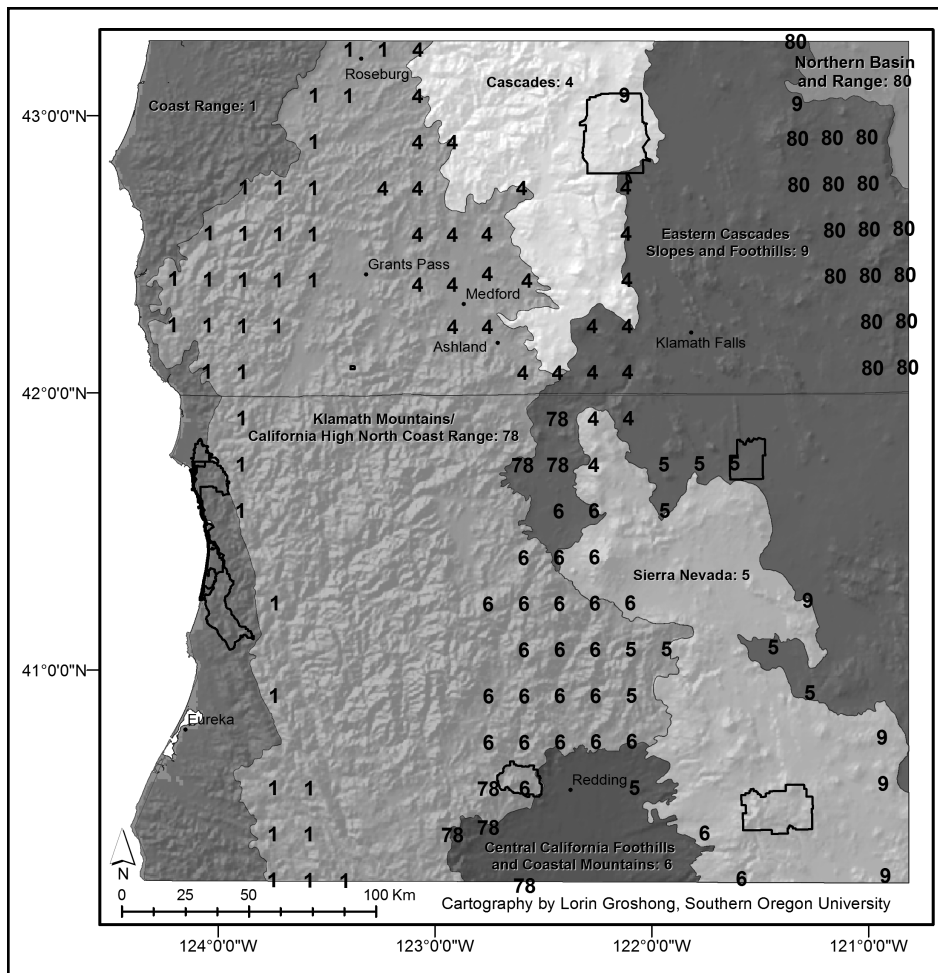


Figure 3. Map of Omernik Revised ecoregions showing misclassified plots based on *resident land bird* assemblages. Large bold numbers indicate a misclassified plot, and the number indicates the erroneous ecoregion assignment based on the discriminant analysis function of Canonical Analysis of Principal Coordinates (CAP). The actual ecoregion numbers follow the ecoregion names (e.g., Klamath Mountains / California High North Coast Range: 78).

been excluded and reassigned, and the total number of misclassifications is used for an overall misclassification error.

A strong ecoregional classification will minimize the number of misclassifications, whereas a weak classification will be characterized by many misclassifications. This method of assessing ecoregions is strongly affected by the total number of ecoregion groups (e.g., an ecoregion scheme with a large number of groups is more likely to have misclassifications than an ecoregion scheme with a low number of groups). Despite this limitation, the CAP misclassification rate still provides an estimate of potential error rates associated with each scheme. It can also be used to assess the relative success of ecoregion schemes across taxonomic groups (e.g., Does the

Bailey ecoregion classification provide a stronger classification for resident birds than amphibians?). Finally, and perhaps most importantly, mapping the locations of plots that were misclassified can offer insights into where ecoregion classifications may be improved. We performed CAP analyses using the software Permanova+ (version 1.0.2, Primer-E Ltd., Plymouth, UK). Because CAP analysis requires at least two replicates of each group, where there was only a single sample for a region, we considered the bordering points in the cardinal directions to be a part of that region to increase the nominal sample size of that group (this occurred only once in the Omernik classification, where the Sierra Nevada zone in the southeastern corner of the study area only had a single point).

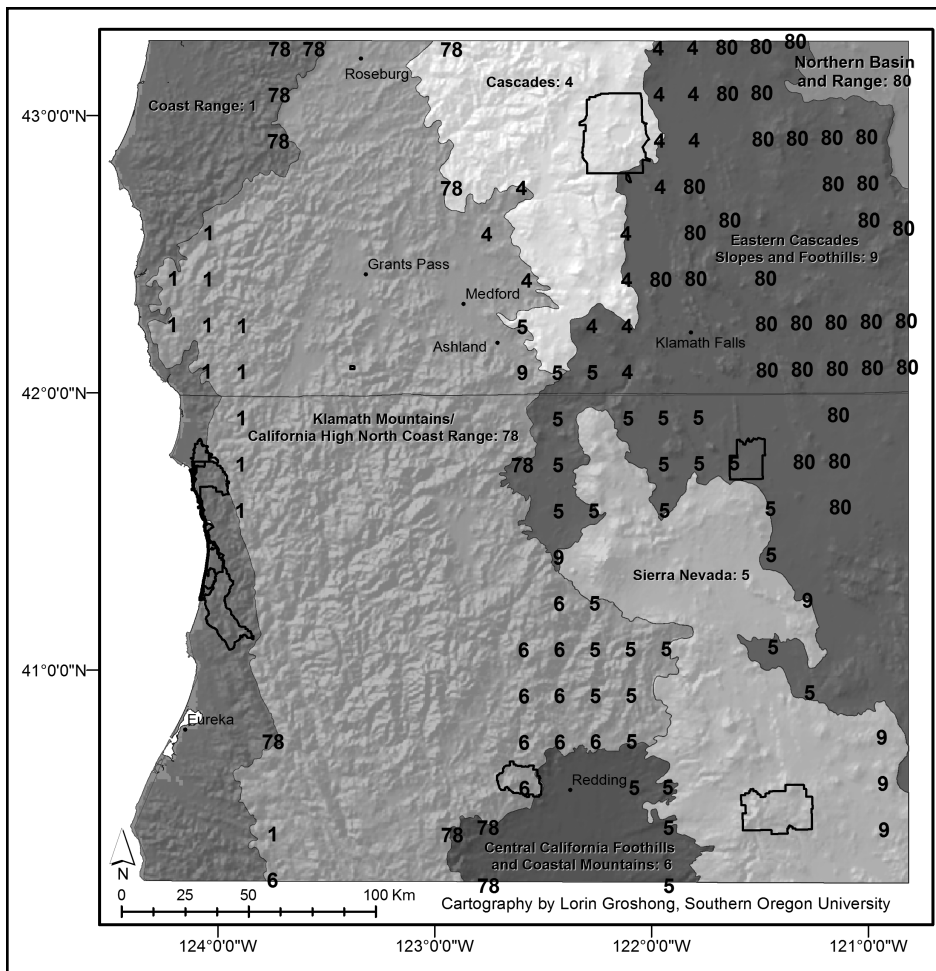


Figure 4. Map of Omernik Revised ecoregions showing misclassified plots based on *migratory land bird* assemblages. Large bold numbers indicate a misclassified plot, and the number indicates the erroneous ecoregion assignment based on the discriminant analysis function of Canonical Analysis of Principal Coordinates (CAP). The actual ecoregion numbers follow the ecoregion names (e.g., Klamath Mountains / California High North Coast Range: 78).

grouping strength in the Bailey classification, and Small Mammals had the highest grouping strength in the Omernik Revised classification. Grouping strength for Large Mammals was generally low, and grouping strength for Trees was generally high for all classifications except for the Climate Zones (Table 1). The reclassification of the southern Cascades section of Omernik's original scheme into an expanded Sierra Nevada class in the Omernik Revised classification improved the average group strength from the second weakest average to being the strongest overall.

