AN ABSTRACT OF THE THESIS OF

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Abstract approved: Signature redacted for privacy.

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I classified the environment of the Klamath Mountains region into physical habitat types using climate and soil variables and a geographic information system (GIS). I used principal components analysis to find four variables representing most regional climate variation: average annual precipitation, the difference between December and July precipitation, average annual temperature, and the difference between July and January average temperatures. I used soil depth and soil water-holding capacity to represent soil quality. I used the four climate variables and two soil variables for cluster analysis to classify the region into 19 physical habitat types. To test the habitat classification, I surveyed woody vegetation in 97 plots throughout the region. I recorded 29 tree species and 53 shrub species.

Mantel tests showed significant correlations between woody vegetation and the environmental variables used in the classification. Multiresponse permutation procedures (MRPP) showed woody plant assemblages differ significantly between physical habitat types. Overlaying Gap Analysis Program (GAP) vegetation types with the physical habitat types showed multiple physical habitats occurring within most vegetation types, a possible indication of the beta diversity within GAP vegetation types. Wilderness areas covered 14% of the study area, but regional physical habitat diversity was poorly represented in the wilderness reserve system. Five of the 19 physical habitat types had at least 25% of their areas in wilderness, and all 5 of those types were in the mountains. Nine physical habitat types had less than 10% of their areas in wilderness, and 3 low interior fertile types had no area in wilderness. Wilderness areas and Late Successional Reserves (LSRs) made up 40% of the study area, but three lowland physical habitat types had less than 25% of their areas in wilderness and LSRs, and three other lowland physical habitat types had less than 10%of their areas in in wilderness and LSRs.

I used conservation planning software to select two examples of more fully representative reserve networks based on existing wilderness areas. One represented at least 10% of each physical habitat type and the other at least 25%. Two-thirds of the region is in public ownership, but private lands would be needed to represent lowland warm fertile habitat types in reserves. GIS and newly available environmental data sets allowed cost-effective mapping of physical habitat diversity for conservation planning.

PHYSICAL HABITAT CLASSIFICATION FOR CONSERVATION PLANNING IN THE KLAMATH MOUNTAINS REGION

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INTRODUCTION

The current rate of species extinctions may be a thousand times greater than the rate over most of evolutionary time (Wilson 1992). Although a number of factors contribute to extinctions, habitat loss is generally considered the primary cause. Habitat protection and restoration are essential to save species from extinction, and three different, but complementary, approaches have been used in the past to identify important areas for habitat conservation (Noss 1996a). The 'special elements' approach attempts to identify known locations of rare, sensitive, threatened, and/or endangered species, communities, and/or ecosystems for protection. This approach is critical to effective protection of elements of biodiversity known to be in danger of extinction, but can be a very complex, time-consuming, and expensive process. It also may overlook species not known to be threatened but which in fact may be. The 'focal species' approach attempts to identify critical habitat for a viable population of some particular species. This approach, a special case of the special elements approach, may protect not only the focal species but all species within the area required for long-term survival of the focal species. Areas not critical to the focal species remain unprotected, however, unless they are of known importance for other special elements. The 'representation' approach supplements the special elements approach by attempting to identify all types of habitat in a region and include areas of each type in a reserve system, under the assumption that if all types of habitat are protected the likelihood of protecting all species--especially those about which little is known--is increased.

The representation approach may define habitat types based on either vegetative or physical (e.g., climate, geology, etc.) characteristics. For example, GAP Analysis projects organized by the U.S. Department of Interior identify types of vegetative habitat so land managers can know of and protect examples of habitat types and associated species within their jurisdiction (Scott et al. 1993). However, plant communities change over time in response to changes in climate, and a reserve system established at one time that represents all types of vegetative habitat may not do so at some future time (Hunter et al. 1988). Representing the full range of physical habitat types in a regional reserve system might increase the likelihood that all vegetative habitat types continue to occur in the reserve system even as climate changes, particularly if the physical habitat types are contiguous so plant communities can migrate within the reserve system in response to changing climate (Peters and Darling 1985, Hunter et al. 1988). Indeed, Hunter et al. (1988) argue that representation of physical environments should often take priority over plant community representation in reserve selection for maximum long-term protection of biodiversity.

In areas of the world where few data on plant communities have been collected but data on physical factors are readily available, identification of physical habitat types based on climate, geology, topography, or other factors may be a more pragmatic approach to habitat representation for conservation than identification of vegetative habitat types (Belbin 1993, Kirkpatrick and Brown 1994, Burnett et al. 1998, Nichols et al. 1998). Yet, even in areas where vegetative types have been identified, representing physical habitat types as well as vegetative types may help protect the plant and animal taxa that have different distributions than the species used to define vegetative habitat (Belbin 1993, Noss 1996b). Vegetation types are often delineated based on dominant species--frequently trees--that may not respond to subtle environmental variation important to other plant and animal species (Hunter et al. 1988). In a comparison of the use of physical habitat types versus vascular plants and communities for reserve planning in Tasmania, Kirkpatrick and Brown (1994) concluded that the two approaches complement one another and their combined use should more fully represent regional biodiversity. Young et al. (1998), in their study of bird species diversity in relation to Holdridge life zones in Costa Rica (Holdridge et al. 1971), concluded the life zones, which are based on annual temperature and precipitation, have value for conservation planning in regions lacking sufficient bird data.

The Klamath Mountains region of southwest Oregon and northwest California is widely recognized as a global center of biodiversity (Wallace 1992, Dellasala et al. 1997). A project to assess biodiversity in the Klamath Mountains region and propose an expanded reserve network capable of protecting that biodiversity is currently under way (Vance-Borland et al. 1995/96). This thesis examines physical habitat diversity in the Klamath Mountains region as part of that project.

OBJECTIVES

The general goal of this thesis is to identify a network of sites representing the full diversity of physical habitat types within the Klamath Mountains Province. A network has been defined as "...the constellation of patches of potentially suitable, potentially connected habitat across a large landscape..." (Noss et al. 1997). Four specific objectives of the research are:

1) classifying regional physical habitats based on climate and soils;

2) mapping the resulting physical habitat types of the region;

3) selecting one or more networks of sites that fully represent regional physical habitat diversity, using generally accepted reserve design principles; and

4) comparing the network(s) with the existing reserve system.

LITERATURE REVIEW

Plants and the Physical Environment

A number of vegetation studies in or near the Klamath Mountains Province have shed light on the relation between plants and the physical environment. One of the earliest of these was an analysis of vegetation in relation to environmental gradients in the Siskiyou Mountains (Whittaker 1960). In that study, species populations and communities were shown to respond to the east-west climatic gradient, the elevational gradient, the 'topographic moisture gradient'--from mesic north-facing valleys to xeric south-facing ridges--, and three different soil types. Waring and Major (1964) found significant relationships between vegetation and gradients of moisture, light, temperature, and soil nutrients in the California coastal redwood region. Zobel et al. (1976) found temperature and moisture stress distinguished among vegetation zones and plant communities in the central western Cascades of Oregon.

Ohmann and Spies (1998) used data from nearly 2,500 plots to examine relationships between forest woody plant variation and the environment for five subregions in Oregon, the east and west halves of the state, and all of the state. They found that in the Klamath subregion winter precipitation, elevation, and ultramafic soils--in that order--were most explanatory of vegetation variation; in western Oregon elevation, growing season moisture stress, and summer precipitation had the most explanatory power; and for the entire state elevation, annual precipitation, and summer precipitation explained most. Richerson and Lum (1980), using distribution descriptions for 5,902 plants in 94 geographic regions of California, found mean annual precipitation, mean annual temperature, and topographic heterogeneity explained most of the variance in gamma diversity (number of species) among those regions.

Genetic variation within plant species has also been correlated with variation in the physical environment. Sorensen's (1983) study of genetic variation of Douglas-fir seedlings from a coast-inland transect in the Siskiyou mountains found that patterns of variation among such factors as seed size, germination rate, growth, and phenology were apparently determined by adaptation to variation in temperature and moisture regimes along that transect. More generally, variation in phenology and growth of Douglas-fir seedlings is significantly related to physiographic measures, mainly elevation, latitude, and distance of the trees from the ocean, in southwest Oregon (Campbell 1986) and northwest California (Griffin and Ching 1977). Variation in growth and phenology of sugar pine seedlings from southwest Oregon have been found to be associated with annual precipitation, elevation, latitude, and distance to the ocean (Campbell and Sugano 1987). The geographic component of total genetic variation among white pine trees in southern Oregon mainly reflects the strong precipitation gradient there (Campbell and Sugano 1989). Variation in growth and phenology in the noble fir (*Abies procera*)-Shasta red fir (*A. magnifica* var. *shastensis*)-California red fir (*A. magnifica*) complex is most strongly related to latitude, and secondarily to elevation, distance from the Cascade crest, and other local factors (Sorensen et al. 1990).

While plant community types are often named and described for the sake of simplifying communication on a complex topic, the concepts of plant associations and climax communities as discreet units (Clements 1936) has been largely replaced by the concept that species respond individualistically to environmental gradients (Gleason 1926, Whittaker 1951). Thus, Whittaker (1960) found that beta diversity (the change in community composition along environmental gradients) increases from trees to shrubs to herbs and increases for all three life forms along the coast-inland gradient he sampled in the Siskiyous. Likewise, Zobel et al. (1976) found beta diversity to be higher for herbs than for trees and shrubs in the central western Cascades of Oregon, and Ohmann and Spies (1998) found higher beta diversity of shrubs than trees in all regions and at all levels of their study in Oregon. These findings indicate that among the life forms studied, herbs are most sensitive to environmental differences, and shrubs may be more sensitive than trees in that respect.

Animals and the Physical Environment

The physical environment can have both direct and indirect effects on animals (Andrewartha and Birch 1984). Examples of direct effects include the generally increasing maximum cruising speed of goldfish in response to increasing water temperature; the generally declining number of hours for fruit flies to pass through egg, larval, and pupal stages as a function of increasing temperature; the decline in number of days for grasshopper eggs to hatch as a function of increasing temperature if the eggs have undergone diapause (exposure to cold), in contrast to the increase in number of days to hatch with increased temperature if the eggs have not undergone diapause; and the number of days for locust nymphs to become adults and reach mating age, and the number of eggs laid by female adult locusts, as a function of both temperature and vapor pressure (Lowry 1967). Soil conditions, including texture and bulk density, affected burrowing rate and energy expenditure of pocket gophers (*Geomys bursarius*) (Anderson 1987).

In other cases it is not clear whether observed correlations between environmental variables and animals are direct or indirect effects. Kiester (1971) observed a positive correlation between amphibian species density in the U.S. and annual precipitation, with species maxima in the southeast and Pacific Northwest. Schall and Pianka (1978) found species density of frogs in the U.S. positively correlated with annual precipitation, annual temperature, and frost-free period, and negatively correlated with insolation and variation in annual precipitation. Those factors, particularly temperature and precipitation, may have had direct impacts on amphibian survival or may have had indirect impacts, such as on amount of food resources.

In a landscape-level study, Terborgh (1977) found distributional differences among trophic subdivisions of the bird fauna along an elevational gradient in the Peruvian Andes. Although total bird species diversity declined from lowlands to ridge top, insectivores decreased 5-fold, frugivores decreased 2-fold, and nectivores showed no decrease. Possible explanations for these patterns include simplified vegetation (providing less habitat diversity) and reduced food resources (especially insects and fruit) with elevation, both of which are influenced by climatic factors such as temperature, light intensity, and transpiration, as well as soil factors such as decomposition rate, water-holding capacity, and pH (Terborgh 1977).

Young et al. (1998) analyzed the diversity of understory birds in relation to five Holdridge life zones (Holdridge et al. 1971) in the Tilaran Mountains of Costa Rica. They found a concordance between the distribution and beta diversity of bird species and life zones, which are based on annual temperature, precipitation, and potential evapotranspiration. A possible ecological explanation is that diverse plant assemblages result from the diverse climates represented by the life zones, and it is the diverse vegetation that directly influences the distribution and abundance of bird species (Young et al. 1998).

On a continental scale, Pianka (1967) concluded that the correlation he observed between growing season length and lizard species diversity increasing from north to south in North American deserts is potentially causal, in that a longer growing season allows greater vegetative growth, leading to greater vegetative structural diversity, which in turn allows greater lizard diversity. Kiester (1971), having observed a strong correlation between North American reptile diversity and total annual sunfall--both increasing north to south--also discussed the possibility that vegetative structural diversity leads to increased reptile diversity. Schall and Pianka (1978) found 82% of the variance in lizard species density in the U.S. accounted for by seven environmental factors: sunfall, annual temperature, summer temperatures, topographic relief, differences between summer and winter precipitation, differences between January and July temperatures, and average annual precipitation. They also found correlations between turtle and snake species diversity in the U.S. and five climate measures: sunfall, annual precipitation, variation in annual precipitation, frost-free period, and annual temperature.

Schall and Pianka (1978) also calculated correlations between bird species diversity and five climate measures for the U.S. They found positive correlations for insectivorous birds with all five climate measures: annual sunfall, annual precipitation, variation in annual precipitation, frost-free period, and annual temperature. However, seed-eating birds and all birds combined were positively correlated only with variation in annual precipitation and annual sunfall, and were negatively correlated with annual precipitation, annual temperature, and frost-free period.

Simpson (1964) discussed a possible negative correlation between annual precipitation and species density of North American mammals from east to west at the continental scale, including the possibility that the observed increase in mammal species might actually be caused by increased topographic complexity in the west. Schall and Pianka (1978) also observed a negative correlation between mammal species diversity in the U.S. and annual precipitation, and in addition reported a negative correlation with frost-free period and annual temperature and a positive correlation with annual hours of sunshine and coefficient of variation of annual precipitation.

As with plants, the distribution and abundance of animal species in response to the physical environment varies among taxa. Terborgh's (1977) bird study described above found different responses among insectivores, frugivores, and nectivores. Patterson et al. (1998) found bird and bat species diversity to decline but mouse species diversity to remain constant with increasing elevation in the Peruvian Andes. Flather et al. (1997) combined published species density maps for birds, amphibians, reptiles, mammals, trees, and tiger beetles in the U.S. and southern Canada and found little coincidence in the locations of maximum species densities among the various taxa. These studies show that the use of indicator species or other taxonomic groups in conservation planning as surrogates for overall species diversity may be unreliable.

Habitat Representation in Conservation Planning

There is no well-established and universally-applicable figure for the amount of habitat needed for adequate representation of biotic or abiotic diversity (Noss 1996a). The Brundtland Commission of the United Nations (World Commission on Environment and Development 1987) suggested that all nations place 12% of their land area in protected status, but this figure was based on political considerations, not scientific research (Noss 1996a). Few studies of the amount of habitat needed to protect species or communities in an area have found such a low percentage to be adequate. One study found that 3.9% of the land area of Idaho was needed to represent each of the 357 vertebrate species in the state, 7.2% to represent each of the 118 vegetation classes, and 7.7% to represent each of the 61 federally listed endangered, threatened, or candidate plant and vertebrate species at least once (Kiester et al. 1996), but there was no minimum occupancy area requirement for species and communities in that study. That is, maintaining viable populations would require more area. Complete representation of floral diversity required 24% of the botanically-rich Fynbos region of South Africa (Rebelo and Siegfried 1990). In western New South Wales, Australia, 45% of the land area was required to represent each of 128 land types--defined by landform, soils, and vegetation--at least once, using ownership parcels as selection units (Pressey and Nicholls 1989). In an Australian floodplain 50% of the total wetland area was required to represent each plant species at least once, but 75% was required to represent each species and each wetland type (Margules et al. 1988). In deciduous woodlands of western Norway, 28% of the area of woodlands was needed to represent all bird species occurring in deciduous woods at least once, 71% to represent all native plant species at least once, and 75% to represent both plants and birds (Saetersdal et al. 1993). Beta diversity is high in that study area because of a steep climatic gradient from the coast to the interior. Places with lower beta diversity may require less area to represent biotic diversity (Saetersdal et al. 1993).

Studies exploring the value of physical habitat representation for conservation planning have used varying levels of habitat representation. Bedward et al. (1992) compared the results from using 1000ha plus either 5% or 20% of the remainder of each ‘environmental domain’--defined by climate, terrain, and soil attributes--for reserve network selection in New South Wales, Australia. They found that because they were adding to existing reserves and using a 1000ha minimum area for each domain, the difference between an additional 5% versus 20% amounted to only 4.4% of the study area but resulted in greater continuity of reserved lands. Kirkpatrick and Brown (1994) used 5%, 10%, 20%, and 30% targets for physical habitat types--based on geology, elevation, climate, and solar radiation--in a series of site selections that were compared to known distributions of species, communities, and taxonomic groups in Tasmania. Not surprisingly, greater biodiversity representation was achieved as the physical habitat targets increased. Many of the taxa missed by the physical habitat selections are associated with historical climate and disturbance events rather than current environmental conditions (Kirkpatrick and Brown 1994).

STUDY AREA

The study area is located in southwest Oregon and northwest California, USA (latitude 121°45' to 124°35'W; longitude 39°45' to 43°15'N) (Figure 1). It is defined by the boundary of the Klamath Mountains geological province (Diller 1902) extended outward to the nearest subwatershed boundary. The total area is approximately 4.2 million ha, one-third in Oregon and two-thirds in California. Elevation ranges from sea level to 2710 m. Steep temperature and precipitation gradients occur from the coast to the interior, and to a lesser degree from north to south. The climate near the coast is wet and mild, with annual precipitation from about 160 to 450 cm and average annual temperature of about 9 to 12°C. The interior is drier, with annual precipitation of about 40 to 230 cm, and warmer in summer but cooler in winter, with average annual temperature of about 4 to 17°C. In addition, the northern portion of the study area is generally cooler and moister than the southern portion. The 'winter boundary' (Mitchell 1976), a major climatic gradient between cold polar air and warmer sub-tropical air in the western US from November to March, occurs at about 41-42°N in the Klamath region. Pacific air masses moderate the winter boundary near the coast, especially in December and January.

The Klamath Mountains region consists of four mountain ranges: the Siskiyous, Marbles, Trinity Alps, and Yolla Bollys, from north to south. It is an area of great topographic complexity, with high peaks and ridges flanked by steeply cut valleys. The mountains, ridges, and valleys lie in all directions, and the area has been

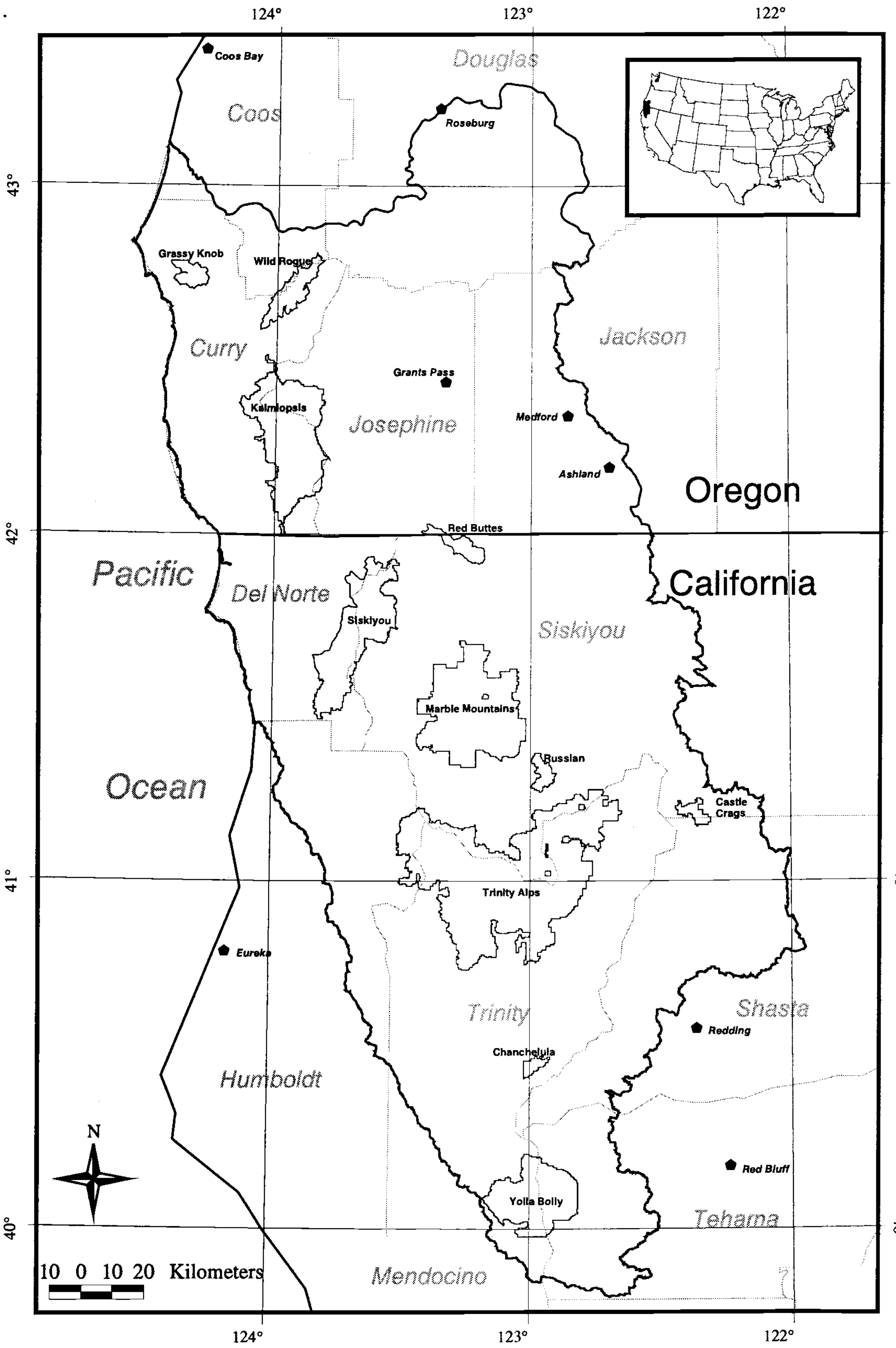


Figure 1. Klamath Mountains Region study area, with counties and wilderness areas.

called the 'Klamath Knot' because of this complexity (Wallace 1983). The topographic complexity is a consequence of the long geologic history of the region (Diller 1902). The Klamaths were first formed during the late Triassic or early Jurassic periods--about 200 million years ago (mya)--along, and in line, with the Sierra Nevada Mountains of California and the Blue Mountains complex of eastern Oregon, as the eastward moving Pacific plate sank beneath the westward moving North American plate, piling up mountain ranges on what was then the edge of the continent (Alt and Hyndman 1978). In the early to middle Cretaceous period (about 100-150 mya) the Klamath Mountains broke away from the Sierra Nevada and Blue Mountains and moved about 60 miles west, forming an offshore island separated from the mainland by a shallow seaway. By the Eocene epoch (about 50 mya) that seaway had filled in and the Klamath Mountains were again part of the mainland. The southern Oregon coast range and western Cascades also began to form at about this time (Alt and Hyndman 1978). Over this long period of time, a series of subsidences and uplifts combined with depositional and erosional episodes to increase the geological and topographic complexity of the region. In more recent geologic time, Pleistocene glaciation was limited to mountain glaciers that affected the highest parts of the Klamath Mountains, but not lower elevations (Irwin 1966). Major parent materials in the region include a jumbled mix of Triassic volcanic greenstone, Jurassic greenstone, shale, and mudstone, Cretaceous sandstone, as well as andesite, gabbro, diorite, granite, marble, and some of the largest serpentinite and peridotite formations in North America (Irwin 1966, Alt and Hyndman 1978).

The flora of the Klamath Mountains is as complex and diverse as the geology. In the warm, moist time of the late Oligocene (about 25 mya) the Klamath region was covered by the mesophytic Arcto-Tertiary geoflora, a mix of coniferous and broad-leaved trees that extended throughout much of Eurasia and North America in what is now the temperate zone (Whittaker 1961). The gradual drying trend during the Miocene (5-25 mya) allowed the xerophytic Madro-Tertiary geoflora, typified by schlerophyllous hardwoods, to migrate northward and displace the Arcto-Tertiary forests in much of the southern and eastern portions of the Klamath region by about 10 mya (Axelrod 1958). By the mid-Pliocene, about 2-5 mya, the present mix of Klamath vegetation had been largely established: mesic coastal forests, mixed evergreen forests in the cooler and drier interior, and oak woodlands and chaparral in the hot, dry eastern and southern portions of the region (Whittaker 1961). More recent climate extremes have also influenced the Klamath flora. Relicts of boreal vegetation from the Pleistocene remain in the higher mountains, while relicts of xerophytic vegetation from the Hypsithermal Interval of 4,000-8,000 years ago remain on drier slopes in the eastern Klamath region (Whittaker 1961, Detling 1961).

The defining vegetation type of the Klamath Mountains region is the mixed evergreen forest, in which conifers and sclerophyllous hardwoods mingle. Typical components of the mixed evergreen forest include Douglas-fir (*Pseudotsuga menziesii*), sugar pine (*Pinus lambertiana*), canyon live oak (*Quercus chrysolepsis*), Pacific madrone (*Arbutus menziesii*), tanoak (*Lithocarpus densiflorus*), and golden chinkapin (*Castanopsis chrysophylla*) (Sawyer et al. 1977, Franklin and Dyrness

1988). Whittaker (1961) argues that the numerous vegetation types found in the region are variations of the mixed evergreen forest: toward the coast the sclerophylls are reduced and Douglas-fir and other conifers such as western hemlock (*Tsuga heterophylla*), Sitka spruce (*Picea sitchensis*), Port-Orford-cedar (*Chamycyparis lawsoniana*), and coast redwood (*Sequoia sempervirens*) dominate; at higher elevations and toward the north the broadleaves also decline and the conifer component becomes dominated by species such as white fir (*Abies concolor*) or mountain hemlock (*Tsuga mertensiana*); in the drier interior Douglas-fir declines and the broadleaf forest becomes more open, gradating to oak woodland; in the south of the region the mixed evergreen forests change to broad-sclerophyll forests and eventually to chaparral; and on the serpentine soils common in the region mixed evergreen forest changes to plant communities, such as Jeffrey pine (*Pinus jeffreyi*) savannas, unique to such parent material.

It has been estimated that over 3500 species of vascular plants, including 281 endemics, occur in northwestern California and southwestern Oregon, an area which includes the North Coast Ranges of California in addition to my study area (Smith and Sawyer 1988). Although the California Klamath Mountains and North Coast Ranges make up only 15% of the California Floristic Province they include about 65% of the plant species found there (Smith and Sawyer 1988). The Klamath region is renowned for its high number of conifer species, 30 in all, seven of them endemics; 60 broadleaf tree species also occur there (Dellasala et al. 1997). Seventeen conifer species have been reported from a 2.6-km^2 (one-square-mile) area near Russian Peak (Cheatham et al. 1977).

The Klamath region is within the range of seven federally listed threatened or endangered species: northern spotted owl (*Strix occidentalis caurina*), marbled murrelet (*Brachyramphus marmoratus*), American peregrine falcon (*Falco peregrinus anatum*), bald eagle (*Haliaeetus leucocephalus*), Sacramento River winter chinook salmon (*Oncorhyncus tshawytscha*), coho salmon (*Oncorhyncus kisutch*), and sea-run cutthroat trout (*Oncorhyncus clarki*) (FEMAT 1993). Two other listed species, gray wolf (*Canis lupus*) and grizzly bear (*Ursus arctos horribilis*) formerly occurred there but have been extirpated from the region. Other animal species include 69 mammals, 189 breeding birds, 19 amphibians, 19 reptiles, 141 butterflies, and 58 molluscs (Dellasala et al. 1997, Trail et al. 1997, Bury 1997).

Land ownership is about one-third private and two-thirds public, the latter being mainly U.S. Forest Service and Bureau of Land Management lands, with some state lands. The 56,000-ha Hoopa Indian reservation is in the southwest of the study area. In 1993, the Forest Ecosystem Management Assessment Team (FEMAT) determined that 33% of forested public lands in the Klamath region was mature (80+ years) or old-growth conifer forests with medium to large (generally 53cm diameter at breast height or larger) trees and two or more canopy layers (FEMAT 1993). This was the highest percentage of such forests in any of the 11 bioregions considered in that study, and nearly twice the average distribution (18%) in the other bioregions. While fire has long played an important role in regional vegetation patterns (Agee 1993) and mining activities have caused severe local disturbances since gold was first discovered there in 1848 (Irwin 1966), logging, livestock grazing, and fire suppression are the major disturbances affecting the Klamath region today (McKay and Pace 1992, Franklin and Dyrness 1988, Riegel et al. 1992).

METHODS

Environmental Data

My physical habitat classification proceeded from the finding from other studies that climate is the primary factor influencing the distribution and abundance of organisms at the scale of my study, and soils are an important secondary factor (Whittaker 1960, Waring and Major 1964, Waring 1969, Ohmann and Spies 1998). Whittaker intended to collect climate data for his sample sites in the Great Smoky Mountains when he did his PhD work there in the late 1940s, but his instruments were destroyed by animals and he resorted to using a topographic moisture index instead (Westman and Peet 1982). I used GIS layers of climate data from the Precipitation-elevation Regressions on Independent Slopes Model (PRISM) (Daly et al. 1994) and soils data from the State Soils Geographic Database (STATSGO) (Soil Survey Staff 1992) for physical habitat classification.

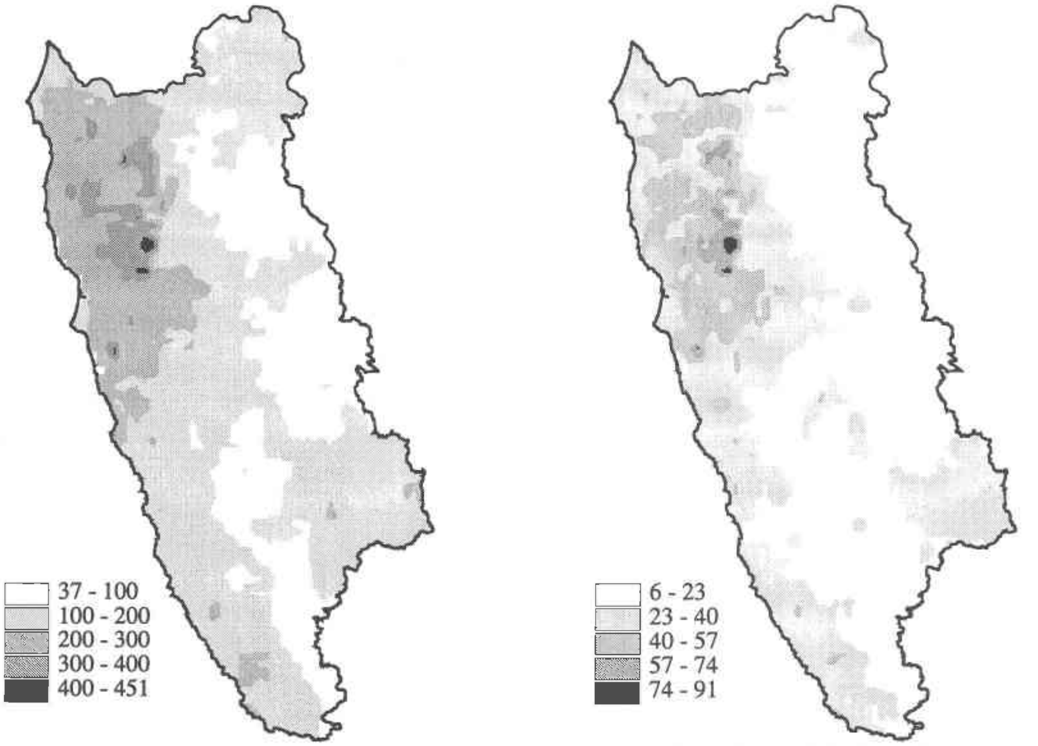
The PRISM algorithm interpolates precipitation and temperature across the landscape between weather stations with at least 30 years of records, based upon major topographic features, maritime and arctic influences, latitude, and other relevant factors. Data are available as digital raster maps having a resolution of approximately 4km. There are 36 precipitation and temperature variables available from PRISM, three for each month: mean precipitation, mean minimum temperature, and mean maximum temperature. However, the classification routines in ARCINFO GIS (Environmental Systems Research Institute, Redlands, California) will take a maximum of 20 variables. Also, using a large number of climate variables but only 2 soils variables (see below) would result in a classification that gave much more weight to climate than to soils. Therefore, I used Principal Components Analysis (PCA) to identify the main components of variation in climate across the region. The PCA on 12 months of mean precipitation showed that 2 components accounted for about 91% of regional variation in precipitation. The first component included about 80% of the variation and was basically an index of annual precipitation, because it gave about equal weight to each month. The second component represented winter/summer contrast in precipitation because December, January, and February had high negative values, June, July, and August had high positive values, and spring and fall months had values near zero. I also ran PCA on 12 mean temperature variables, calculated as the average of mean minimum and mean maximum temperatures. The results were similar to the precipitation PCA, with two principal components accounting for about 97% of regional temperature variation, the first representing mean annual temperature and the second winter/summer temperature contrast.