Classification strength (W-B) results were similar to the ANOSIM *R*-value evaluation, with the exception that the top two strongest classifications were tied (Bailey

and WWF) at 0.15 (Table 2). Breeding Birds and Large Mammals had the lowest classification strengths, demonstrating that these taxa have high amounts of similarity (a large shared percentage of species) between ecoregions. Taxa groups with higher classification strengths (typically Trees and Amphibians), however, have fewer shared species between ecoregions.

Percent correct allocation based on CAP was sensitive to the number of ecoregions in any one scheme, with Bailey ecoregions having the worst overall average (53% correct), but also the highest number of regions (13) (Table 3, Appendix). Likewise, the group with the highest average correct percentage was the Climate Zones (70%), with only five regions. The revision

to Omernik's classification increased the average percent correct allocation from 60% to 65% (with a constant number of ecoregions; 7).

Evaluating Biogeographic Linkages in the Klamath Region

Based on the success of the Omernik Revised classification in both ANOSIM *R* and Classification Strength techniques, its high percentage of correct classifications in the CAP analysis, and its closest congruence with the Climate Zone classification, we chose to use the Omernik Revised classification as a framework upon which to map the location of misclassified plots and the reclassified grouping for each taxa group (Figures 2–7). The Omernik Revised classification is fairly coarse in scale (only seven ecoregions across our study region), but also biologically robust. The resulting maps provide insights into the biogeographic linkages between ecoregions in the broader Klamath Region and, as discussed below, help identify areas for potential ecoregion refinements.

DISCUSSION

This study illustrated that ecoregional variation differentially affects species with varied life history and vagility. Nonetheless, species distributions appear to provide a coarse illustration of conceptual and spatial domains for natural areas management (hereafter management domains) in the Klamath Region. The CAP analysis, in particular, illustrated areas of gradation between adjacent zones, providing clues as to how the species distributions interface across ecoregional boundaries. In the following discussion, ecoregion names refer to the Omernik Revised classification (Figures 2–7; Appendix) unless otherwise stated.

Ecoregional Classification Accuracy

If ecoregional classifications are judged on their ability to delimit internally homogeneous parts of the larger landscape, none succeeded. Most of the ecoregions identified showed important internal variation. If, however, the goal is to identify interpretable

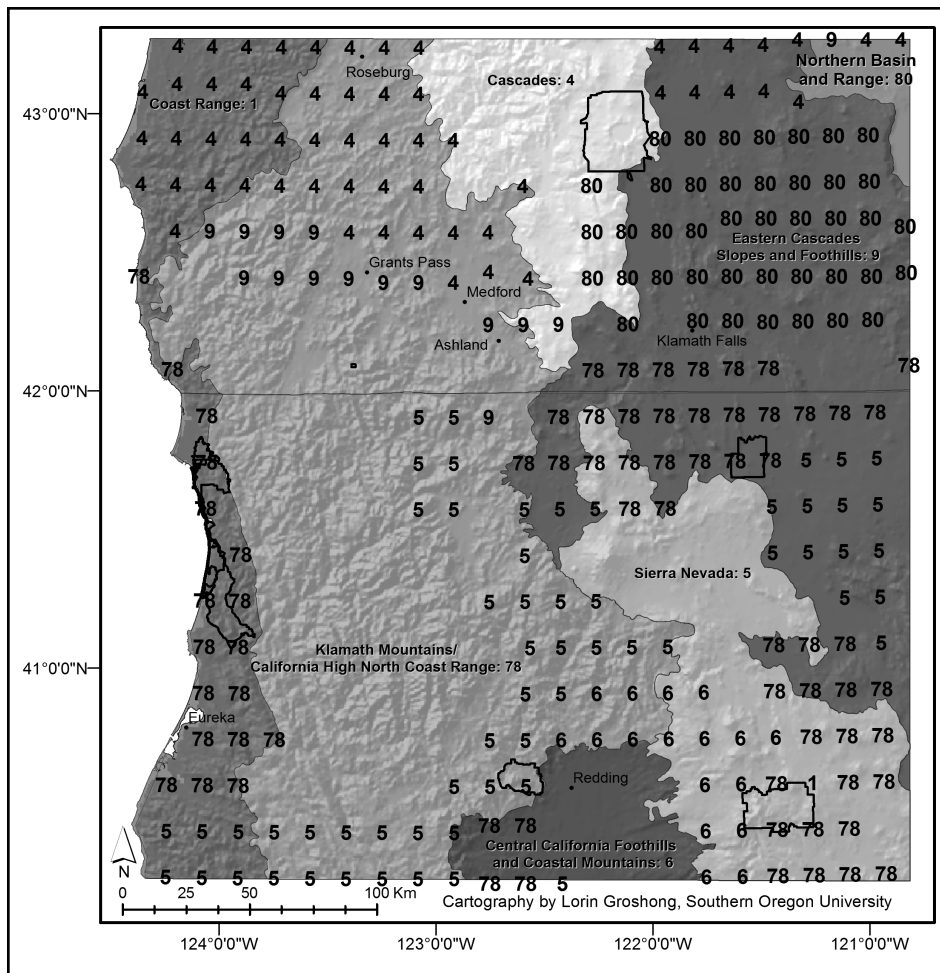


Figure 5. Map of Omernik Revised ecoregions showing misclassified plots based on *large mammal* assemblages. Large bold numbers indicate a misclassified plot, and the number indicates the erroneous ecoregion assignment based on the discriminant analysis function of Canonical Analysis of Principal Coordinates (CAP). The actual ecoregion numbers follow the ecoregion names (e.g., Klamath Mountains / California High North Coast Range: 78).

transitions between ecoregions and to describe the major landscape boundaries in the region, the ecoregional classifications were roughly comparable in accuracy, and with the Climate Zones analysis, helped to paint a broad picture of the ecoregional structure of the Klamath Region.

However, there were some boundaries that failed to capture ecological variation at our scale of analysis. For instance, Bailey’s Klamath Mountains ecoregion extends all the way to the coast in southern Oregon (ecoregion 2 on Figure 1A), whereas all our analyses suggested the coastal zone has many distinctive qualities. The WWF classification seemed to capture the coastal to Klamath Mountains transition particularly well (Figure 1B). On the other hand, the

Bailey classification correctly described the functional connection between the California Cascade Range and the Sierra Nevada Range. Both the WWF and Bailey classifications have especially large ecoregions (ecoregions 16 and 2 on Figures 1B and 1A, respectively) that cover a large area of the Klamath Mountains, a region that has great internal ecological heterogeneity. Neither classification recognized the considerable climatic diversity that we noted in the Climate Zone analysis for the central part of our study region, specifically as identified by the Eastern Klamath/Cascades ecoregion and the westward peninsula of the Great Basin ecoregion (zones 4 and 5, respectively, Figure 1D).

We noted a very implausible boundary in

the distribution of amphibian species at the California–Oregon state border in the Eastern Cascades Slopes and Foothills ecoregion (Figure 2), which is likely due to differences in species inventory completeness (it seems more complete for California) rather than the biogeography of amphibian species distributions. It should be noted that the Bailey classification has an ecoregion boundary in this vicinity (i.e., north of Klamath Falls, Figure 1A), but it is not clear at this time if this boundary identifies aspects of the environment that would affect amphibian species distributions.

Although the Omernik Revised classification (Figures 2–7) uses a somewhat coarser grain than the Bailey and WWF classifications (7 ecoregions, as opposed to 13 and 9 ecoregions for Bailey and WWF, respectively; Appendix), it seemed to capture the most important transitions across our region as a whole. We believe it provides a generalized and intuitive ecoregional framework for use by natural area managers in our region, recognizing that some applications would benefit from finer scale classifications (e.g., Bailey, WWF, and Omernik Level IV). Thus, with regards to research questions 1 and 2 that we posed in the Introduction, we believe the Omernik classification, revised to combine the southern Cascades with the Sierra Nevada ecoregion, provides the most ecologically relevant classification scheme for our region.

Species Vagility and Ecoregional Classifications

Species vagility appeared to be important for evaluating the fit between recorded species ranges and ecoregion classifications (research question 3, Introduction). Trees showed the highest congruence with all classifications (Tables 1–3), suggesting relatively fine scale correspondence with environmental variation. Studying species distributions across geographic gradients in Patagonia, Monjeau et al. (1998) noted that plants responded more markedly to climate variation than did small mammals. McDonald et al. (2005) also noted that species turnover rate with distance was higher for trees than for land birds and

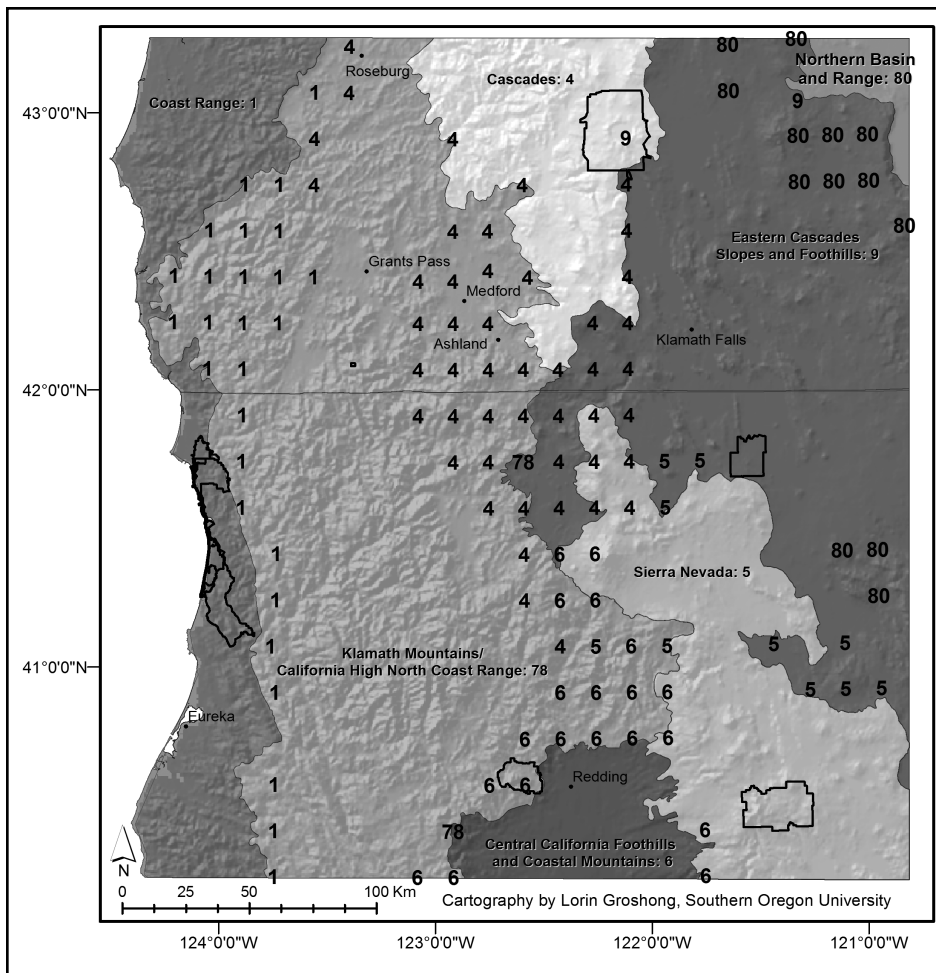


Figure 6. Map of Omernik Revised ecoregions showing misclassified plots based on *small mammal* assemblages. Large bold numbers indicate a misclassified plot, and the number indicates the erroneous ecoregion assignment based on the discriminant analysis function of Canonical Analysis of Principal Coordinates (CAP). The actual ecoregion numbers follow the ecoregion names (e.g., Klamath Mountains / California High North Coast Range: 78).

mammals. Because climatic variation was notable across all the classifications, and such variation is mechanistically linked to plant species distributions (Woodward 1987), these results are not surprising.

Small mammal and amphibian distributions showed modestly high degrees of correspondence to the ecoregional classifications (Tables 1–3). Hess et al. (2006) noted that congruence between ecoregional and species richness turnover for amphibians was among the highest for terrestrial wildlife indicators. In the Pacific Northwest, they also noted that mammal turnover was high. However, large mammals showed the weakest correspondence with the ecoregional classifications we tested (Tables 1–3). Our results are consistent

with the hypothesis that larger mammals, which are highly mobile and can more effectively regulate their body temperature, are less sensitive to some of the climatic or habitat boundaries than are less mobile and ectothermic organisms. However, this finding may also have been affected by the low species richness of large mammals, so our results are not definitive for this group.

Resident and migratory birds showed an intermediate degree of correspondence with the ecoregional classifications we tested (Tables 1–3), but appeared more sensitive to such geographic differences than did large mammals. However, we had many more bird species to analyze, so we believe our results are more likely to be

robust for these groups. The preference of many birds for specific habitat types may be more intentional and fixed than for more wide ranging generalist species that establish territories across a broad range of habitats (e.g., CalPIF 2002a, 2002b, 2004, 2005). Migratory breeding birds showed somewhat weaker correspondence to the ecoregions than did resident species, due perhaps to their lower diversity and shorter period of residence in our region each year. Winter climate is typically considered one of the strongest factors limiting resident bird populations within temperate and boreal regions (Forsman and Mönkkönen 2003).

Ecoregional Features and Biogeographic Linkages

Our results suggest that there are a number of biogeographic linkages among ecoregions in our study area (research question 4, Introduction). Although the number of ecoregions in each classification varied, our analyses suggested that they can be viewed hierarchically, from a three-zone overview of the region that should be relevant to almost all species, to finer scale subdivisions for less widespread species or other ecological processes.

All the classifications differentiated a coast zone from the rest of the ecoregions (Figure 1). Although latitudinal variation does occur in this zone, it is muted within our study region. The uniquely cool, moist climates of the coastal zone are associated with redwood (*Sequoia sempervirens* Endl.) and Sitka spruce (*Picea sitchensis* (Bong.) Carrière) forests, as well as a number of other Pacific Northwest plant and animal species. Interestingly, the summer climate appears to be the primary factor differentiating this zone, as winter precipitation is matched in other areas of the western Klamath Region. Other characteristic species of this region include trees such as red alder (*Alnus rubra* Bong.) and western hemlock (*Tsuga heterophylla* Sarg.), mammals such as the white-footed vole (*Arborimus albipes* Merriam) and yellow-cheeked chipmunk (*Neotamias ochrogenys* Sutt. & Nadl.), and a rich array of salamander species, including California slender salamander (*Batrachoseps attenuates* Eschscholtz)

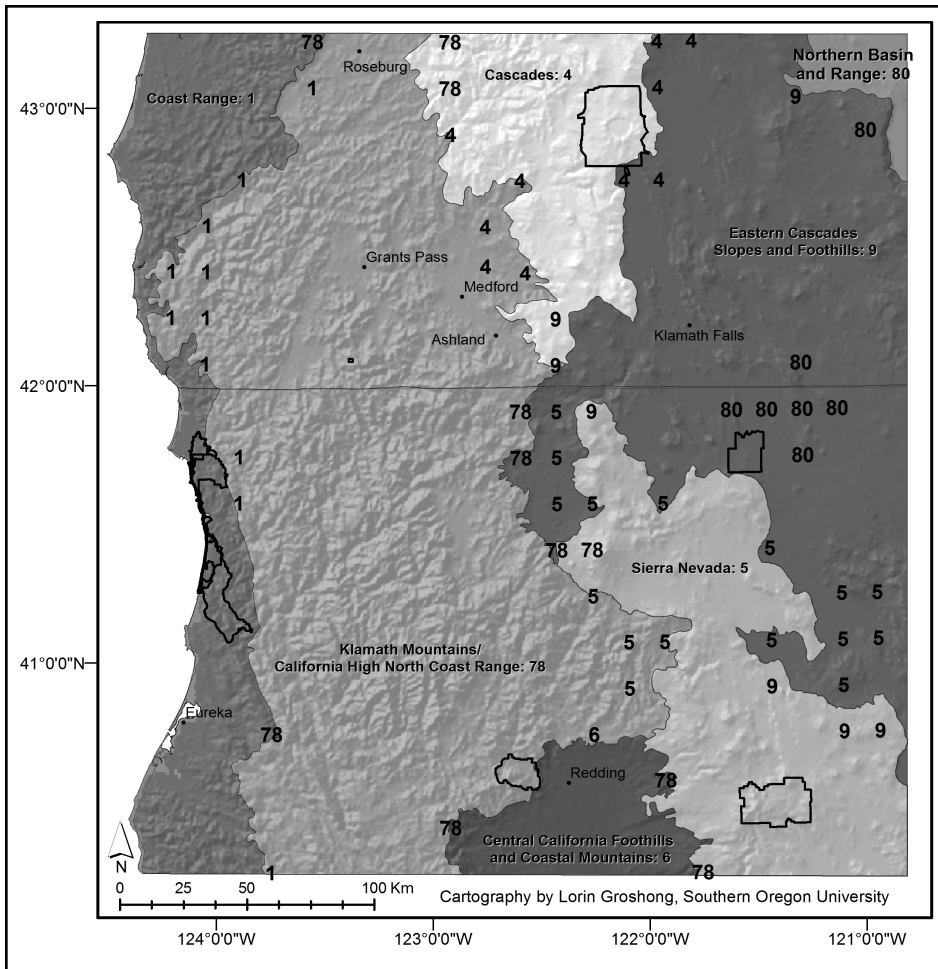


Figure 7. Map of Omernik Revised ecoregions showing misclassified plots based on *tree* assemblages. Large bold numbers indicate a misclassified plot, and the number indicates the erroneous ecoregion assignment based on the discriminant analysis function of Canonical Analysis of Principal Coordinates (CAP). The actual ecoregion numbers follow the ecoregion names (e.g., Klamath Mountains / California High North Coast Range: 78).