Principal components are not ideal for use in classification, however, because the component scores are unitless, difficult to interpret, and meaningless to the general public. I decided to use four precipitation and temperature measures corresponding to the four principal components but having recognizable units of measurement (cm and °C): mean annual precipitation is simply the total of 12 mean monthly precipitation variables; the difference between December (the wettest month) and July (the driest month) precipitation represents winter/summer precipitation contrast; mean annual temperature is the sum of 12 months of mean monthly temperatures, divided by 12; and the difference between July (the hottest month) and January (the coldest month) temperatures represents winter/summer temperature contrast. Summary statistics for the four climate variables are in Table 1, and maps of the climate variable distributions are in Figure 2. PRISM temperature data were converted from °F to °C.

Table 1. Summary statistics for precipitation, temperature, and soil variables used for physical habitat classification.

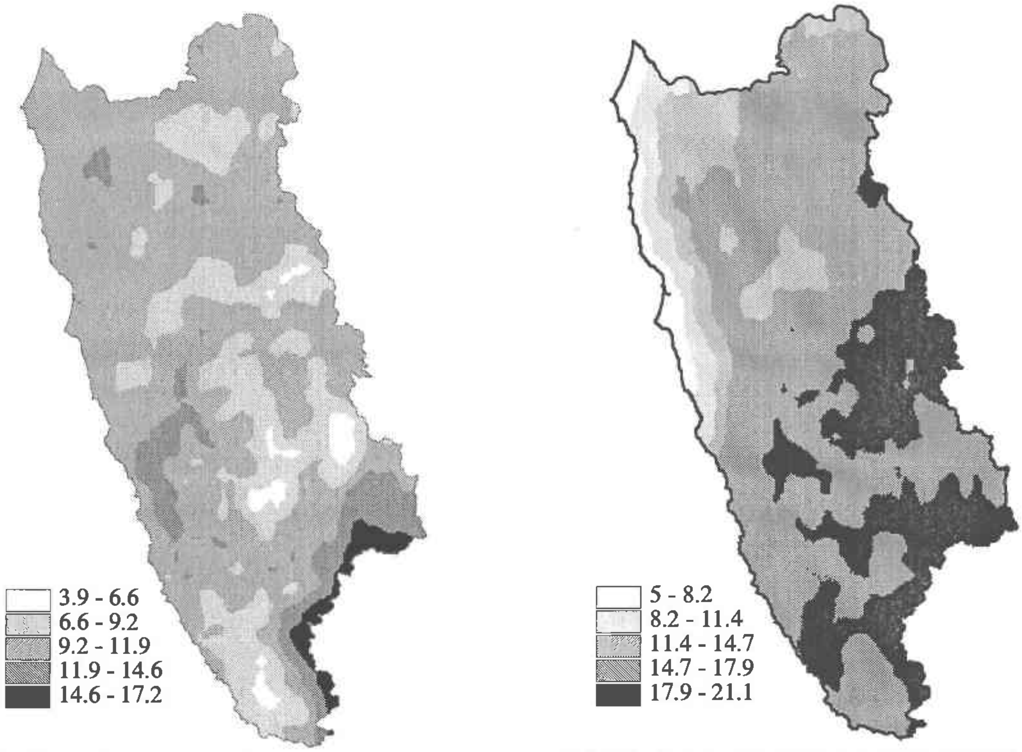
	Annual Precip. (cm)	Dec.-July Precip. Diff.(cm)	Annual Temp. (°C)	July-Jan. Temp. Diff.(°C)	Soil Depth (cm)	Soil Water Capacity (cm^3/cm^3)
Minimum	37	6	3.9	5.0	0	0.00
Maximum	451	91	17.2	21.1	152	0.30
Mean	149	25	10.1	16.2	94	0.12
Standard Deviation	70	12	1.8	2.8	26	0.03

Three sets of digital soils data were available from the Natural Resources Conservation Service (NRCS). The three data sets are hierarchical, consisting of county-, state-, and national-level maps of soil characteristics. The county-level data are appropriate for site-specific analyses and planning, state-level data for multi-county or regional analyses, and national-level data for whole- or multi-state analyses (Soil Survey Staff 1992). I used soil data from the State Soil Geographic Database (STATSGO), as it is the most appropriate of the three for a study area the size of the Klamath Mountains region. With minimum mapping units of approximately 400



2a. Annual precipitation (cm)

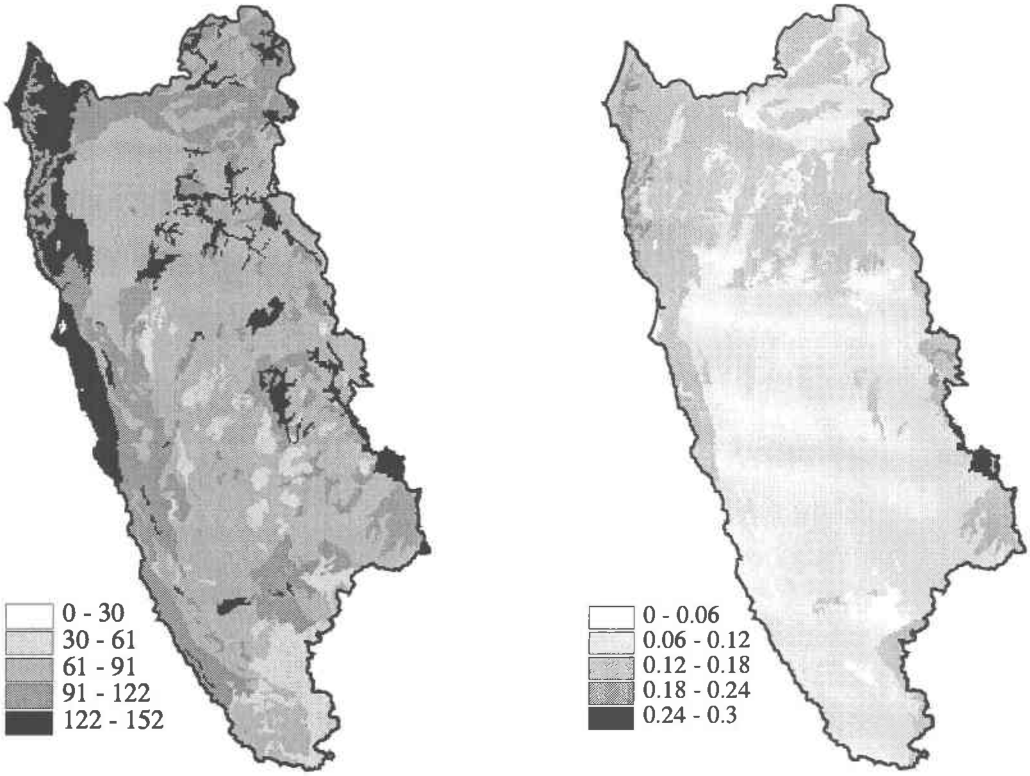
2b. December-July precipitation difference (cm)



2c. Annual temperature C)

2d. July-January temperature difference (C)

Figure 2. Precipitation, temperature, and soil variables.



2d. Soil depth (cm)

2e. Soil available water capacity (cm3/cm3)

Figure 2, continued.

hectares, it is also closest to the resolution of PRISM climate data. STATSGO maps were generalized by NRCS soil scientists from more detailed county-level soil maps that were originally drawn based upon a combination of field work (soil pits) and interpretation of various topographic and environmental features such as aspect, topographic position, elevation, parent material, and vegetation.

I used mean soil depth and available water capacity (awc: cm^3 H_2O/cm^3 soil) because the National Soil Survey Handbook (NSSH) (Soil Survey Staff 1993) used those two variables for interpreting suitability of soils to produce habitat for wildlife, specifically birds and mammals (Grant 1972). Whereas many soils characteristics used by the NSSH to determine wildlife habitat, such as texture or soil moisture regime, are categorical (e.g., “poor” to “excellent”), depth and available water capacity are quantitative and thus appropriate for quantitative classification. I computed the mean soil depth (converted from inches to cm) and available water capacity (volume water/volume soil; cm^3H_2O/cm^3 soil here) for each polygon in the study area, following the methods of Lytle et al. (1993). There are 536 polygons in the STATSGO map of the study area, ranging in size from about 250 to over 300,000 ha. Values for soil depth ranged from 0 to 152 cm (mean=94, s.d.=26), and for available water capacity from 0.0 to 0.30 cm^3H_2O/cm^3soil (mean=0.12, s.d.=0.03) (Table 1).

As this project neared completion I learned that the NSSH wildlife interpretations were made by expert opinion to satisfy an agency mandate, and the soil scientists responsible have little faith in their validity (Cathy Staley, NRCS, Corvallis, pers. com.). Although this diminishes the hoped-for relevance of the soils data to wildlife, soils are nonetheless vitally important to a great number of species, both below and above ground.

Physical Habitat Classification

All input variables must be in raster format for ARCINFO classification routines, so I converted the soil depth and AWC maps to raster maps. I used a raster size of 1 km x 1 km (100 ha) because that size would capture the small polygons in the maps but was reasonably close to the raster size of the climate data (4 km x 4 km). In order for all the variables in the classification to have the same raster size, I resampled the climate raster maps from 4 km to 1 km raster size.

I then normalized the six variables to have a mean of zero and a standard deviation of one, by subtracting the mean and dividing by the s.d., so each variable would have equal weight in the clustering. That was necessary because of the disparity in the values of the variables, with AWC ranging from 0 to about 0.3 and annual precipitation ranging from about 40 to 450. After classification, I 'back-normalized' the values by multiplying by the s.d. and adding the mean to put the values for each variable in each cluster (or class) back into recognizable units. I constructed many classifications, starting with two classes and adding one at each new classification, to determine how many physical habitat classes the data could be divided into using GIS.

Classification Testing

Murphy and Noon (1992) suggested that a map and its properties can represent a set of testable hypotheses. In the context of this project, a map of physical habitat types represents two hypotheses: 1) the environmental variables used in the physical habitat classification are related to distributions of species, and 2) different physical habitat types support different species assemblages. Once the physical habitat classification was done I was able to test these hypotheses with field data. I visited 97 sites across the region (Figure 3), the maximum number time would allow, and surveyed woody vegetation--tree and shrub species--at each site. I tried to find sites 1) at least two km from boundaries between physical types to avoid transition zones, 2) at least 100m from roads to avoid road-induced edge effects, and 3) with no evidence of prior logging activities (stumps), in an attempt to survey sites representative of natural vegetation. I included species within 1 m on each side of a 20 m transect for shrubs and 2 m on each side for trees. I recorded the abundance of each species on a scale of 1 to 4, corresponding to percentage contribution to the canopy (for trees) or understory (for shrubs).

I used two non-parametric multivariate statistical methods in the program PC-ORD (McCune and Mefford 1995) to test my hypotheses: the Mantel test (Mantel and Valand 1970, Burgman 1987, Mandrak 1995, Sokal and Rohlf 1995) assessed correlation between environmental variables and vegetation, and the multiresponse permutation procedures (MRPP) (Berry et al. 1983, Reich et al. 1991, Hix and Pearcy 1997) tested for differences between physical habitat types based on woody vegetation.

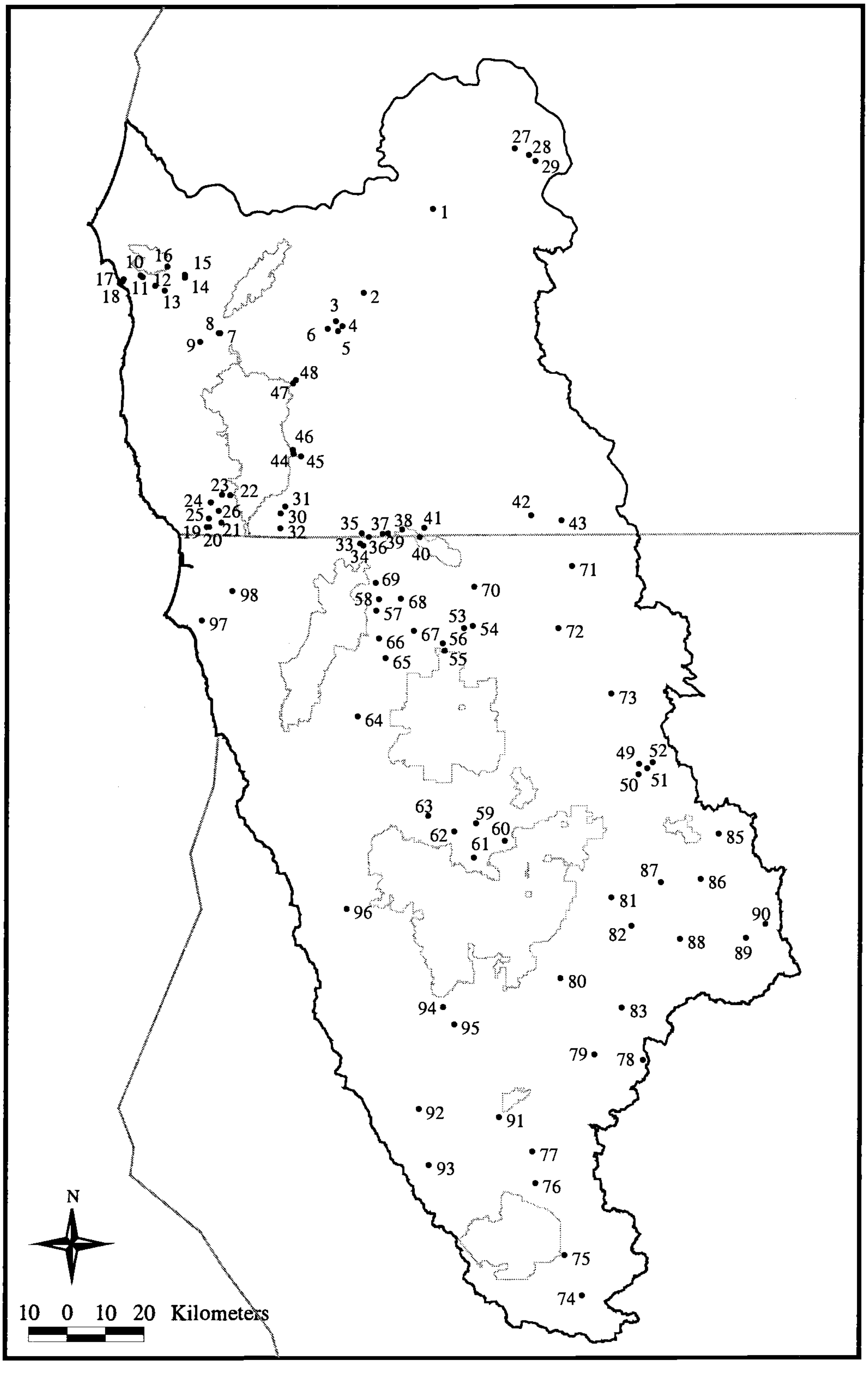


Figure 3. Locations of vegetation survey plots.

I used both methods on the set of 97 sites with abundance data for all species, for trees only, and for shrubs only.

Physical and Vegetative Habitats Combined

To explore possible interactions between physical habitat types and vegetative habitat types, I did a map overlay of the physical habitat types and the 29 vegetative habitat types that occur in the region, using data from the Oregon and California Gap Analysis Programs (Figure 4). The GAP maps represent alliance-level plant communities recognized by overstory vegetation using LANDSAT TM imagery. Although the two state programs used different minimum mapping units and did not match their vegetation types at the state border, as can be seen in Figure 4, the data are adequate for my purpose.

Physical Habitat Gap Analysis

I conducted three analyses to see how well physical habitat types are represented in different management units in the region. Wilderness areas comprise the majority of public land units that are required by law to be maintained in their 'natural' condition. To determine the extent to which physical habitat types are permanently protected by law, I calculated the total area of each physical habitat type in the region, then the area of each physical habitat type in wilderness. Late-successional reserves (LSRs) in option 9 of the Northwest Forest Plan (Tuchmann et al. 1996) cover substantial areas of the Klamath region outside of wilderness areas. They are not

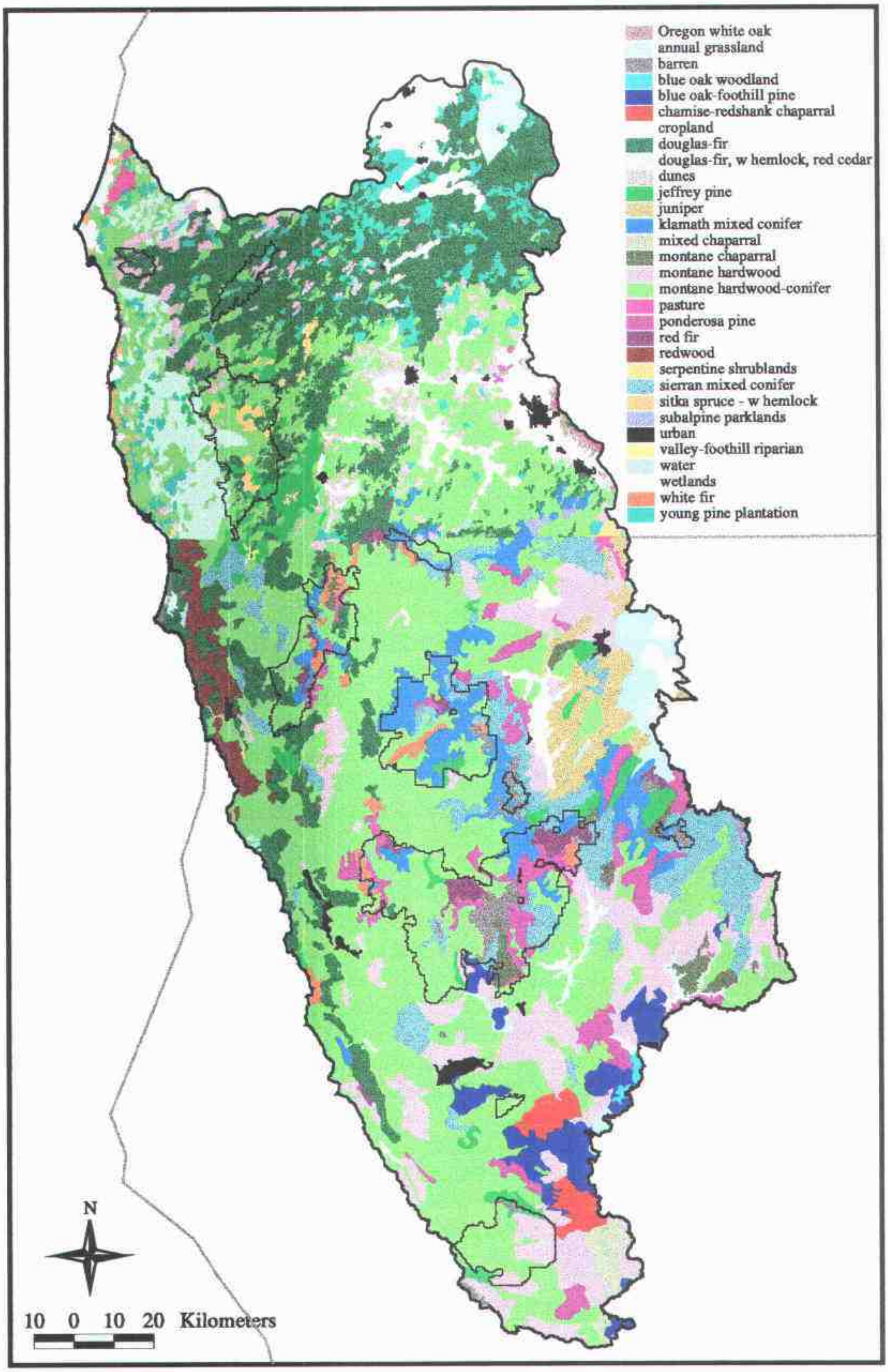


Figure 4. Map of GAP vegetation types in the study area.

required by law to be managed for natural conditions, but the present policy (with some important exceptions) is to manage them thus, and it could be argued that LSRs supplement wilderness areas to form an extensive conservation network. To see how well such a network represents physical habitat types, I calculated the area of each physical habitat in wilderness areas and LSRs combined. Private lands comprise about one-third of the Klamath region and pose a very different problem for conservation planning than public lands. I conducted an analysis to determine how well physical habitat types are represented by ownership, broken down into public and private lands, in the region.

Site Selection for Representative Reserve Networks

I made a digital map of land units by overlaying maps of physical habitat types, watersheds, ownership--public, private, and tribal--and wilderness areas. The resulting map had 4883 land units. I used the C-PLAN conservation planning software being developed by the New South Wales National Parks and Wildlife Service (http:// www.ozemail.com.au/~cplan/) for site selection and reserve design. Using existing wilderness areas as a starting point, I selected sites from public lands wherever possible, and from private lands where necessary to capture habitat types not on public lands. I delineated networks of sites using the following generally accepted reserve design principles (Thomas et al. 1990, Murphy and Noon 1992, Noss et al. 1997) as guidelines:

1) make networks continuous, without isolated habitat patches, in keeping with

the goal of providing for biotic migration in the event of climate change and short-term disturbances;

2) make linkages between larger patches wide enough to provide interior habitat within the linkages;

3) make reserve patches as large as possible given the limited number of cells available, in keeping with the principle that larger patches are better than smaller ones;

4) include more than one patch of each habitat type, in keeping with the principle that redundancy in habitat representation improves reserve effectiveness; and

5) include linkages to adjacent biogeographical regions to provide migration routes to/from those areas.

I selected sites for one reserve network representing 10% of each physical habitat type, and a second reserve network representing 25% of each type, to compare the conservation potential of those two levels of representation.

RESULTS

Physical Habitat Classification

The physical habitat classification resulted in 19 physical habitat types in the region, the maximum number of types the software could distinguish in the data. Although the full spectrum of environmental gradients cannot be adequately represented in a model of discrete habitat types, environmental diversity is more fully represented as the number of types increases (Belbin 1993). Raster map output (Figure 5) shows patches of types across the landscape. In addition to patches with areas of tens to hundreds of km^2, there were many patches of only one or a few km^2, usually embedded in a larger patch. These small patches seemed to be 'noise' rather than having ecological meaning at the scale of my study. They were also smaller than the original minimum mapping units of the data used for the classification. Therefore, I eliminated all patches smaller than 10 km^2 by merging them with the patch in which they were embedded.

The 19 types fall into three sub-regions: coastal, low interior (hereafter Low), and high interior (hereafter High) (Table 2). The six types in the coastal sub-region generally have highest mean annual precipitation (201-352 cm) and December/July precipitation difference (33-59 cm), moderate mean annual temperatures (9.6-11.1°C) with lowest July/January temperature difference (9.3-14.8°C), and good soils (mean depth:85-138 cm; mean awc:0.11-0.26 cm^3/cm^3). The eight types in the Low sub-region generally have lowest mean annual precipitation (64-159 cm) and

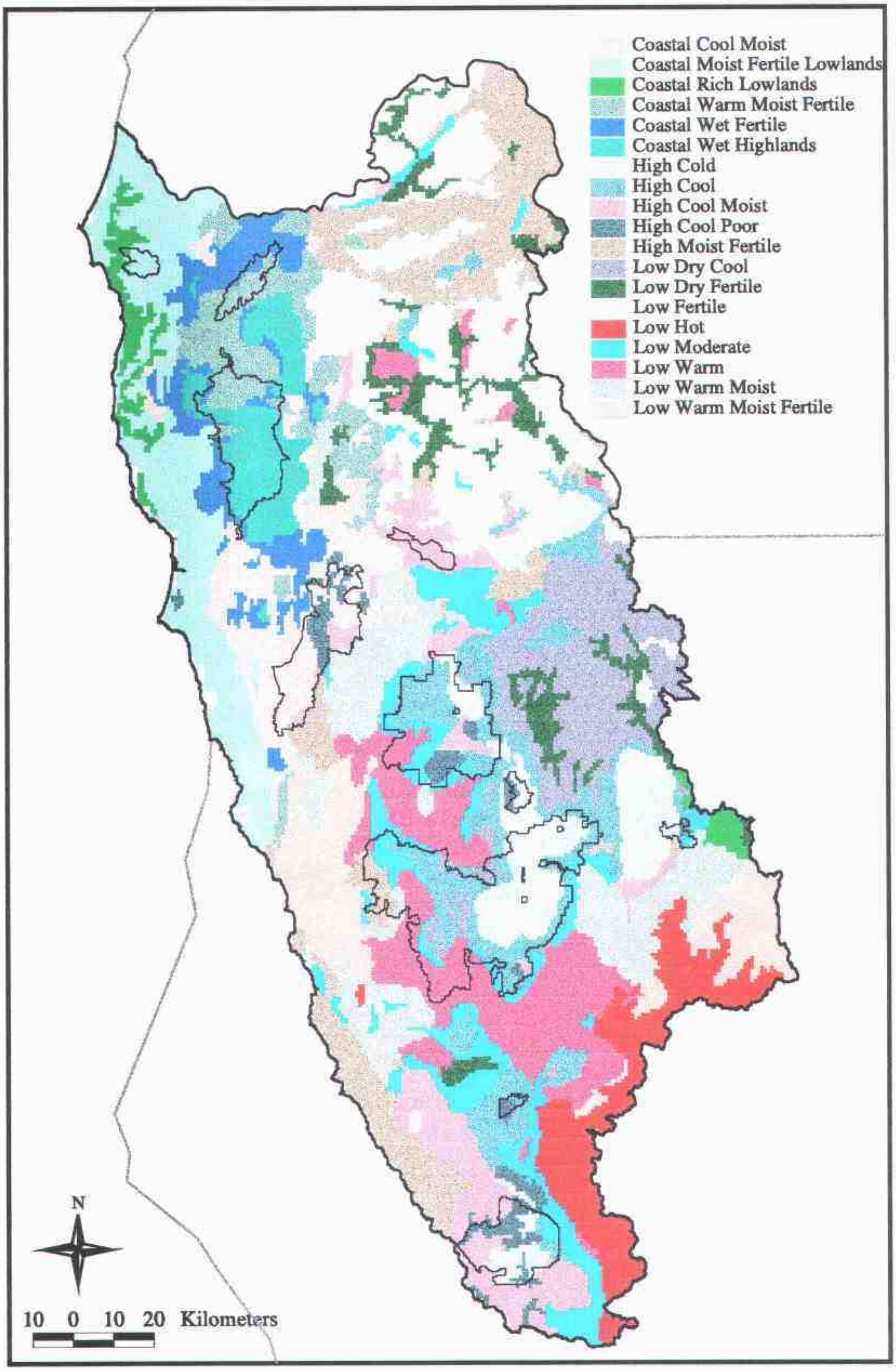


Figure 5. Map of 19 physical habitat types in the study area.

Table 2. Nineteen physical habitat types, named by sub-region and distinguishing characteristics, with alpha codes and mean values of the six environmental variables used in the classification.

Habitat Type	Alpha Code	Annual Precip. (cm)	Dec.-July Precip. Diff.(cm)	Annual Temp (°C)	July-Jan. Temp. Diff.(°C)	Soil Depth (cm)	Soil Water Capacity (cm^3/cm^3)
High Cold	hi_cold	120	19	6.6	17.2	78	0.08
High Cool Poor	hi_cool_po	191	34	7.8	16.2	47	0.07
High Cool	hi_cool	100	16	8.6	17.6	83	0.09
High Cool Moist	hi_cool_mo	168	29	8.4	16.6	84	0.10
High Moist Fertile	hi_mo_fer	134	22	9.6	16.5	117	0.12
Low Dry Cool	lo_dry_cool	64	11	9.7	19.0	82	0.11
Low Dry Fertile	lo_dry_fer	79	14	10.7	17.5	149	0.13
Low Moderate	lo_mod	114	20	10.1	17.4	72	0.09
Low Fertile	lo_fertile	97	15	10.3	16.1	83	0.14
Low Warm	lo_warm	103	17	12.3	17.9	90	0.09
Low Warm Moist	lo_warm_mo	159	28	11.5	17.6	83	0.09
Low Warm Moist Fertile	lo_wa_mo_f	159	29	12.6	17.4	116	0.13
Low Hot	lo_hot	112	19	14.6	19.0	58	0.12
Coastal Cool Moist	co_cool_mo	240	41	9.6	14.0	92	0.11
Coastal Moist Fertile Lowlands	co_mo_f_lo	229	38	11.0	9.3	138	0.15
Coastal Rich Lowlands	co_rich_lo	201	33	10.9	10.8	118	0.26
Coastal Warm Moist Fertile	co_wa_mo_f	213	36	11.1	14.6	89	0.14
Coastal Wet Fertile	co_wet_fer	282	47	10.6	13.9	106	0.14
Coastal Wet Highlands	co_wet_hi	352	59	9.9	14.8	85	0.12

December/July precipitation difference (11-29 cm), highest mean annual temperatures (9.6-14.6°C) and July/January temperature difference (16.1-19.0°C), and good soils (mean depth:58-149 cm; mean awc:0.09-0.14 cm^3/cm^3). The five types in the High sub-region generally have moderate mean annual precipitation (100-191 cm, but more as snowfall than the other sub-regions) and December/July precipitation difference (16-34 cm), lowest mean annual temperatures (6.6-9.6°C) and high July/January temperature difference (16.2-17.6°C), and poor soils (mean depth:47-117 cm; mean awc:0.07-0.12 cm^3/cm^3).

Classification Testing

I found 29 tree species and 53 shrub species at the 97 sites (see Appendix 1). Eight plots in stands with complete canopy closure had no shrub species and two plots in chaparral had no trees. An average of 5.1 survey plots occurred in each physical habitat type (range: 0-12). Some types were not adequately sampled because sites were selected and surveyed before the 19-type classification was done, using an early classification having only nine physical habitat types.