and Del Norte salamander (*Plethodon elongatus* Van Denburgh). Resident birds include the Marbled Murrelet (*Brachyramphus marmoratus* Gmelin) and many other coastal species. This zone's eastern boundary is more definitive for plants than for most of the animals we studied.

Similarly, the easternmost zone is highly distinctive in our study area, showing a markedly different flora and fauna and much less forest cover than the rest of the region. Significantly, the climatic and topographic boundary of the Cascade Range appears to be a more pronounced boundary for small mammals than for many tree species, and although poor in tree species, areas east of the Cascade Range are surprisingly rich in animal species (Appendix). The biodiversity of the region is composed of species with broad distributions in the Great Basin and Intermountain West. Characteristic tree species include western juniper (*Juniperus occidentalis* Hook.) and curl-leaf mountain mahogany (*Cercocarpus ledifolius* Nutt.). Notable animal species include the Great Basin spadefoot toad (*Scaphiopus intermontanus* Cope), pronghorn (*Antilocapra Americana* Ord), least chipmunk (*Tamias minimus* Bachman), and birds of open country, such as the ferruginous hawk (*Buteo regalis* Gray).

The central zone is an exceedingly complex area of major latitudinal and longitudinal transitions between wet coastal forests along the western and northern margins,

Table 1. Ecoregional classification strength as measured by analysis of similarity (ANOSIM) R values for each biota group and ecoregional classification. B = Bailey, C = Climate Zones, O = Omernik, O_R = Omernik Revised, and W = World Wildlife Fund. See text for more information on ANOSIM R values.

Biota Group	ANOSIM R					Average	Rank Order
	B	C	O	O_R	W		
Amphibians	0.69	0.43	0.63	0.67	0.65	0.61	B = O_R > W > O > C
Breeding Birds	0.49	0.6	0.54	0.56	0.6	0.56	C = W > O_R > O > B
Resident Birds	0.61	0.69	0.62	0.67	0.66	0.65	C > O_R > W > O > B
Large Mammals	0.4	0.19	0.3	0.35	0.34	0.32	B > O_R > W > O > C
Small Mammals	0.63	0.63	0.65	0.68	0.67	0.65	O_R > W > O > B = C
Trees	0.73	0.45	0.68	0.72	0.68	0.65	B > O_R > W = O > C
Averages	0.59	0.5	0.57	0.61	0.6	0.57	O_R > W > B > O > C

Table 2. Ecoregional classification strength as measured by Classification Strength values (the weighted mean of the *within* class similarities minus the mean of all *between* class similarities) for each biota group and ecoregional classification. B = Bailey, C = Climate Zones, O = Omernik, O_R = Omernik Revised, and W = World Wildlife Fund. See text for more information on Classification Strength.

Biota Group	Classification Strength					Average	Rank Order
	B	C	O	O_R	W		
Amphibians	0.2	0.16	0.19	0.2	0.21	0.19	W > B = O_R > O > C
Breeding Birds	0.07	0.06	0.06	0.06	0.07	0.06	W = B > C = O_R = O
Resident Birds	0.07	0.07	0.06	0.07	0.07	0.07	W = B = O_R = C > O
Large Mammals	0.06	0.04	0.04	0.05	0.05	0.05	B > W = O_R > C = O
Small Mammals	0.16	0.14	0.14	0.15	0.16	0.15	B = W > O_R > C = O
Trees	0.31	0.22	0.28	0.31	0.31	0.29	W = B = O_R = C > O
Averages	0.15	0.12	0.13	0.14	0.15	0.13	W = B > O_R > O > C

and dry forests, sagebrush steppe, Mediterranean shrublands, and grasslands along the eastern and southern boundaries. The three broad zones described above were recognized by all the classifications, and compose the coarsest ecoregional classification for our region. We next delineate and describe regions within the central zone.

At the northern edge of the central zone, the Oregon Cascades subregion (Cascades 4; Figures 2–7) appears to function as a southward-reaching high elevation peninsula of circumboreal species that do not occur elsewhere in our region. This was especially notable for small mammals, which show a surprising richness in this subregion. Notable species of this ecoregion include Pacific silver fir (*Abies*

amabilis Douglas ex J. Forbes), Engelmann spruce (*Picea engelmannii* Engelm.), subalpine fir (*Abies lasiocarpa* Endl.), such iconic northern mammals as the wolverine (*Gulo gulo* L.) and lynx (*Lynx canadensis* Kerr), small mammals such as the water vole (*Microtus richardsoni* De Kay) and Pacific shrew (*Sorex pacificus* Coues), and high elevation birds, such as the American Three-toed Woodpecker (*Picoides dorsalis* Baird) and Gray Jay (*Perisoreus canadensis* L.).

Similarly, at the southern margin of the central zone, the Central California Foothills and Coastal Mountains ecoregion of the Sacramento Valley (Figures 2–7) presents a northward-reaching peninsula for the rich assemblage of species characteristic of

lowland California. These species include a number of native oaks, such as blue oak (*Quercus douglasii* Hook. & Arn.), valley oak (*Q. lobata* Née), interior live oak (*Q. wislizeni* A. DC.), a rich array of chaparral shrubs, such as toyon (*Heteromeles arbutifolia* M. Roem.) and chamise (*Adenostoma fasciculatum* Hook. & Arn.), small mammals such as the California kangaroo rat (*Dipodomys californicus* Merriam), and southern landbirds such as the California Thrasher (*Toxostoma redivivum* Gambel), and Greater Roadrunner (*Geococcyx californianus* Lesson).

Our analyses suggested the California Cascade Range is climatically and biogeographically more closely allied with the Sierra Nevada than the larger Cascades

Table 3. Ecoregional classification strength as measured by Canonical Analysis of Principal Coordinates (CAP) analyses for each biota group and ecoregional classification. B = Bailey, C = Climate Zones, O = Omernik, O_R = Omernik Revised, and W = World Wildlife Fund. See text for more information on CAP.

Biota Group	CAP (%Correct)					Average	Rank Order
	B	C	O	O_R	W		
Amphibians	55%	67%	66%	64%	61%	63%	C > O > O_R > W > B
Breeding Birds	55%	71%	66%	71%	64%	65%	C = O_R > O > W > B
Resident Birds	58%	83%	69%	68%	66%	69%	C > O > O_R > W > B
Large Mammals	16%	36%	14%	35%	29%	26%	C > O_R > W > B > O
Small Mammals	62%	80%	66%	70%	66%	69%	C > O_R > W = O > B
Trees	71%	82%	81%	84%	81%	80%	O_R > C > W = O > B
Averages	53%	70%	60%	65%	61%	62%	C > O_R > W > O > B

ecoregion described by Omernik (2011). The Bailey and WWF classifications both define a Sierra Nevada ecoregion, but of very different extents in our study region. The California Cascades/Sierra Nevada ecoregion we defined using the Omernik boundaries (Sierra Nevada 5; Figures 2–7) is similar in distribution to the Bailey Sierra Nevada and Southern Cascades ecoregions, but more closely matches the topography and recognizes an important disjunction between the Sierra Nevada and Cascades ecoregions in far northern California. The climatic, biogeographic, and biophysical data suggest such a disjunction is important, despite the underlying volcanic geology.

The Klamath Mountains/California High North Coast Range ecoregion (hereafter Klamath Mountains ecoregion), the most complex and centrally located ecoregion, shows a notable gradient from the windward slopes of the major mountain ranges, where lower elevations are largely forested and receive 100–250 cm of precipitation per year, to the leeward slopes, which receive 40–80 cm of precipitation per year and contain a rich mosaic of more open forests, shrublands, pine-oak woodlands, and grasslands at lower elevations. This pattern suggests that the Klamath Mountains ecoregion might be viewed in terms of western and eastern subregions, with quite varied environments and floras. Waring (1969) proposed that the eastern portion of the Siskiyou Mountains (a northern subrange of the Klamath Mountains) composes a distinct ecological unit within which many characteristic woody plant species of the western Siskiyou Mountains are absent or rare. While many of the endemic and moisture-adapted woody species are indeed restricted to the western Siskiyou Mountains, vascular plant species diversity is notably higher in the eastern zone (Whittaker 1960), with a greater array of plant communities, especially of drought-adapted species.

Viewed across all the taxa groups we studied, the western Klamath Mountains subregion can be viewed as a major reservoir of mesic forest species with northern distributions into the maritime forests of the coastal zone and Pacific Northwest.

Although they are distinguished from the immediate coastal forests by greater plant diversity and endemism, western Klamath Mountains sites were often misclassified as coastal sites for resident land birds, small mammals, and amphibians, suggesting strong connections between these moist, largely forested ecoregions (Figures 2, 3, and 6).

The eastern Klamath Mountains subregion shows more varied biogeographic influences. The Climate Zone analysis suggested that climates typical of the eastside of the Cascade Range extend nearly to the eastern foothills of the Marble Mountains (a high range in the central Klamath Mountains), which mirrored western range extensions of many drought-adapted plant and animal species typically found east of the Cascade Range. The eastern ridges and valleys show evidence of Sierran and Californian influences, respectively. In the northeast, Cascadian influences are also notable. The general character is of great spatial variability and surprising juxtapositions of different floras and faunas.

The strong influence of Sierran species throughout the Californian Cascades and into the eastern Klamath Mountains ecoregion is most likely a result of the unique evolutionary, geologic, and climatic history of these adjacent ecoregions. The ancient Klamath Mountains and Sierra Nevada, with many shared geologic characteristics and a great diversity of habitats, evolved a globally distinct and uncommonly diverse flora and fauna (Whittaker 1961; Stebbins and Major 1965). With the later rise of the Cascade Range, the species-rich communities of the adjacent Klamath Mountains and Sierra Nevada were able to readily colonize the new volcanic landscapes, intermix, and with subsequent climate-driven migrations, establish a general biogeographic continuity across the highlands of northeast California.

Implications for Natural Areas Management in the Klamath Region

The uniquely complex array of ecoregions and environments within the Klamath Region creates practical challenges for natural area managers. There are many

distinct combinations of climate, geology, and biodiversity, yet there is not a corresponding level of site-specific management knowledge for many issues. Klamath Region managers often must import concepts and resource management approaches developed in adjacent regions, yet the geographic domains of such management approaches are rarely stated explicitly.

This study provides potential insights into the relevant management domains of the Klamath Region. For instance, the wet and productive landscape of the coast, western Klamath Mountains, and Oregon Cascades subregions seem to show strong connections to the management domain of the maritime Pacific Northwest (e.g., Swanson and Franklin 1992; Carey 1998; Naiman et al. 2000; Spies et al. 2002; Altman and Alexander 2012). These landscapes are dominated by highly productive conifer-dominated forests with many shade-tolerant, moisture-adapted plant and animal species. Many of the ecological processes (e.g., large, relatively infrequent fires, debris flows and geomorphic, flood, and wind events, rafting and damming of large wood in large perennial streams, etc.) are well studied in this region. In this productive landscape, uniquely biodiverse habitats, such as rare plant communities, are likely to be associated with geologically distinct areas or relatively rare early and late successional stages (Odion and Sarr 2007).

East of the crest of the Klamath Mountains, the management domains become blurred and broadly overlapping. Southern and low elevation zones, with open woodland, grassland, and chaparral environments have strong connections with Californian and Sierran ecosystems and management literatures (e.g., SNEP 1996; Odion and Davis 2000; CalPIF 2002a, 2002b, 2004; Keeley 2002; Agee and Skinner 2005). Species diversity and landscape heterogeneity are very high, summer drought is severe, and fire and invasive species are major concerns, especially at low and middle elevations. Although fire and fuels restoration approaches developed in the southwestern United States are often applied to these fire-adapted ecosystems (e.g., Covington et al. 1997) in natural areas, it is important to note

that Mediterranean plant communities are richer in endemic species than most Interior West ecosystems, and warrant distinctive management approaches. Shrublands and associated species, especially, are critical reservoirs for biodiversity (Cody 1986), not simply ladder fuels or competitors with desired tree species.

East of the Cascades and Sierra Nevada ecoregions, the Interior West influence is increasingly important, although higher elevation areas have notable affinities with drier Sierran forest landscapes. The Eastern Cascades Slopes and Foothills and Northwest Basin and Range ecoregions in this area (Figures 2–7) have the strongest affinities with the other semiarid and subhumid ecoregions of the Interior Northwest and Great Basin, and resource management literature from those regions (e.g., Hemstrom et al. 2002; CalPIF 2005; Chambers et al. 2007) may be quite relevant for many of the most pressing management issues. The notable summer drought in this area suggests our eastern regions are likely to fall in the management domains of the western Great Basin and Columbia Basin.

We found that a revision of the most recent Omernik ecoregional classification (Figures 2–7) provided a relatively general geographic framework that captured most of the broad biogeographic zones and subregions of the Klamath Region. A more precise delineation of western and eastern Klamath Mountains subregions appears worthy of future study, but awaits finer scale data sources. The Omernik Revised classification we devised is sufficiently general to be used by managers to place their protected areas in a larger regional context and to help identify linkages to more widespread ecoregions and management domains.

Although the Klamath Region can be viewed as a nexus for more broadly distributed Maritime Temperate, Mediterranean, and Interior West ecoregions and species assemblages, such a peripheral role does not fully capture its emergent properties. It is important to recognize that it is also a region of globally significant biodiversity and endemism (Whittaker 1960; Stebbins and Major 1965; DellaSala et al. 1999; Vander

Schaaf et al. 2004). Such evolutionary centers, refugia (Whittaker 1961; Tzedakis et al. 2002), and hot spots (Myers et al. 2000) may have exceptional importance for teaching us about the mechanisms whereby species coexist and persist in space and time. Tzedakis et al. (2002) demonstrated that many tree species survived Quaternary climate fluctuations in the mountains of western Greece, a region with many parallels to the Klamath Region. Much of the research to date in the Klamath Region has been botanical. We need comparable work for other life forms, especially the less studied taxa (e.g., arthropods).

Current climate figures strongly in the spatial structure of ecoregions in the Klamath Region and elsewhere; however, projected climate change will shift the geographic distribution of climate conditions (Wiens et al. 2011) and those shifts will likely reshuffle existing ecoregional patterns (Stralberg et al. 2009). Landscapes that have functioned as past refugia are likely to be of exceptional importance during future changes (Ashcroft 2010). It seems reasonable to hypothesize that the Klamath Region has the potential, if managed well, to carry many native species into an uncertain future (Olson et al. 2012). Major goals for a Klamath Region management domain might, therefore, be inventory, monitoring, and research that strengthens our understanding of the patterns and origins of native biodiversity and helps to ensure it will be conserved for future generations.

CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

Our study of ecoregional structure and biotic distributions in the Klamath Region highlights the complex array of ecological patterns across the region. A hierarchical view of ecoregions, starting from a coarse three-region overview to finer ecoregional subdivisions, provides a comprehensive and yet flexible framework suitable for understanding and managing for native biodiversity. At broad scales, general climate-driven patterns seem to affect the distributions of most species in the Klamath Region. At finer scales, spe-

cies life history and other factors, such as environmental history and land use, can cause varied responses to landscape boundaries. Our findings supported the hypothesis that immobile species (plants, fungi) and low vagility species (small mammals, amphibians) are likely to show narrower distributions than wider ranging taxa (birds, large mammals). However, for most other taxa, inventories are not complete, nor are range maps available (e.g., most arthropods). Thus, for many natural areas management applications, managers may want to consider more general ecoregional classifications that are likely to be relevant to multiple species.