The null hypothesis of no correlation between the distribution of woody vegetation and the distribution of the environmental variables used in the physical habitat classification was tested with the Mantel test. Results of the Mantel test of correlation between two data matrices include the standardized Mantel statistic, r, which ranges from 0 to 1. A value of 0 indicates no association between the two matrices (the null hypothesis), and a value of 1 means the two matrices are identical. A p-value--the proportion of 1000 randomized (Monte Carlo) runs with more positive association between matrices than observed--is given for each r, indicating the probability of a type I error in rejecting the null hypothesis. The Sorensen distance measure was used for each test. Results of Mantel tests are: for all 82 woody species in all 97 plots (n=97), r=0.146 (p<0.001); for 29 tree species in 95 plots (n=95), r=0.086 (p=0.01); and for 53 shrub species in 89 plots (n=89), r=0.173 (p<0.001). Correlations between all woody species and the environmental variables and between shrubs and the environmental variables are significant at the 0.1% level: none of the 1000 randomizations had higher r-values than observed. The correlation between trees and the environmental variables is significant at the 1% level: nine of the 1000 randomizations had higher r-values than observed. Therefore, I rejected the null hypothesis that r=0.

The null hypothesis of no difference between groups of vegetation plots--grouped by the physical habitat type they occur in--was tested with MRPP, using species abundances in plots (see Appendix 2). Results of the MRPP test include the test statistic, T, which is the observed weighted average of differences among grouped plots minus expected differences, divided by the standard deviation of expected differences. If observed differences among grouped plots are less than expected, the T-statistic is negative. Expected differences are determined from the Pearson type III distribution, which approximates the distribution of differences among randomly grouped plots. The squared Euclidian distance measure was used. Fewer than 19 physical habitat types were included in the tests because of inadequate sampling.

Results of MRPP tests of grouping vegetation survey plots by the physical habitat type in which they occur are: for all 82 woody species in 96 plots and 17 habitat types, T=-9.495 (p<0.001); for 29 tree species in 94 plots and 17 habitat types, T=-7.008 (p<0.001); and for 53 shrub species in 88 plots and 16 habitat types, T=-7.591 (p<0.001). The average of differences between woody species assemblages in physical habitat types is significant at the 0.1% level. I therefore rejected the null hypothesis.

Physical and Vegetative Habitats Combined

The number of physical habitat types in which a GAP vegetative type occurs varies considerably (Table 3). Two vegetative types (Montane Hardwood and Montane Hardwood-Conifer) occur in all 19 physical types, although they are each more common in some physical types than in others. Two of the vegetative types (Blue Oak Woodlands and Subalpine Parklands) occur in only one physical type (Low Hot and High Cold, respectively). The other 24 vegetative types range between those two extremes. For example, the Oregon White Oak vegetative type occurs on almost 5,100 ha in the Low Fertile physical habitat type, 200 ha in the Low Dry Fertile physical type, and over 400 ha in the High Moist Fertile type. The Redwood vegetative type occurs on 42,100 ha in the Coastal Moist Fertile Lowlands physical type, 3,400 ha in the Coastal Cool Moist type, 200 ha in the Coastal Warm Moist Fertile type, and 100 ha in the Coastal Wet Fertile type. The Juniper vegetative type occurs on 74,700 ha in the Low Dry, Low Dry Fertile, and Low Fertile physical types, but also on 3,300 ha in the High Cool and High Cold types.

Table 3. Area (ha) of physical habitat types within GAP vegetation types*, for the entire study area. Bold figures = no representation in the current reserve system (wilderness areas), italics = <10%, underlined = 10-25%, and plain = >25%. Physical habitat codes are as in Table 2.

GAP type	hi_cold	hi_cool_po	hi_cool	hi_cool_mo	hi_mo_fer	lo_dry_cool	lo_dry_fer	lo_mod	lo_fertile	lo_warm	lo_warm_mo	lo_wa_mo_f	lo_hot	co_cool_mo	co_mo_f_lo	co_rich_lo	co_wa_mo_f	co_wet_fer	co_wet_hi
ag	**3622**		**722**		**16**	**21577**	**12442**	**38**	**6959**	**3029**			**3354**		**1472**	**255**			
b	20159	4105	3492	1151	4	170		1191		21	141				**1078**	**426**			
bf		**111**	*4465*	**62**			**285**	*14393*		*13317*	**57**	**6323**	**44362**						
bow													**4237**						
c			**279**	**523**	**3877**	**22289**	**64424**	**3400**	**80179**	**2456**	**1246**	**2817**		**3**	**10636**	**1052**	**2262**		
crc			**924**					*5174*		**3127**		**667**	**23532**						
d															**552**	**76**			
df	*2164*	*1050*	*6741*	10833	*164574*	**177**	**8673**	**6909**	*116046*	*4372*	*16726*	**21661**		*43086*	*47845*	1073	76718	56621	53623
dhc				**795**	**22934**		**18**		**3334**					**3541**	*59705*	**7419**	1071	*26625*	8303
j	**211**		**3111**			**63654**	**10179**		**1033**										
jp	*13228*	5252	6413	*6323*	**693**	*5702*	**726**	2950		1230	**7322**	**1281**		*15028*	**268**	**7**	3745	*5290*	22389
kmc	57384	10715	34560	19176	3355	**3764**	**366**	11753	**326**	224	1895			6016				**149**	
mc	5024	2541	7070	*734*		**3043**	**80**	*2322*			**461**	**4233**	**9682**	2003					
mh	7853	3734	15584	*29810*	**16997**	**44759**	**9206**	*38146*	**17605**	*60345*	*43051*	**34103**	**42113**	**3712**	12650	*2206*	9315	*6033*	231
mhc	43798	31833	104980	123048	*98573*	*50919*	**24904**	124140	*172827*	202679	*160392*	**109873**	**24473**	91222	*88166*	*29839*	67832	38306	35456
mxc								**541**		**118**			**19203**		**774**				
owo					**437**		**205**		**5094**										
p			**12**			**1805**	**1378**		**448**						**3896**	**2158**			
pp	25022	2851	22990	9870	11428	10698	**3178**	12161	**2201**	**8518**	*4310*	**1238**	**11563**	1929		**2394**			
r														**3435**	**42142**		**203**	**110**	

Table 3 continued

GAP type	hi_ cold	hi_ cool_ po	hi_ cool	hi_ cool_ mo	hi_ mo_ fer	lo_ dry_ cool	lo_ dry_ fer	lo_ mod	lo_ fertile	lo_ warm	lo_ warm _mo	lo_ wa_ mo_f	lo_ hot	co_ cool_ mo	co_ mo_f _lo	co_ rich_ lo	co_ wa_ mo_f	co_ wet_ fer	co_ wet_ hi
rf	10819	2009	9179	2041	**905**	913		910	*152*					3259			**95**		
sh															**2674**	**1443**			
smc	24310	1420	45342	9567	*5547*	*22277*	**2223**	*15839*	**1920**	*6507*	*35493*	**21141**	**922**	*17525*	**1906**	**11173**		**2014**	**934**
sp	**3295**																		
ss			**40**		**387**	**225**			**2354**					**857**			2769	121	8541
vfr							**55**							**447**	**1255**	**322**		**382**	**22**
w		901			**952**		**1008**	**20**	**42**	**5552**	**3296**	**716**	**8806**	**70**	**3404**	**4**			
wf	573	4178	2414	1038	5120			5758		3058	**857**			2796					
ypp	**336**		**4076**	**2054**	**25993**	**157**	**2602**	**4333**	**27847**	**659**				**1870**	**15713**	**3854**	5284	1833	**1201**

*GAP type codes are: ag=annual grassland; b=barren; bf=blue oak-foothill pine; bow=blue oak woodlands; c=croplands; crc=chamise-redshank chaparral; d=dunes; df=Douglas-fir; dhc=Douglas-fir-w. hemlock-redcedar; j=juniper; jp=jeffrey pine; kmc=Klamath mixed conifer; mc=montane chaparral; mhc=montane hardwood-conifer; mxc= mixed chaparral; owo=Oregon white oak; p=pasture; pp=ponderosa pine; r=redwood; rf= red fir; sh=sitka spruce-w. hemlock; smc=sierran mixed conifer; sp=subalpine parklands; ss=serpentine shrublands; u=urban; vfr=valley-foothill riparian; w=wetlands; wf=white fir; ypp=young pine plantation.

Physical Habitat Gap Analysis

Ten of the 19 physical habitat types have at least 10% of their area in the 11 wilderness areas that make up 14% of the Klamath Mountains region, but 9 of the types have less than 10% in wilderness, and 3 types (Low Hot, Low Dry Fertile, and Low Warm Moist Fertile) have no area at all in wilderness status (Table 4). It would require an additional 186,800 ha to represent 10% of every physical type in a reserve network based on current wilderness areas. Only 5 of the 19 types have at least 25% of their area in wilderness areas, and those 5 types are all in the mountains of the coastal and high interior sub-regions. It would require an additional 607,600 ha to represent 25% of every physical type. Wilderness and LSRs together make up about 40% of the region. Three physical habitat types have less than 10% of their area represented in those two land-management types and an additional three types have less than 25%. The six under-represented types (with percent representation) are all lowlands: Low Warm Moist Fertile (24%), Low Hot (23%), Low Dry (9%), Low Dry Fertile (3%), Coastal Moist Fertile Lowlands (17%), and Coastal Rich Lowlands (7%). Full 10% representation would require 15,700 ha more than all wilderness and LSRs combined, and full 25% representation would require 114,700 ha. All public lands together make up approximately 64% of the region, and two physical habitat types have less than 25% of their areas in public ownership: Low Dry Fertile (8%) and Coastal Rich Lowlands (10%). Full 10% representation would require 2,800 ha of private lands, and full 25% representation would require 36,600 ha.

Table 4. Physical habitat representation. Physical habitat codes are as in Table 2. For each habitat type, 'Area' is the total area (ha) in the study area; 'Tribal Area' and 'Private Area' are the ha. on tribal or private lands; 'Public Area' is the ha. on public lands, excluding wilderness areas; 'Wild. Area' is the ha. in wilderness areas; 'Wild. + LSR Area' is ha. in wilderness and LSRs; percents ('%') are the percentage of (total) 'Area' in the ownership or management classes.

Physical Habitat Code	Area	Tribal Area	Triba l %	Private Area	Private %	Public Area	Public %	Wild. Area	Wild. %	Wild.+ LSR Area	Wild. + LSR %
hi_cold	217668			27387	12.6	87815	40.3	102466	47.1	131520	60.4
hi_cool_po	70448			3423	4.9	22450	31.9	44575	63.3	55800	79.2
hi_cool	272504			59884	22.0	112211	41.2	100409	36.9	135620	49.8
hi_cool_mo	219665			28273	12.9	155078	70.6	36314	16.5	56310	25.6
hi_mo_fer	370451	737	0.2	130944	35.4	228052	61.6	10718	2.9	32280	8.7
lo_dry_cool	255833	107	<0.1	183857	71.9	59576	23.3	12293	4.8	174500	68.2
lo_dry_fer	156873			144343	92.0	12530	8.0			4400	2.8
lo_mod	251130			52072	20.7	157416	62.7	41642	16.6	70740	28.2
lo_fertile	453231			253293	55.9	199938	44.1			34930	7.7
lo_warm	317105	330	0.1	95302	30.1	179816	56.7	41657	13.1	63810	20.1
lo_warm_mo	275937			57467	20.8	214229	77.6	4241	1.5	128350	46.5
lo_wa_mo_f	211385	39937	18.9	66942	31.7	104506	49.4			21270	10.1
lo_hot	195990			113022	57.7	82968	42.3			4260	2.2
co_cool_mo	197491	789	0.4	17143	8.7	142038	71.9	37521	19.0	90820	46.0
co_mo_f_lo	318355	12937	4.1	210313	66.1	88382	27.8	6723	2.1	80840	25.4
co_rich_lo	68354			60846	89.0	6224	9.1	1284	1.9	14000	20.5
co_wa_mo_f	170621	1463	0.9	34644	20.3	105309	61.7	29205	17.1	45200	26.5
co_wet_fer	137394			15819	11.5	110788	80.6	10787	7.9	101660	74.0
co_wet_hi	130716			869	0.7	80173	61.3	49674	38.0	69820	53.4

Site Selection for Representative Reserve Networks

As expected intuitively, reserve design guidelines are not met as well with 10% representation as with 25% (Figures 6 and 7). The 10% representation network (Figure 6) has numerous isolated patches; linkages between the few connected patches are relatively narrow and nowhere greater than 8 km wide. Six habitat types (Low Dry Cool, Low Fertile, Low Hot, Low Warm Moist Fertile, Coast Moist Fertile Lowlands, and Coast Rich Lowlands) are represented in only one patch, although some of those patches are extensive. Only one linkage to a bordering ecoregion (California North Coast) is made, although isolated patches are adjacent to the Pacific Ocean, Sierra Nevada, and California Central Valley ecoregions. In contrast, the 25% representation network (Figure 7) is nearly continuous, exceptions being Castle Crags and Chanchellula wilderness areas in the southeast and south, which remain isolated; linkages between larger patches are at least 3 km wide at almost all locations and are greater than 15 km wide in some places. Each physical habitat type is represented in more than one patch, with the exception of Coast Rich Lowlands, which is represented once near Grassy Knob wilderness. At least one, and as many as three, linkages are made to each of the bordering ecoregions: Oregon Coast, Pacific Ocean, California North Coast, Southern Cascades, Sierra Nevada, and California Central Valley.

As expected, private lands had to be included for both the 10% and 25% representation networks. Of the 219,600 ha selected in addition to wilderness areas for the 10% network, 29,600 ha were from private lands (Table 5). Of the 729,000 ha selected for the 25% network, 156,500 ha were from private lands. Sites on private

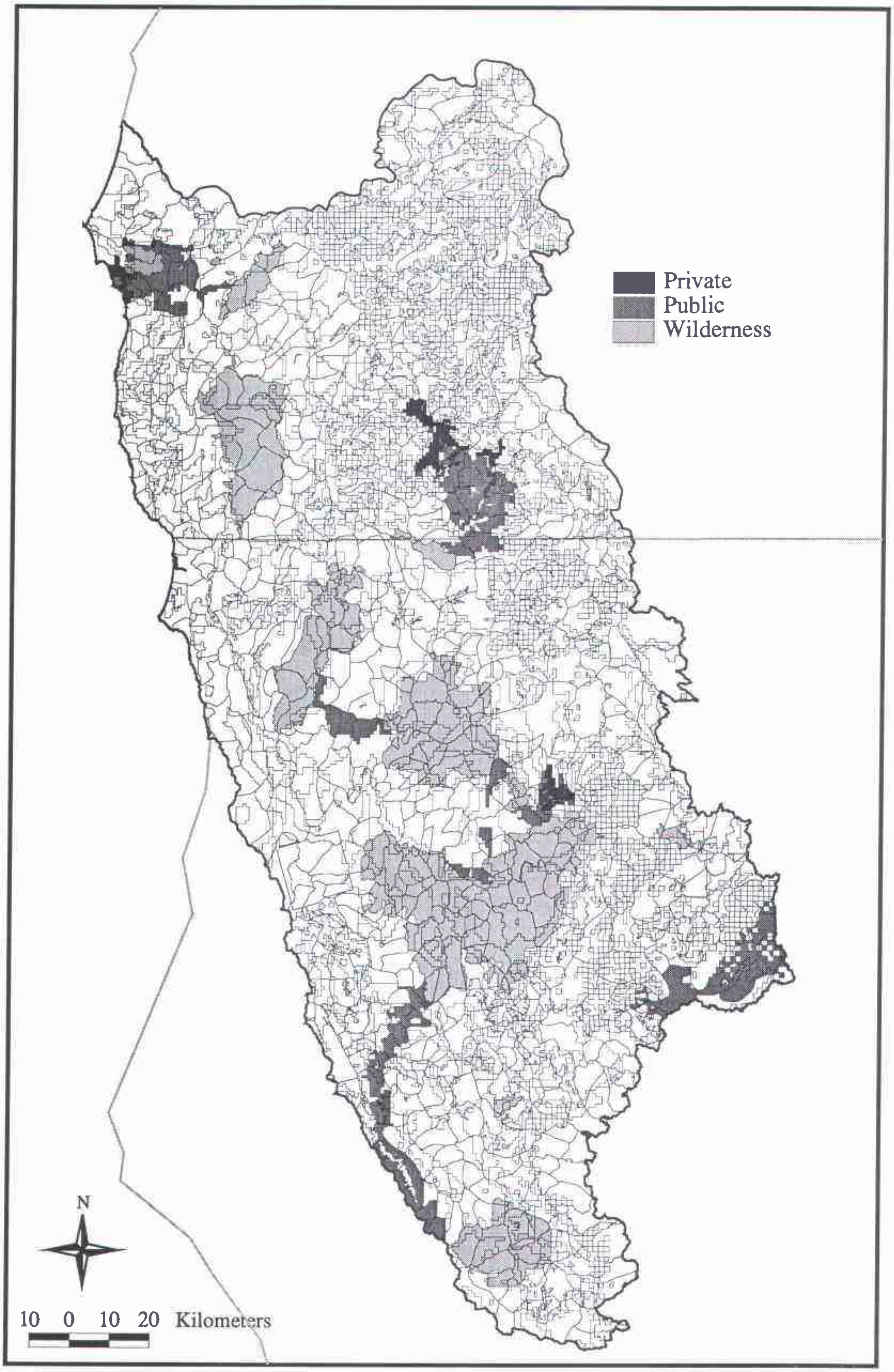


Figure 6. Land units and 10% representation network.