It is also important to recognize that precise, taxon-specific classifications are unlikely to be broadly relevant management domains for natural area managers, who often must make decisions that are suitable for many species and ecological processes. In our study, we found that an intermediate level of resolution, as in the Omernik Revised classification, captured sufficient ecoregional detail to be broadly relevant, yet easily understood and communicated. Similar resolution ecoregional classifications may be useful for natural areas management applications in other regions, particularly in other coastal mountainous regions with levels of ecoregional complexity comparable to that of the Klamath Region.

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LITERATURE CITED

- Agee, J.K., and C.N. Skinner. 2005. Basic principles of forest fuel reduction treatments. *Forest Ecology and Management* 211:83-96.
- Altman, B., and J. Alexander. 2012. Habitat conservation for landbirds in the coniferous forests of western Oregon and Washington. Version 2.0. Oregon-Washington Partners in Flight. Accessed 20 February 2014 <http://www.orwapif.org/sites/default/files/Western_Conifer_Plan_new.pdf>.
- Anderson, M.A., R.N. Gorley, and K.R. Clarke. 2008. PERMANOVA+ for PRIMER: Guide to software and statistical methods. PRIMER-E Ltd., Plymouth, UK.
- Ashcroft, M.B. 2010. Identifying refugia from climate change. *Journal of Biogeography* 37:1407-1413.
- Bailey, R.G. 1983. Delineation of ecosystem regions. *Environmental Management* 7:365-373.
- Bailey, R.G. 1998. *Ecoregions: The Ecosystem Geography of the Oceans and Continents*. Springer, New York.
- Baker, F.S. 1944. Mountain climates of the western United States. *Ecological Monographs* 14:225-254.
- Ball, G.H., and D.J. Hall. 1965. ISODATA, a novel method of data analysis and pattern classification. Stanford Research Institute Technical Report, April 1965. Stanford Research Institute, [Menlo Park, CA.]
- [CalPIF] California Partners in Flight. 2002a. The coniferous forest bird conservation plan: A strategy for protecting and managing coniferous forest habitats and associated birds in California (J. Robinson and J. Alexander, lead authors). Version 1.1. Point Reyes Bird Observatory, Stinson Beach, California. Accessed 20 February 2014 <<http://www.prbo.org/calpif/plans.html>>.
- [CalPIF] California Partners in Flight. 2002b. The oak woodland bird conservation plan: A strategy for protecting and managing oak woodland habitats and associated birds in California (S. Zack, lead author). Version 2.0. Point Reyes Bird Observatory, Stinson

Beach, California. Accessed 7 January 2008 <<http://www.prbo.org/calpif/plans.html>>.

- [CalPIF] California Partners in Flight. 2004. The coastal scrub and chaparral bird conservation plan: A strategy for protecting and managing coastal scrub and chaparral habitats and associated birds in California (J. Lovio, lead author). Version 2.0. PRBO Conservation Science, Stinson Beach, California. Accessed 7 January 2008 <<http://www.prbo.org/calpif/plans.html>>.
- [CalPIF] California Partners in Flight. 2005. The sagebrush bird conservation plan: A strategy for protecting and managing sagebrush habitats and associated birds in California. Version 1.0. PRBO Conservation Science, Stinson Beach, California. Accessed 7 January 2008 <<http://www.prbo.org/calpif/plans.html>>.
- Carey, A. 1998. The ecological foundations of biodiversity: lessons from natural and managed forests of the Pacific Northwest. *Northwest Science* 72:127-133.
- Chambers, J.C., B.A. Roundy, R.R. Blank, S.E. Meyer, and A. Whittaker. 2007. What makes Great Basin sagebrush ecosystems invulnerable by *Bromus tectorum*? *Ecological Monographs* 77:117-145.
- Clarke, K.R., and R.H. Greene. 1988. Statistical design and analysis for a 'biological effects' study. *Marine Ecology Progress Series* 46:213-226.
- Clarke, K.R., and R.M. Warwick. 2001. *Change in Marine Communities*, 2nd ed. PRIMER-E Ltd., Plymouth, UK.
- Cody, M.L. 1986. Diversity, rarity, and conservation in Mediterranean-climate regions. Pp. 122-152 in M.E. Soule, ed., *Conservation Biology: The Science of Scarcity and Diversity*. Sinauer, Sunderland, MA.
- Covington, W.W., P.Z. Fulé, M.M. Moore, S.C. Hart, T.E. Kolb, J.N. Mast, S.S. Sackett, and M.R. Wagner. 1997. Restoring ecosystem health in ponderosa pine forests of the southwest. *Journal of Forestry* 95:23-29.
- DAYMET. 2007. Climatological summaries for the conterminous United States, 1980-1997. University of Montana, Numerical Terradynamic Simulation Group. Accessed 24 April 2007 <<http://daymet.ornl.gov>>.
- DellaSala, D.A., S.T. Reid, T.J. Frest, J.R. Strittholt, and D.M. Olson. 1999. A global perspective on the biodiversity of the Klamath-Siskiyou ecoregion. *Natural Areas Journal* 19:300-319.
- Duff, A., and T. Morrell. 2007. Predictive occurrence models for bat species in California. *Journal of Wildlife Management* 71:693-700.
- ESRI. 2003. ArcGIS ArcInfo Desktop (version 9.3) Environmental Systems Research

- Institute Inc., Redlands, CA.
- Forsman, J.T., and M. Mönkkönen. 2003. The role of climate in limiting European resident bird populations. *Journal of Biogeography* 30:55-70.
- Grinnell, J. 1917. The niche relationships of the California thrasher. *The Auk* 21:364-382.
- Hansen, A.J., and J.J. Rotella. 2002. Biophysical factors, land use, and species viability in and around nature reserves. *Conservation Biology* 16:1-12.
- Hawkins, C.P., R.H. Norris, J. Gerritsen, R.B. Hughes, S.K. Jackson, R.K. Johnson, and R.J. Stevenson. 2000. Evaluation of the use of landscape classifications for the prediction of freshwater biota: synthesis and recommendations. *Journal of the North American Benthological Society* 19:541-556.
- Hemstrom, M.A., M.J. Wisdom, M.M. Rowland, B. Wales, W.J. Hann, and R.A. Gravenmier. 2002. Sagebrush-steppe vegetation dynamics and potential for restoration in the Interior Columbia Basin, USA. *Conservation Biology* 16:1243-1255.
- Henderson, J. 1997. The PNV Model – A gradient model for predicting environmental variables and potential natural vegetation across a landscape. Unpublished Technical Report on file at Mt. Baker-Snoqualmie National Forest, Mountlake Terrace, WA.
- Hess, G.R., R.A. Bartel, A.K. Leidner, K.M. Rosenfeld, S.B. Snider, and T.H. Ricketts. 2006. Effectiveness of biodiversity indicators varies with extent, grain, and region. *Biological Conservation* 132:448-457.
- Holdridge, L.R. 1947. Determination of world plant formations from simple climatic data. *Science* 105:367-368.
- Host, G.E., P.L. Polzer, D.J. Mladenoff, M.A. White, and T.R. Crow. 1996. A quantitative approach to developing ecosystem classifications. *Ecological Applications* 6:608-618.
- Hurlbert, A.H., and E.P. White. 2005. Disparity between range map- and survey-based analyses of species richness: patterns, processes and implications. *Ecology Letters* 8:319-327.
- Johnson, K.N., F. Swanson, M. Herring, and S. Greene, eds. 1999. *Science at the Crossroads of Management and Policy*. Island Press, Washington, DC.
- Keeley, J.E. 2002. Fire management of California shrubland landscapes. *Environmental Management* 29:395-408.
- McDonald, R., M. McKnight, D. Weiss, E. Selig, M. O'Connor, C. Violin, and A. Moody. 2005. Species compositional similarity and ecoregions: do ecoregion boundaries represent ones of high species turnover? *Biological Conservation* 126:24-40.
- McLaughlin, S.P. 1989. Natural floristic areas of the western United States. *Journal of Biogeography* 16:239-248.
- McNab, W.H., and P.E. Avers. 1994. *Ecological Subregions of the United States*. Technical Report WO-WSA-5, prepared in cooperation with Regional Compilers and the ECOMAP Team of the Forest Service, July 1994. Accessed 16 April 2004 <<http://www.fs.fed.us/land/pubs/ecoregions/>>.
- Merriam, C.H., and L. Steineger. 1890. Results of a biological survey of the San Francisco Mountain region and desert of the Little Colorado in Arizona. *North American Fauna* 3:1-136.
- Mitchell, V.L. 1976. The regionalization of climate in the western United States. *Journal of Applied Meteorology* 15:920-926.
- Mock, C.J. 1996. Climatic controls and spatial variations of precipitation in the western United States. *Journal of Climate* 9:1111-1125.
- Monjeu, J.A., E.C. Birney, L. Ghermandi, R.S. Sikes, L. Margutti, and C.J. Phillips. 1998. Plants, small mammals, and the hierarchical landscape classifications of Patagonia. *Landscape Ecology* 13:285-306.
- Myers, N., R.A. Mittermeier, C.G. Mittermeier, G.A.B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853-858.
- Naiman, R.J., R.E. Bilby, and P.A. Bisson. 2000. Riparian ecology and management in the Pacific coastal rain forest. *BioScience* 50:996-1011.
- Odion, D.C., and F.W. Davis. 2000. Fire, soil heating, and the formation of vegetation patterns in chamise chaparral. *Ecological Monographs* 70:149-169.
- Odion, D., and D. Sarr. 2007. Managing disturbance regimes to maintain biodiversity in forested ecosystems of the Pacific Northwest. *Forest Ecology and Management* 246:57-65.
- Ohmann, J., and T. Spies. 1998. Regional gradient analysis and spatial pattern of woody plant communities of Oregon forests. *Ecological Monographs* 68:151-182.
- Olson, D., D.A. DellaSala, R.F. Noss, J.R. Strittholt, J. Kass, M.E. Koopman, and T.F. Allnutt. 2012. Climate change refugia for biodiversity in the Klamath-Siskiyou ecoregion. *Natural Areas Journal* 32:65-74.
- Olson, D.M., E. Dinerstein, E.D. Wikramanayake, N.D. Burgess, G.V.N. Powell, E.C. Underwood, J.A. D'Amico, I. Itoua, H.E. Strand, J.C. Morrison, C.J. Loucks, T.F. Allnutt, T.H. Ricketts, Y. Kura, J.F. Lamoreux, W.W. Wettengel, P. Hedao, and K.R. Kassem. 2001. Terrestrial ecoregions of the world: a new map of life on Earth. *BioScience* 51:933-938.
- Omernik, J.M. 1987. Ecoregions of the conterminous United States. Map (scale 1:7,500,000). *Annals of the Association of American Geographers* 77:118-125.
- Omernik, J.M. 2011. Level III Ecoregions of the Continental United States (Revised December 2011). National Health and Environmental Effects Research Laboratory, US Environmental Protection Agency, [Research Triangle Park, NC]. Accessed 26 March 2013 <http://www.epa.gov/wed/pages/ecoregions/level_iii_iv.htm>.
- Palik, B., and R.T. Engstrom. 1999. Species composition. Pp. 66-94 in M. Hunter, ed., *Maintaining Biodiversity in Forest Ecosystems*. Cambridge University Press, Cambridge, UK.
- Ricketts, T.H., E. Dinerstein, D.M. Olson, C.J. Loucks, W. Eichbaum, D. DellaSala, K. Kavanagh, P. Hedao, P.T. Hurley, K.M. Carney, R. Abell, and S. Walters. 1999. *Terrestrial Ecoregions of North America: A Conservation Assessment*. Island Press, Washington, DC.
- Root, T. 1988. Energy constraints on avian distributions and abundances. *Ecology* 69:330-339.
- Sarr, D., D. Odion, S. Mohren, E. Perry, R. Hoffman, L. Bridy, and A. Merton. 2007. Klamath Network Vital Signs Monitoring Plan. Natural Resource Report NPS/KLMN/NRR-2007/016. National Park Service, Fort Collins, CO.
- Shine, R., E.G. Barrott, and M.J. Elphick. 2002. Some like it hot: effects of forest clearing on nest temperatures of montane reptiles. *Ecology* 83:2808-2815.
- [SNEP] Sierra Nevada Ecosystem Project. 1996. *State of the Sierra Nevada: Final Report to Congress, Volumes I-III plus summary and addendum*. Wildland Resources Reports 37-40, University of California Air and Wildland Resources, Davis, CA.
- Spies, T.A., D.E. Hibbs, J.L. Ohmann, G.H. Reeves, R.J. Pabst, F.J. Swanson, C. Whitlock, J.A. Jones, B.C. Wemple, L.A. Parendes, and B.A. Schrader. 2002. The ecological basis of forest ecosystem management in the Oregon Coast Range. Pp. 31-67 in S.D. Hobbs, J.P. Hayes, R.L. Johnson, G.H. Reeves, T.A. Spies, J.C. Tappeiner, and G.E. Wells, eds., *Forest and Stream Management in the Oregon Coast Range*. Oregon State University Press, Corvallis.
- Stebbins, G.L., and J. Major. 1965. Endemism and speciation in the California flora. *Ecological Monographs* 35:1-35.
- Stralberg, D., D. Jongsomjit, C.A. Howell, M.A. Snyder, J.D. Alexander, J.A. Wiens, and T.L. Root. 2009. Re-shuffling of species

-
- with climate disruption: a no-analog future for California birds? *PLoS ONE* 4(9):e6825. doi:10.1371/journal.pone.0006825.
- Swanson, F., and J.F. Franklin. 1992. New forestry principles from ecosystem analysis of Pacific Northwest forests. *Ecological Applications* 2:262-274.
- Thompson, R., S.L. Shafer, K.H. Anderson, L.E. Strickland, R.T. Pelletier, P.J. Bartlein, and M.W. Kerwin. 2005. Topographic, bioclimatic, and vegetation characteristics of three ecoregion classification systems in North America: comparisons along continent-wide transects. *Environmental Management* 34(1)Supplement:S125-S148.
- Thornton, P.E., S.W. Running, and M.A. White. 1997. Generating surfaces of daily meteorological variables over large regions of complex terrain. *Journal of Hydrology* 190:214-251.
- Tzedakis, P.C., I.T. Lawson, M.R. Frogley, G.M. Hewitt, and R.C. Preece. 2002. Buffered tree population changes in a Quaternary refugium: evolutionary implications. *Science* 297:2044-2047.
- US Geological Survey. 1999. Digital representation of "Atlas of United States Trees" by Elbert L. Little, Jr. US Geological Survey Professional Paper 1650, [Lakewood, CO]. Accessed 19 May 2005 <<http://gec.cr.usgs.gov/data/little>>.
- Van Sickle, J., and R.M. Hughes. 2000. Classification strengths of ecoregions, catchments, and geographic clusters for aquatic invertebrates in Oregon. *Journal of the North American Benthological Society* 19:370-384.
- Vander Schaaf, D., M. Schindel, D. Borgias, C. Mayer, D. Tolman, G. Kittel, J. Kagan, T. Keeler-Wolf, L. Serpa, J. Hak, and K. Popper. 2004. Klamath Mountains Ecoregional Conservation Assessment. The Nature Conservancy, Portland, OR.
- Wallace, A.R. 1869. *The Malay Archipelago: The Land of the Orang-utan, and the Bird of Paradise*. Harper & Brothers Publishers, New York.
- Walter, H. 1973. *Vegetation of the Earth in Relation to the Eco-Physiological Conditions*. Springer-Verlag, New York.
- Waring, R.H. 1969. Forest plants of the eastern Siskiyou, their environmental and vegetational distribution. *Northwest Science* 43:1-17.
- Welsh, H.H. 1994. Bioregions: an ecological and evolutionary perspective and a proposal for California. *California Fish and Game* 80:97-124.
- Whittaker, R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30:279-338.
- Whittaker, R.H. 1961. Vegetation history of the Pacific coast states and the central significance of the Klamath region. *Madroño* 16:5-23.
- Wiens, J.A., N.E. Seavy, and D. Jongsomjit. 2011. Protected areas in climate space: what will the future bring? *Biological Conservation* 144:2119-2125.
- Woodward, F.I. 1987. *Climate and Plant Distribution*. Cambridge University Press, Cambridge, UK.
- Wright, R.G., M.P. Murray, and T. Merrill. 1998. Ecoregions as a level of ecological analysis. *Biological Conservation* 86:207-213.