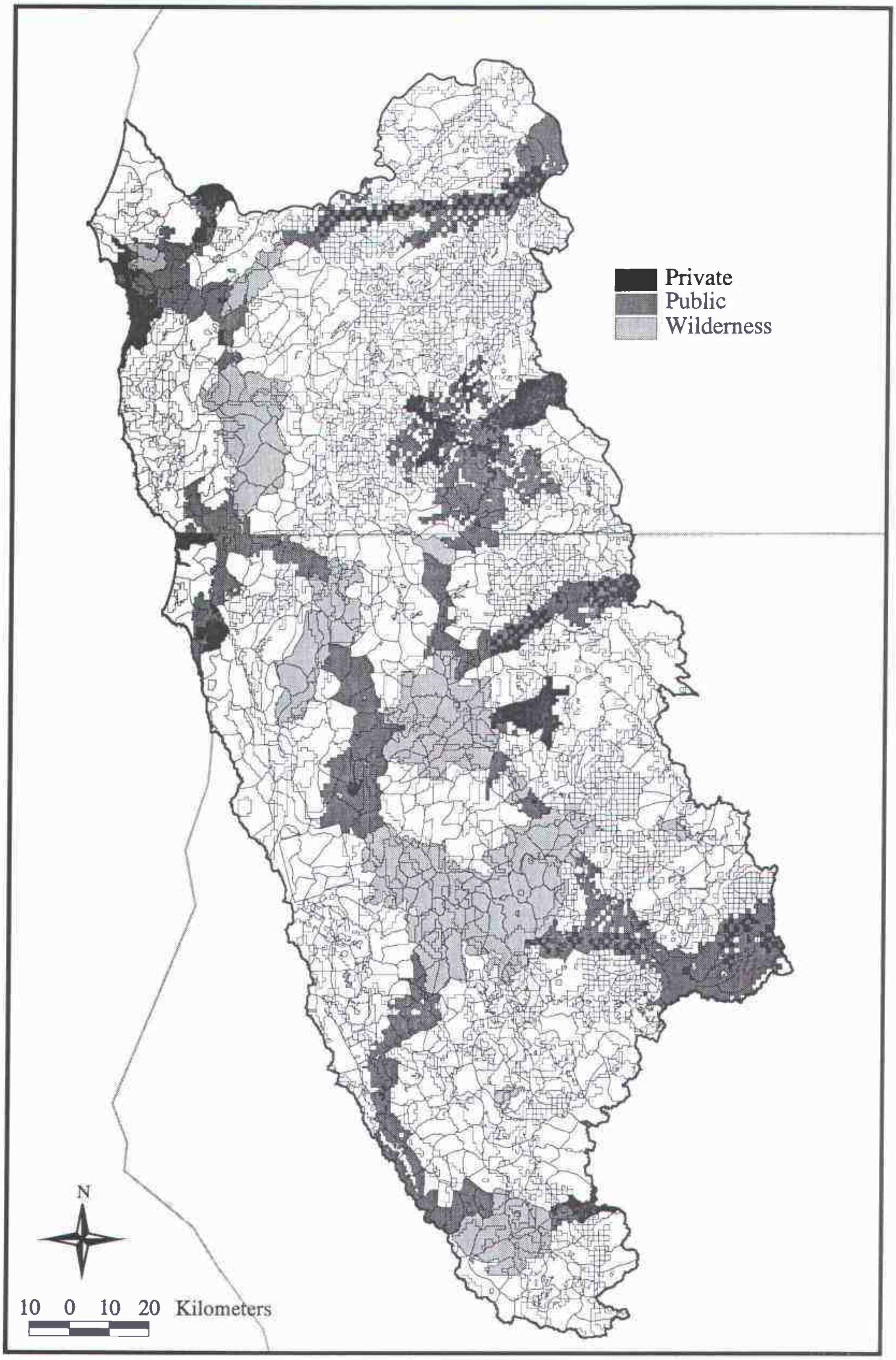


Figure 7. Land units and 25% representation network.

Table 5. Physical habitat representation in wilderness, 10%, and 25% reserve networks, with areas (ha) of public and private land. Habitat codes are as in Table 2. Percents ('%') are percentages of the total area of each habitat type represented in each network.

Physical Habitat Code	Wild. Area	Wild. %	10% Network Private Area	10% Network Public Area	10% Network Total Area	10% Network %	25% Network Private Area	25% Network Public Area	25% Network Total Area	25% Network %
hi_cold	102466	47.1		3377	105843	48.6		4845	107311	49.3
hi_cool_po	44575	63.3			44575	63.3		2603	47178	67.0
hi_cool	100409	36.9		4966	105375	38.7	1754	13022	115184	42.3
hi_cool_mo	36314	16.5			36314	16.5		18156	54470	24.8
hi_mo_fer	10718	2.9	601	28817	40136	10.8	17111	72154	99983	27.0
lo_dry_cool	12293	4.8	6660	8841	27794	10.9	19453	27748	59494	23.3
lo_dry_fer			14511	1310	15821	10.1	37749	2582	40331	25.7
lo_mod	41642	16.6		1768	43410	17.3	468	24780	66890	26.6
lo_fertile			2287	42423	44710	9.9	16675	98649	115323	25.4
lo_warm	41657	13.1		1471	43128	13.6	4989	34242	80887	25.5
lo_warm_mo	4241	1.5		25484	29725	10.8	4173	70528	78941	28.6
lo_wa_mo_f			201	21981	22183	10.5	7047	45402	52449	24.8
lo_hot				20759	20759	10.6	6854	42524	49378	25.2
co_cool_mo	37521	19.0			37521	19.0	757	20628	58906	29.8
co_mo_f_lo	6723	2.1	1209	21785	29717	9.3	23016	50001	79740	25.1
co_rich_lo	1284	1.9	4120	1507	6910	10.1	14577	1507	17368	25.4
co_wa_mo_f	29205	17.1			29205	17.1	1861	15299	46364	27.2
co_wet_fer	10787	7.9		4662	15449	11.2	105	26484	37376	27.2
co_wet_hi	49674	38.0		433	50108	38.3		867	50541	38.7

lands were selected either because they were the only place a particular habitat type--such as Low Dry Fertile or Coastal Rich Lowlands--occurred, or because they were needed to meet a reserve design goal. An example of the latter would be private lands lying along a route connecting the reserve network to a neighboring bioregion, as was the case in the far south of the study area where the Yolla Bolly wilderness was connected to the California Central Valley via a privately held patch of Low Hot habitat (Figure 7).

DISCUSSION

Physical Habitat Classification

The ARCINFO software was able to divide the climate and soils data into only 19 classes. If environmental heterogeneity is more fully represented as the number of physical habitat classes increases (Belbin 1993), this is a serious limitation. Other studies (Mackey et al. 1988, Kirkpatrick and Brown 1994) used more classes, and it would have been useful to have that option. A GIS with the capability of delineating larger numbers of physical habitat types from complex environmental data would be a valuable tool for this type of research.

Just as any designation of plant communities is an arbitrary division of continuous change in species assemblages across environmental gradients and spatial scales (Whittaker 1975), any designation of physical habitat types is an arbitrary division of continuous change in environmental gradients. Because the 19 physical habitat types of my classification (Figure 5) represent complex gradients, variation in climate and soils exists within each of them. Environments near centers of habitat patches are probably closest to the mean values (Table 2) for each type. Environments near borders with other habitat types are similar to those types, and "fuzzy" boundaries would be more realistic representations of borders than simple lines.

I used a few readily-available environmental variables--macroclimate and soils--to represent environmental heterogeneity in a physical habitat classification just as others might use a few plant species--trees and shrubs--to represent botanical heterogeneity in a plant community classification. Many other environmental factors besides the six I used influence the distribution and abundance of species, just as many species besides trees and shrubs occur in plant communities. My physical habitat classification does not attempt to represent all environmental heterogeneity in the region, just variation in four climate and two soils variables according to the PRISM and STATSGO models.

It would be useful to construct physical habitat classifications at finer and coarser scales (smaller and larger areas) than the landscape-level study I present here, in order to identify appropriate scales of habitat classification for conservation planning projects of different geographic extents. Finer scales might include the patch or ecosystem level, whereas a coarser scale would be the biome. A variety of environmental variables could be tested for association with biotic variation to find those variables most appropriate to each scale of classification, as no single set of environmental variables can represent patterns in biotic variation across all scales (Levin 1992).

Classification Testing

Belbin (1993) argues that even where no biological data are available to validate physical habitat models they should still be used in reserve planning to identify areas of environmental homogeneity. My physical habitat classification was validated by field data in two respects: the environmental variables used in the classification were found to be significantly correlated with at least one taxonomic group (woody plants), and at least one portion of the total biota (woody species assemblages) were found to differ significantly between physical habitat types. These results should increase the confidence with which this physical habitat classification is used in conservation planning in the Klamath Mountains region, as well as the confidence with which these methods--including GIS, newly available environmental data, multivariate statistical techniques, and validation with field data--could be applied to conservation planning in other regions.

The environmental variables used in this study were chosen not for their importance to woody plants but because they were readily available and seemed broadly applicable to a variety of taxa. Because of the individualistic response of species and other taxonomic groups to environmental gradients, devising a single physical habitat classification that reflects the major environmental determinants for multiple taxonomic groups would be difficult.

Because I tested my classification with woody plants, I cannot say whether it works for other taxa, but it is reasonable to suppose it might. It might also work better or worse for various taxa. An example is suggested by my woody vegetation data. According to the MRPP tests, shrub species assemblages differ between physical habitat types only slightly more than do tree species assemblages ($T=-7.591$ vs. $T=-7.008$, respectively), although this difference is probably not significant ($p<0.001$ in both cases). According to the Mantel tests, however, shrubs are significantly more correlated with the environmental variables ($r=0.173$, $p<0.001$) than trees ($r=0.086$, $p=0.01$). Are non-woody vascular plants more correlated with these environmental variables than trees or shrubs? Do non-woody plant assemblages differ between physical habitat types more than tree or shrub assemblages? Whittaker's (1960) work at low elevations in the Siskiyou Mountains, where he found the rate of change in species composition along the topographic moisture gradient to double from trees to shrubs to herbs, suggests the answer to both questions might be yes. A survey of non-woody vegetation would allow a test of the hypothesis that these physical habitat types differentiate non-woody vascular plant assemblages as well as, or better than, they do woody plant assemblages. More generally, any systematic survey, whether of herbs, fungi, lichens, soil macroinvertebrates, butterflies, herps, ground-dwelling small mammals, birds, or any other taxa, would allow testing of the validity of this habitat classification for those taxa. Such data would provide valuable information on the utility of this classification for conservation planning in the Klamath region and perhaps on the utility of these methods for conservation planning in general.

Physical and Vegetative Habitat Combined

GAP vegetation classes (Figure 4) are based on remote sensing, a technology well-suited to describe the broad-scale distribution of overstory plant communities (usually trees in my study area) but inadequate to describe finer-scale variation within those communities (Levin 1992), much less the variation in understory and below-ground plant and animal communities. According to my data, tree and shrub assemblages vary between physical habitat types in my classification. When I overlaid GAP vegetation types with physical habitat types, I found multiple physical habitat types within most GAP vegetation types. This suggests that combining GAP vegetation and physical habitat types may be a way to depict variation within GAP types, a refinement of the GAP process that could prove valuable for conservation planning.

Conservation of population-level genetic diversity may be essential to species conservation because of threats such as climate change and exotic pests and pathogens (Millar and Libby 1991). Genetic variation in a number of tree species in the Klamath Mountains region has been shown to be significantly correlated with temperature and precipitation gradients (Sorensen 1983, Campbell and Sugano 1987, 1989). Conserving genetic variation in the tree species that define GAP vegetation types may be furthered by protecting stands in each physical habitat type occurring within GAP types.

Whittaker (1960) defined beta diversity as the "extent of change of community composition, or degree of community differentiation, in relation to a complex-gradient of environment..." If combining GAP vegetation types and physical habitat types is a way to depict variation in GAP types, it may be an approach to depicting beta diversity within the plant communities represented by those GAP types. This hypothesis could be tested by selecting one or more GAP vegetation types, sampling abundances of tree, shrub, and herb species (and as many other taxa as resources allow) in all physical habitat types occurring in the GAP types, and calculating beta diversity among those samples. If the hypothesis was supported by data it would be strong evidence in favor of using merged GAP vegetation types and physical habitat types to select sites for representation in nature reserves in the Klamath region, and possibly in other regions.

Flather et al. (1997) advocate incorporating knowledge of ecological processes underlying biotic patterns into conservation planning efforts to improve the functional value of the product. As climatic and edaphic factors are among the major influences on vegetation and, secondarily, animal distribution patterns, combining these physical habitat types with GAP vegetation types is in accord with their recommendation and may improve the effectiveness of the Klamath-Siskiyou biodiversity conservation plan.

Physical Habitat Gap Analysis

Wilderness areas were not established with representation of physical habitat diversity (or biodiversity) as a criterion, so it is not surprising they fail to represent that diversity even at a minimum level. LSRs were not intended to represent physical habitat diversity either. That the combination of wilderness areas and LSRs does rather well at representing physical habitats may be because those two management types are broadly dispersed and comprise 40% of the study area, much more than most regions. Still, four lowland habitat types--Low Dry Fertile, Low Dry, Coastal Rich Lowlands, and Coastal Moist Fertile Lowlands--have much less than 25% of their extent in wilderness and LSR areas, and nearly 115,000 ha would be needed to represent 25% of each of those types. Whereas LSRs were selected in part to meet habitat requirements of the northern spotted owl and threatened salmonids, the configuration of sites in the wilderness/LSR system may not meet conservation goals such as connectivity between reserve areas and linkages to neighboring bioregions.

Uncertainty about both the immediate and long-term effectiveness of LSRs as protected areas means it cannot be assumed that physical habitat types with insufficient representation in wilderness areas are adequately protected simply because they are more fully represented in LSRs. There has been a considerable amount of timber harvest in LSRs, most notably under the “salvage rider” to the Recissions Bill of 1995 (H.R. 1944) that provided emergency relief to victims of the Oklahoma City bombing. LSRs were established by administrative rules and as part of Option 9 of the President’s forest plan for management of Pacific Northwest forests. Administrations and administrative rules change, and LSRs could be abolished by future administrative rulings. If LSRs were made permanent by legislation, however, it would render that argument obsolete and necessitate a thorough reevaluation of conservation needs in the Klamath region.

Public lands alone are not sufficient to represent 25% of each physical habitat type in the region because three habitat types--Low Dry Fertile, Low Dry Cool, and Coastal Rich Lowlands--have less than 25% of their areas in public ownership. At least 36,000 ha of private lowlands are needed for 25% representation of all habitat types. Hence, private lands must be a part of any conservation plan that adequately represents regional physical habitat diversity.

Site Selection for Representative Reserve Networks

My physical habitat classification represents hypotheses I was able to test with vegetation data. The reserve networks I selected also represent testable hypotheses: reserve networks designed from accepted conservation concepts to represent physical habitat diversity are more likely to protect biodiversity in the event of climate change than the present reserve system. Spatially-explicit dynamic modeling programs could be used to model future distributions of plants or animals under different climate and conservation regimes (Baker 1989, Bartlein et al. 1997), providing a means of testing those hypotheses. Dynamic modeling could also be used to compare the long-term consequences of the Klamath-Siskiyou conservation plan with and without physical habitat representation, to explore the value of physical habitat representation to the conservation network. Or dynamic modeling could be used to explore the long-term outcome of using the present management system and reserve areas rather than adopting the Klamath-Siskiyou proposal.

My example of a 25% representation network includes linkages to neighboring bioregions, a feature entirely missing from the present reserve system. In his preliminary conservation plan for the Oregon Coast Range, Noss (1993) intended that proposed network to eventually be linked to the Siskiyou Mountains to allow demographic and genetic exchange and aid recovery of carnivores, such as the fisher. Conservation plans are in various stages of development for the Central Cascades of Oregon and Washington (Platt 1998) and the Sierra Nevada and North Coast regions of California (Hunter 1998). Examples of possible linkages to each of these regions, and the California Central Valley as well, are included in my 25% representation example. If such interregional linkages were ever implemented, however, they would be selected using many criteria in addition to physical habitat considerations and would almost certainly not be located exactly as they are in my example.

The physical habitat types I have delineated will be integrated with biological data in the Klamath-Siskiyou biodiversity conservation planning project. One possible way this will happen is that the general form of the reserve network will first be determined by selecting areas for their biological value, and the amount of each physical habitat type included at that stage will be computed. Sites will then be selected for physical habitat types that remain underrepresented, probably in locations contributing to other reserve design goals such as buffering biologically sensitive areas, connecting isolated areas, or connecting to other bioregions. Another possibility is that the physical habitat types will be merged with GAP vegetation types, and sites representing each combination of physical habitat and GAP vegetation will be selected for the proposed reserve.

The 10% and 25% reserve networks I have selected are intended to be examples of possible reserve networks given area constraints and well-accepted guidelines for designing reserves rather than 'optimal' designs or as the only possible ways to lay out representative networks of habitat patches. Flexibility is an asset in reserve design and implementation (Pressey et al. 1996). If a complete reserve network were implemented at one time, it is unlikely that every site identified in the planning process would be agreeable to all parties concerned. Flexibility allows consideration of options that would accommodate such conflicts while still meeting conservation goals. If, as is more likely, a reserve network were implemented in stages over time, perhaps including sites other than those in the original plan, flexibility allows for re-evaluation of priority areas and revisions in the plan after each stage of implementation.

In the U.S., western states and Alaska have much more land in public ownership than states east of the Rocky Mountains. The majority of sites for regional conservation networks would be on private lands in most eastern states, requiring significant expenditures for land acquisition (e.g., Florida, R. Noss, pers. comm.). Two-thirds of the Klamath region is in public ownership, and I preferentially selected sites on public lands whenever possible. Nearly 90% of the 25% reserve example was accomplished on public lands. Still, over 150,000 ha of private lands are included in my example, mainly chosen to represent physical habitat types with less than 25% of their area in public ownership--Coastal Rich Lowlands, Low Dry Fertile, and Low Dry Cool--but also including sites needed for intraregional and interregional connectivity. If an expanded reserve network in the Klamath region is ever to become a reality, implementation strategies will have to be different for public and private lands. Conservation advocates will need to work with state and federal agencies, legislators, and existing or new laws to implement conservation reserves on public lands. On private lands, advocates will need to seek voluntary conservation practices by well-intentioned property owners, sales or donations of land or conservation easements by property owners, or other creative approaches to conservation implementation currently being used in eastern states (Freyfogle 1995/96, Sayen 1996, Smith 1997).

Conclusion

GIS and newly available environmental data sets allow cost-effective mapping of physical habitat diversity for conservation planning. In this study I have demonstrated the use of GIS to integrate spatial climate and soils data for physical habitat classification as part of a conservation planning effort for the Klamath Mountains Province. The physical habitat classification was tested with and supported by woody vegetation data collected in the field. Although the current system of reserves, consisting of congressionally designated wilderness areas and administratively withdrawn Late Successional Reserves, covers approximately 40% of the study area, my physical habitat gap analysis shows that the full diversity of physical habitats is not included in these reserves. I have presented examples of more fully representative reserve networks. For the Klamath Mountains Province, with its diverse physical environment, the internationally declared goal of placing 10-12% of land area in conservation status appears inadequate, and something on the order of 25% of land area may be needed to represent physical habitat diversity in a reserve network designed using accepted conservation concepts. Considerably more than 25% of the area may be needed to meet additional conservation goals, such as protecting viable populations of all species (including anadramous fish and large carnivores) and representing all plant community types across the full range of seral stages. Public lands do not include sufficient amounts of all physical habitat types, so private lands must be part of any adequate reserve network for the area.

My analysis of physical habitat types is one component of the Klamath-Siskiyou biodiversity conservation planning project. Physical habitats mapped in this study will be incorporated into a conservation proposal for the region, along with rare species and community occurances, biodiversity hot spots, carnivore habitat requirements, and GAP vegetation representation. Potential contributions of this study to biodiversity conservation in the Klamath Mountains region include representing diverse environments important for little-known or unknown species, representing heterogeneity within GAP vegetation types, and providing paths for species migrations in the event of climate change. More light could be shed on the potential contribution of physical habitats to conservation planning by additional research on three testable hypotheses suggested by this project: the physical habitat types mapped in this study are correlated with other taxonomic groups besides woody vegetation; beta diversity within GAP vegetation types can be represented in reserve networks by combining physical and vegetation habitat types for site selection; and reserve networks that represent physical habitat diversity in the Klamath Mountains region will protect biodiversity better than the present reserve system in the event of climate change.

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APPENDICES

Appendix 1. Species recorded in woody vegetation surveys.

Scientific Name	Code	Common Name
Abies concolor	ABCO	white fir
Abies grandis	ABGR	grand fir
Abies magnifica	ABMA	California red fir
Abies procera	ABPR	noble fir
Acer circinatum	ACCI	vine maple
Acer glabrum	ACGL	Rocky Mountain maple
Acer macrophyllum	ACMA	bigleaf maple
Adenostoma fasiculatum	ADFA	chamise
Alnus rubra	ALRU	red alder
Amalanchier alnifolia	AMAL	western serviceberry
Apocynum androsaemifolium	APAN	spreading dogbane
Arbutus menziesii	ARME	Pacific madrone
Arctostaphylos canescens	ARCA	Sonoma manzanita
Arctostaphylos nevadensis	ARNE	pinemat manzanita
Arctostaphylos patula	ARPA	greenleaf manzanita
Arctostaphylos viscida	ARVI	whiteleaf manzanita
Berberis aquifolium	BEAQ	tall Oregongrape
Berberis nervosa	BENE	dwarf Oregongrape
Calocedrus decurrens	CADE	incense-cedar
Castanopsis chrysophylla	CACH	golden chinquapin
Ceanothus cuneatus	CECU	wedgeleaf ceanothus
Ceanothus integerrimus	CEIN	deerbrush ceanothus
Ceanothus prostratus	CEPR	squawcarpet ceanothus
Ceanothus sanguineus	CESA	redstem ceanothus
Cercocarpus betuloides	CEBE	mountain mahogany
Chamaecyparis lawsoniana	CHLA	Port-Orford-cedar
Comandra umbellata	COUM	bastard toad-flax
Cornus nuttallii	CONU	Pacific dogwood
Corylus cornuta californica	COCO	California hazel
Disporum hookeri	DIHO	Oregon fairy-bell
Disporum smithii	DISM	Smith fairy-bell
Garrya fremontii	GAFR	Fremont silktassel
Gaultheria ovatifolia	GAOV	slender salal
Gaultheria shallon	GASH	salal
Heteromeles arbutifolia	HEAR	Christmas berry, toyon
Holodiscus discolor	HODI	creambush oceanspray
Juniperus occidentalis	JUOC	western juniper, Sierra juniper

Scientific Name	Code	Common Name
Leucothoe davisiae	LEDA	Sierra laurel
Linnaea borealis longiflora	LIBO	western twinflower
Lithocarpus densiflora	LIDE	tanoak
Lonicera ciliosa	LOCI	orange honeysuckle
Lonicera hispidula	LOHI	hairy honeysuckle
Menziesia ferruginea	MEFE	rusty menziesia
Pachistima myrsinites	PAMY	Oregon boxwood
Phlox diffusa	PHDI	spreading phlox
Picea breweriana	PIBR	Brewer spruce
Pinus jeffreyi	PIJE	Jeffrey pine
Pinus lambertiana	PILA	sugar pine
Pinus monticola	PIMO	western white pine
Pinus ponderosa	PIPO	ponderosa pine
Pinus sabiniana	PISA	gray pine
Prunus virginiana	PRVI	common chokecherry
Pseudotsuga menziesii	PSME	Douglas-fir
Quercus chrysolepis	QUCH	canyon live oak
Quercus garryana	QUGA	Oregon white oak
Quercus kelloggii	QUKE	California black oak
Quercus sadleriana	QUSA	Sadler oak
Quercus vaccinifolia	QUVA	huckleberry oak
Rhamnus californica	RHCA	California coffeeberry
Rhamnus purshiana	RHPU	cascara
Rhododendron macrophyllum	RHMA	Pacific rhododendron
Rhododendron occidentale	RHOC	western azalea
Ribes roezlii	RIRO	Sierra gooseberry
Rosa eglanteria	ROEG	sweet-brier
Rosa gymnocarpa	ROGY	baldhip rose
Rubus ursinus	RUUR	trailing blackberry
Rubus vitifolius	RUVI	wild blackberry
Salix scouleriana	SASC	Scouler's willow
Sequoia sempervirens	SESE	coast redwood
Styrax officinalis	STOF	snowdrop bush
Symphoricarpos albus	SYAL	common snowberry
Symphoricarpos mollis	SYMO	creeping snowberry
Taxus brevifolia	TABR	Pacific yew
Tsuga heterophylla	TSHE	western hemlock
Umbellularia californica	UMCA	California laurel
Vaccinium membranaceum	VAME	thin-leaved huckleberry

Scientific Name	Code	Common Name
Vaccinium ovatum	VAOV	evergreen huckleberry
Vaccinium parvifolium	VAPA	red huckleberry
Whipplea modesta	WHMO	whipplevine

Appendix 2. Values of environmental variables, physical habitat type, and species abundances (in parentheses) for each vegetation survey plot. Physical habitat type codes are as in Table 2. Species codes are as in Appendix 1. Species abundances are by percent cover, with 1 = 1-25%, 2 = 26-50%, 3 = 51-75%, and 4 = 76-100%.

Plot	Annual Precip. (cm)	Dec.-July Precip. Diff.(cm)	Annual Temp. (°C)	July-Jan. Temp. Diff.(°C)	Soil Depth (cm)	Soil Water Capacity (cm^3/cm^3)	Physical Habitat Type	Species Codes(with abundances)
1	130.3	18.5	10.6	15	119.9	0.125	hi_mo_fer	ACMA(1),ARME(1),BENE(1),CEIN(1), COCO(1),HODI(1),LOCI(1),LOHI(1),PSME (1),QUCH(1),RHDI(2),ROGY(1),RUUR(1), SYMO(1),WHMO(1)
2	92.1	14.7	8.5	15.6	84	0.139	lo_fertile	ARME(1),CACH(1),CEIN(1),COCO(1), CONU(1),LIDE(2),LOCI(1),PSME(1),QUCH (1),RHDI(1)
3	118.8	19	10	15.6	84	0.139	lo_fertile	ARME(1),LIDE(1),PSME(3),QUCH(1), QUKE(1),RUUR(1)
4	104.6	17.1	10	15.6	84	0.139	lo_fertile	ACMA(2),ALRU(1),ARME(1),LIDE(1), PSME(1)
5	106.2	17.7	9.5	15.6	84	0.139	lo_fertile	ARME(1),LIDE(1),LOCI(1),PSME(1), QUCH(2),RHDI(1)
6	134.7	22.3	9.4	15.6	84	0.139	lo_fertile	ARME(1),BENE(1),CACH(2),CHLA(1), GASH(1),LOCI(1),PSME(1),RHDI(1), ROGY(1),WHMO(1)
7	214.3	35.4	12.2	13.4	84	0.139	co_wa_mo_f	ACMA(1)CACH(1),CONU(1),GASH(1), LIDE(1),PSME(1),RHDI(1),UMCA(1) VAOV(4)
8	214.8	35.5	12.2	13.5	84	0.139	co_wa_mo_f	LIDE(2),PIPO(1),PSME(1),RHCH(1),UMCA (1),VAOV(3)
9	245.1	39.9	12.2	13.9	84	0.139	co_wa_mo_f	ALRU(1),LIDE(2),PSME(1),RHCH(1), UMCA(1),VAOV(1)
10	223.8	36.1	11.1	9.9	141.3	0.169	co_mo_f_lo	LIDE(1),PSME(2),TSHE(1),VAOV(1)

Plot	Annual Precip. (cm)	Dec.-July Precip. Diff.(cm)	Annual Temp. (°C)	July-Jan. Temp. Diff.(°C)	Soil Depth (cm)	Soil Water Capacity (cm^3/cm^3)	Physical Habitat Type	Species Codes(with abundances)
11	226.4	36.4	11.1	10	142.5	0.166	co_mo_f_lo	BENE(1),LIDE(4),PSME(1)
12	266.1	42.3	10.6	10.1	142.5	0.166	co_mo_f_lo	CACH(1),GASH(1),LIDE(2),PSME(3),TSHE (1),VAPA(1)
13	278.2	44.2	10.6	10.6	142.5	0.166	co_mo_f_lo	BENE(1),CACH(1),GASH(4),LIDE(1), PSME(2),RHCA(1)
14	284.8	45.8	10.4	12.2	142.5	0.166	co_mo_f_lo	BENE(1),CHLA(2),GASH(1),LIDE(1), PSME(2),RHCA(1),TSHE(1),VAOV(1)
15	285.2	45.9	10.4	12.2	142.5	0.166	co_mo_f_lo	ACCI(2),BENE(1),COCO(1),GASH(1),LIDE (2),PSME(2),RHCA(1),RUUR(1),RUVI(1), VAOV(1)
16	249.2	40	11.1	11.1	142.5	0.166	co_mo_f_lo	ACCI(1),BENE(1),CONU(1),GASH(1),LIDE (4),QUCH(1),TSHE(1),UMCA(1),VAPA(1)
17	236.1	37.9	11.7	8.2	115.8	0.244	co_rich_lo	LIDE(3),PSME(1),RHDI(1)
18	232.6	37.4	11.7	8	115.8	0.244	co_rich_lo	ABGR(1),GASH(1),LIDE(2),PSME(2), ROGY(1),RHDI(1),RUPA(1),RUUR(1), UMCA(1)
19	239.9	40.6	11.6	8.9	110.2	0.161	co_mo_f_lo	ACMA(1),LIDE(1),PSME(2),UMCA(2), VAOV(1)
20	238.2	40.3	11.3	8.9	110.2	0.161	co_mo_f_lo	LIDE(2),PSME(2),UMCA(1),VAOV(1)
21	236.5	39.5	11.1	10.1	110.2	0.161	co_mo_f_lo	PSME(2),UMCA(2),VAOV(1)
22	318.8	52.9	11.7	14.3	142.5	0.166	co_wet_fer	LIDE(1),PSME(3),UMCA(1)
23	339.5	56.8	11.7	13.8	142.5	0.166	co_wet_fer	LIDE(4),UMCA(1),VAOV(1)
24	279.1	46.6	11.7	11.8	110.2	0.161	co_wet_fer	LIDE(1),PSME(1),RHCA(1),SESE(1), UMCA(1),VAOV(1)
25	244	41	11.1	9.8	110.2	0.161	co_mo_f_lo	LIDE(3),PSME(2),UMCA(1),VAOV(1)
26	246.7	40.3	11.1	11.3	110.2	0.161	co_wet_fer	ACMA(1),LIDE(2),RHCA(2),UMCA(1), VAOV(2)