Appendix. Ecoregional classification schemes and average taxa richness for each group examined. Variance is represented as standard deviation. Number of plots refers to the number of points within each ecoregional polygon for that zone. Zone numbers are unique to each original ecoregional scheme and have no inherent meaning other than their original context. Zone names come from the original ecoregional scheme as well.

Zone Number	Zone Name	Number of plots	Breeding			Large Mammals		Small Mammals		Trees	Total
			Amphibians	Birds	Resident Birds	Mammals	Mammals				
Bailey											
2	Klamath Mountains	160	14 ± 1.9	44 ± 3.3	83 ± 4.7	8 ± 1.1	37 ± 3.6	33 ± 6.7	219 ± 11		
3	Northern California Coast	19	16 ± 0.7	44 ± 1.8	79 ± 1.1	8 ± 0.5	35 ± 1.7	31 ± 5.3	213 ± 6		
8	Great Valley	7	9 ± 1.1	50 ± 1.6	89 ± 1.2	5 ± 1	33 ± 1.1	12 ± 2.4	197 ± 3		
9	Sierra Nevada Foothills	8	12 ± 0.5	52 ± 0.5	85 ± 1.6	5 ± 0.5	35 ± 2.1	17 ± 3.3	206 ± 5		
10	Sierra Nevada	2	5 ± 2.1	49 ± 0	84 ± 2.1	8 ± 0	40 ± 0.7	13 ± 1.4	197 ± 1		
11	Southern Cascades	59	9 ± 3	50 ± 1.9	86 ± 2.8	8 ± 1.3	41 ± 3.9	17 ± 5.8	209 ± 10		
12	Modoc Plateau	53	7 ± 0.8	51 ± 1.1	86 ± 1.7	8 ± 1.1	39 ± 1.8	6 ± 3.6	195 ± 6		
13	Eastern Cascades	53	7 ± 2.2	51 ± 1.9	89 ± 3.1	10 ± 0.8	39 ± 3.2	10 ± 4.6	205 ± 10		
14	Western Cascades	13	15 ± 2.7	47 ± 0.7	86 ± 4	10 ± 0.3	41 ± 2.8	24 ± 2.5	222 ± 5		
28	Northwestern Basin and Range	3	5 ± 0	50 ± 1	81 ± 2	8 ± 0.6	34 ± 0.6	2 ± 0.6	180 ± 3		
164	Northern California Interior Coast Ranges	4	11 ± 0.6	46 ± 1.2	89 ± 0.5	8 ± 0	35 ± 1	18 ± 4.2	205 ± 4		
168	Northern California Coast Ranges	11	16 ± 0.7	47 ± 1.6	81 ± 1.3	8 ± 0.5	37 ± 2.4	35 ± 2.7	222 ± 2		
1482	Oregon and Washington Coast Ranges	10	15 ± 0.4	39 ± 1.1	75 ± 1.3	10 ± 0	29 ± 1.2	31 ± 2	198 ± 3		
WWF											
1	California Central Valley Grassland	8	9 ± 1.5	50 ± 1.7	89 ± 1.2	5 ± 0.9	33 ± 1	12 ± 2.2	198 ± 3		
2	California Interior Chaparral and Woodlands	10	11 ± 0.7	48 ± 3.3	87 ± 2.7	7 ± 1.3	35 ± 1.1	19 ± 3.7	205 ± 4		
8	Central and Southern Cascades Forests	28	14 ± 2.8	47 ± 1.2	86 ± 4.6	10 ± 0.4	41 ± 3.4	22 ± 3.9	219 ± 7		
9	Snake/Columbia Shrub Steppe	10	5 ± 0.3	51 ± 0.7	83 ± 2.5	9 ± 0.7	36 ± 2.1	5 ± 2.5	187 ± 7		
10	Central Pacific Coastal Forests	22	15 ± 0.7	39 ± 1.2	75 ± 1.6	10 ± 0.7	30 ± 1.5	32 ± 6.9	199 ± 7		
12	Eastern Cascades Forest	113	7 ± 1.2	51 ± 1.5	88 ± 2.6	9 ± 1.5	40 ± 2.9	8 ± 4.2	201 ± 9		
16	Klamath-Siskiyou Forests	165	14 ± 2.2	45 ± 3.2	84 ± 4.1	8 ± 1	38 ± 3.4	32 ± 6.9	220 ± 9		
19	Northern California Coastal Forests	22	16 ± 0.6	44 ± 1.7	79 ± 1.2	8 ± 0.5	35 ± 1.6	32 ± 5.3	214 ± 6		
27	Sierra Nevada Forests	24	8 ± 3.5	51 ± 2.0	83 ± 1.7	7 ± 1	37 ± 1.7	17 ± 5.8	202 ± 7		

Continued

Appendix (Continued)

Zone Number	Zone Name	Number of plots	Breeding			Large Mammals		Small Mammals		Trees	Total
			Amphibians	Birds	Resident Birds	Mammals	Mammals				
Omerik											
1	Coast Range	43	16 ± 0.8	42 ± 3.2	77 ± 2.6	9 ± 1.2	32 ± 3.3	32 ± 5.9	207 ± 10		
4	Cascades	77	10 ± 4.1	49 ± 2.4	85 ± 3.3	8 ± 1.6	40 ± 3.4	18 ± 6.2	210 ± 11		
5	Sierra Nevada	1	3	49	85	8	40	12	196		
6	Central California Foothills and Coastal Mountains	17	10 ± 1.4	49 ± 2.9	88 ± 2.4	6 ± 1.5	34 ± 1.7	15 ± 4	201 ± 5		
9	Eastern Cascades Slopes and Foothills	99	7 ± 1.5	51 ± 1.5	88 ± 2.6	9 ± 1.5	40 ± 2.9	8 ± 4.7	201 ± 9		
78	Klamath Mountains/California High North Coast Range	156	14 ± 1.8	45 ± 3.1	84 ± 4.3	8 ± 1	37 ± 3.3	33 ± 6.6	221 ± 9		
80	Northern Basin and Range	9	5 ± 0	50 ± 0.7	83 ± 2.5	9 ± 0.7	35 ± 1.7	4 ± 2.5	186 ± 7		
Omerik Revised											
1	Coast Range	43	16 ± 0.8	42 ± 3.2	77 ± 2.6	9 ± 1.2	32 ± 3.3	32 ± 5.9	207 ± 10		
4	Cascades	28	14 ± 2.8	7 ± 1.1	86 ± 4.5	10 ± 0.4	41 ± 3.4	22 ± 3.9	220 ± 6		
5	Sierra Nevada	50	8 ± 2.7	50 ± 1.8	85 ± 2.2	7 ± 0.8	39 ± 3	16 ± 6.1	204 ± 8		
6	Central California Foothills and Coastal Mountains	17	10 ± 1.4	49 ± 2.9	88 ± 2.4	6 ± 1.5	34 ± 1.7	15 ± 4	201 ± 5		
9	Eastern Cascades Slopes and Foothills	99	7 ± 1.5	51 ± 1.5	88 ± 2.6	9 ± 1.5	40 ± 2.9	8 ± 4.7	201 ± 9		
78	Klamath Mountains/California High North Coast Range	156	14 ± 1.8	45 ± 3.1	84 ± 4.3	8 ± 1	37 ± 3.3	33 ± 6.6	221 ± 9		
80	Northern Basin and Range	9	5 ± 0	50 ± 0.7	83 ± 2.5	9 ± 0.7	35 ± 1.7	4 ± 2.5	186 ± 7		
Climate Zones											
1	Coastal	65	16 ± 0.7	42 ± 2.8	78 ± 2.6	9 ± 1	33 ± 3	35 ± 6.6	210 ± 10		
2	Western Klamath	63	15 ± 1.6	44 ± 2.6	82 ± 4.2	9 ± 1	37 ± 3.3	32 ± 7.4	219 ± 10		
3	Californian	93	12 ± 2.6	48 ± 2.6	86 ± 2.6	7 ± 1.1	37 ± 2.5	25 ± 7.6	215 ± 11		
4	Eastern Klamath/Cascades	69	10 ± 2.8	49 ± 2.5	90 ± 2.1	10 ± 1.1	41 ± 3.4	19 ± 9.8	218 ± 9		
5	Great Basin	112	7 ± 2.2	50 ± 1.3	86 ± 1.9	8 ± 1.2	39 ± 2.4	10 ± 7.4	199 ± 11		