Plot	Annual Precip. (cm)	Dec.-July Precip. Diff.(cm)	Annual Temp. (°C)	July-Jan. Temp. Diff.(°C)	Soil Depth (cm)	Soil Water Capacity (cm^3/cm^3)	Physical Habitat Type	Species Codes(with abundances)
27	123.1	18.7	10	16.1	119.9	0.125	hi_mo_fer	ABGR(1),ACCI(1),ACMA(1),ARME(1), CADE(2),GASH(1),HODI(1),LOCI(1),PSME(1),QUCH(1),RUUR(1),WHMO(1)
28	131.3	20	9.4	16.1	119.9	0.125	hi_mo_fer	ABGR(1),ARME(1),BENE(1),CACH(1), GASH(4),HODI(1),PSME(3),SYMO(1), TABR(1),WHMO(1)
29	138.6	20.8	10	16.1	118.8	0.151	hi_mo_fer	BENE(1),CADE(1),PSME(2),RHCA(1), TSHE(1),VAPA(1)
30	370	63.5	9.4	15	88.8	0.113	co_wet_hi	BENE(1),CACH(2),DISM(1),GASH(3),LIDE(1),PILA(1),PSME(1),QUSA(3),QUVA(1), RHMA(3),RUUR(1),VAPA(1)
31	350.2	61.6	9.4	15	88.8	0.113	co_wet_hi	CACH(1),PSME(4),QUCH(1),QUSA(1)
32	355.7	61.1	9.4	15	88.8	0.113	co_wet_hi	CHLA(1),GASH(3),LIBO(1),LIDE(1),PSME(1),QUSA(2),RHMA(2),VAPA(1)
33	244.8	41.8	8.9	14.3	82.4	0.098	co_cool_mo	ABCO(1),BENE(1),DISM(1),HODI(1),LIDE(1),PSME(4),ROGY(1),RUUR(1),SYMO(1), WHMO(1)
34	235.4	39.6	8.5	13.9	82.5	0.098	co_cool_mo	ABCO(2),ABPR(1),CADE(1),COCO(1), DISM(1),HODI(1),PSME(2),ROGY(1), SYMO(1)
35	242.3	40.6	9.1	14.1	82.9	0.103	co_cool_mo	ABCO(1),ACCI(1),BENE(1),CHLA(1), COCO(1),DIHO(1),LIBO(1),PAMY(1), PSME(1),ROGY(1),WHMO(1)
36	225.2	37.6	8.3	13.9	82.8	0.099	co_cool_mo	ABCO(1),CADE(1),QUSA(1),RHPU(1), ROGY(1)
37	202.7	34.3	8.3	13.9	82.8	0.101	co_cool_mo	ABCO(1),ABMA(1),PAMY(1),ROGY(1), SYAL(1)

Plot	Annual Precip. (cm)	Dec.-July Precip. Diff.(cm)	Annual Temp. (°C)	July-Jan. Temp. Diff.(°C)	Soil Depth (cm)	Soil Water Capacity (cm^3/cm^3)	Physical Habitat Type	Species Codes(with abundances)
38	176.1	27.9	7.8	13.3	83	0.107	hi_cool_mo	ABCO(3),ABMA(1),APAN(1),BENE(1), CADE(1),LIBO(1),PAMY(1),PSME(1), QUSA(1),ROGY(1)
39	195.9	33.5	8	13.9	82.8	0.101	hi_cool_mo	ABCO(2),ACGL(1),COCO(1),QUSA(1), RHPU(1),ROGY(1)
40	181.3	28.2	7.8	13.3	82.8	0.099	hi_cool_mo	ABCO(2),ABMA(1),AMAL(1),BENE(1), CACH(1),LIBO(1),PSME(2),QUSA(1), ROGY(1),RUUR(1),VAME(1)
41	166.7	25.7	7.8	13.3	82.8	0.101	hi_cool_mo	BENE(1),CACH(1),GAOV(1),LIBO(1), PAMY(1),PIBR(1),PILA(1),PSME(3),QUSA(1),RHMA(2),RUUR(1),TABR(1),VAME(1), VAPA(1)
42	123.9	18.8	8.1	15.6	82.8	0.101	hi_cool	ABCO(2),BENE(1),HODI(1),PSME(1), ROGY(1)
43	129.9	19.2	6.1	15.6	77.8	0.079	hi_cold	ABCO(2),PILA(1),PSME(1)
44	364.7	62	8.9	14.4	82.8	0.101	co_wet_hi	ABCO(1),BENE(1),CACH(1),LIBO(1),LIDE(1),PIBR(1),PSME(1),QUSA(2),VAPA(1)
45	338.5	61	8.9	14.4	87.9	0.111	co_wet_hi	ARCA(1),CADE(1),LIDE(1),PILA(1),PSME(1),QUVA(1),ROGY(1)
46	361.5	62.4	8.9	14.7	82.8	0.101	co_wet_hi	ABCO(1),BENE(1),CADE(1),LIBO(1), PSME(2),RHOC(1),ROGY(1),RUUR(1), SYMO(1)
47	355.4	56.7	10	15	73.8	0.086	co_wet_hi	ABCO(1),CACH(1),CADE(1),PIMO(1)PIPO(1),PSME(1),QUSA(1),VAPA(1)
48	356.4	56.9	10	15	73.8	0.086	co_wet_hi	ABCO(1),BENE(1),CACH(1),CADE(1), GASH(1),LEDA(3),PIMO(1),PSME(1), QUSA(1),RUUR(1)
49	103.2	15.7	6.1	17.8	61.7	0.09	hi_cold	ABCO(1),AMAL(1),ARPA(2),CEPR(1),PIJE(1),PRVI(1),QUVA(3),RHCA(1)

Plot	Annual Precip. (cm)	Dec.-July Precip. Diff.(cm)	Annual Temp. (°C)	July-Jan. Temp. Diff.(°C)	Soil Depth (cm)	Soil Water Capacity (cm^3/cm^3)	Physical Habitat Type	Species Codes(with abundances)
50	99.4	15.1	5.3	17.8	85.7	0.099	hi_cold	ABCO(1),PHDI(1),PIMO(1),QUVA(1)
51	117.1	18.1	5.4	17.8	81.4	0.097	hi_cold	ABCO(1),CADE(1),PIMO(1),PSME(1),ROGY(1)
52	114.2	17.5	5.9	17.8	85.7	0.099	hi_cold	ABCO(1),BENE(1),CADE(1),GAFR(1),PAMY(1),QUVA(1),ROGY(1)
53	148.7	26.6	8.7	15.1	83.3	0.075	hi_cool_mo	ABCO(1),AMAL(1),BENE(1),CADE(1),HODI(1),PSME(1),ROGY(1),SYAL(1),SYMO(1)
54	151.6	27.8	8.3	15.2	83.3	0.075	hi_cool_mo	ABCO(1),BEAQ(1),PILA(1),PIPO(1),PSME(1),QUCH(1)
55	157.1	18.8	8.3	15	84.4	0.085	hi_cool_mo	ABCO(1),ROGY(1),SYMO(1)
56	160.8	21	8.9	15.3	83.3	0.075	hi_cool_mo	ABCO(2),BENE(1),PAMY(1),PILA(1),PSME(2),QUCH(1),SYMO(1)
57	229.3	39.7	9.4	15.6	85.7	0.099	co_cool_mo	ABCO(2),PSME(3),QUCH(1),QUSA(1)
58	208.5	36.3	9.5	15.2	85.7	0.099	co_cool_mo	ABCO(3),ARNE(1),CACH(1),GAFR(1),PILA(1),PSME(1),QUSA(1),SASC(1)
59	80.6	14.1	9.6	18.3	83.3	0.075	hi_cool	AMAL(1),PIPO(1),PSME(1),QUCH(2),QUGA(2)
60	99.7	19.1	8.7	18.3	69.7	0.073	hi_cool	ABCO(2),ARME(1),LIDE(2),PAMY(1),PILA(1),PIPO(1),PSME(1),QUCH(1)
61	90.7	15.4	10	17.8	80.5	0.093	lo_warm	ACMA(1),ARME(3),COCO(1),PSME(4),QUKE(1)
62	99.9	17.8	11.1	17.8	80.5	0.093	lo_warm	PILA(1),PSME(1),QUCH(3),RHDI(1)
63	109.3	19.5	12.2	17.8	80.5	0.093	lo_warm	PSME(4),QUCH(4),RHDI(1),SYAL(1)
64	139.6	27	12.1	17.5	80.5	0.093	lo_warm_mo	ARME(1),LIDE(1),PILA(1),PSME(1),QUCH(3),RIRO(1),SYAL(1)
65	169.6	32.8	11.7	17.8	103.5	0.096	lo_warm_mo	ACMA(3),COCO(2),CONU(1),LIDE(1),PSME(4),RHDI(1),UMCA(1)

Plot	Annual Precip. (cm)	Dec.-July Precip. Diff.(cm)	Annual Temp. (°C)	July-Jan. Temp. Diff.(°C)	Soil Depth (cm)	Soil Water Capacity (cm^3/cm^3)	Physical Habitat Type	Species Codes(with abundances)
66	199.4	35.6	11.1	17.2	80.5	0.093	lo_warm_mo	ACMA(2),ARME(2),CEIN(1),LIDE(1),QUCH(3),QUKE(1)
67	161.7	30.2	11.7	17.8	80.5	0.093	lo_warm_mo	ARME(1),BEAQ(1),BENE(1),CEIN(1),CONU(1),LIDE(2),PSME(3),QUCH(1),RHDI(1),SYAL(1)
68	171.5	31.5	11.1	16.7	80.5	0.093	lo_warm_mo	ARME(1),CONU(1),LIDE(1),PILA(1),PSME(2),QUCH(3),RHDI(1)
69	205.2	34.3	9.5	15.1	85.7	0.099	co_cool_mo	BENE(1),CACH(3),CONU(1),PAMY(1),PILA(1),PSME(2),QUKE(1),RHDI(1),SYAL(1),TABR(1)
70	87.3	18.6	10	16.7	80.5	0.093	lo_mod	ARME(1),CONU(1),PILA(1),PSME(4),QUCH(1),QUKE(1),RHDI(1),ROGY(1),SYAL(1)
71	72.9	11.9	9.4	18.3	103.5	0.096	lo_dry_cool	PILA(1),PIPO(1),PSME(1),QUCH(1),QUKE(1)
72	83.1	8.9	8.3	18.3	82.8	0.078	hi_cool	ABCO(2),CEPR(1),PILA(1),PSME(1),RIRO(1),SYAL(1)
73	86.5	11.9	8.3	17.8	75.3	0.116	lo_dry_cool	ARPA(1),CEBE(1),CECU(1),JUOC(1),QUGA(1)
74	148.8	27.2	8.3	16.1	67.7	0.09	hi_cool_mo	CADE(1),PILA(1),PSME(2),SYMO(1)
75	128.6	24.2	8.1	16.7	67.7	0.09	hi_cool_mo	BEAQ(1),CADE(1),PSME(3)
76	117.7	21	8.7	17.1	45	0.052	hi_cool_po	ABGR(1),PIPO(1),PSME(1),QUCH(1),SYMO(1)
77	98.6	15.6	11	18.3	41.8	0.102	lo_mod	ADFA(2),RHDI(1)
78	134.9	22.2	15.7	19.4	88.1	0.101	lo_hot	HEAR(1),PISA(1),QUCH(1),QUKE(1),RHDI(1),STOF(1)
79	104.5	14.8	10.1	17.3	83.8	0.075	lo_warm	ABCO(1),ARPA(2),CADE(1),CEPR(2),LIDE(2),PILA(1),PIPO(1)

Plot	Annual Precip. (cm)	Dec.-July Precip. Diff.(cm)	Annual Temp. (°C)	July-Jan. Temp. Diff.(°C)	Soil Depth (cm)	Soil Water Capacity (cm^3/cm^3)	Physical Habitat Type	Species Codes(with abundances)
80	102.5	18.1	11.7	18.3	99.7	0.082	lo_warm	ACMA(1),COCO(1),CONU(1),PSME(3),ROGY(1),SYMO(1)
81	164.5	26.8	11.7	18.3	80.5	0.093	lo_warm_mo	CADE(1),PILA(1),PSME(3),QUKE(1)
82	185.4	31	10	17.8	80.5	0.093	lo_warm_mo	CADE(2),COCO(1),PILA(1),PIPO(1),PSME(2),QUCH(1),QUKE(1),ROGY(1),SYMO(1)
83	116.5	19.4	13.3	18.3	63.7	0.097	lo_hot	ADFA(1),CECU(1)
85	157.1	27.8	11.7	17.2	122.9	0.302	co_rich_lo	ACMA(1),CADE(1),COUM(1),LIDE(1),PILA(1),PSME(1),QUCH(2),QUKE(1),RHDI(1)
86	167.6	25.8	12.9	17.8	80.5	0.093	lo_warm_mo	CADE(1),COUM(1),LIDE(2),PILA(1),PSME(1),QUCH(1),QUKE(1),RHDI(1)
87	151.7	26.9	10.1	17.4	85.7	0.099	lo_warm_mo	ABCO(1),AMAL(1),ARPA(1),CADE(1),CEPR(1),PHDI(1),PIJE(1),PILA(1),QUVA(3),RHCA(1)
88	172.6	29.5	14.4	18.9	66	0.108	lo_hot	ARVI(4),CESA(1),PISA(1),QUCH(1),QUGA(1),QUKE(1),RHDI(1)
89	170.6	29.2	13.9	18.3	117.6	0.14	lo_wa_mo_f	LIDE(1),PSME(1),QUCH(1),QUKE(1),RHDI(1),STOF(1)
90	191.2	33.7	13.3	17.8	117.6	0.14	lo_wa_mo_f	ARME(1),BEAQ(1),COCO(1),CONU(1),COUM(1),PILA(1),PSME(2),QUCH(2),QUKE(1),RHDI(1),ROEG(1),SYMO(1)
91	108.4	22.9	8.3	17.8	87.3	0.099	hi_cool	LIDE(1),PIJE(1),PILA(1),PSME(1),QUCH(1)
92	234.2	43	8.9	17.8	80.5	0.093	co_cool_mo	BENE(1),COCO(1),PSME(1),ROGY(1),SYMO(1),TABR(1)
93	174.2	31.1	8.9	18.3	108	0.115	hi_mo_fer	ABCO(2),AMAL(1)
94	118	20.5	11.1	17.8	80.5	0.093	lo_warm	ARME(1),CACH(1),CEIN(1),PILA(1)PSME(2),QUCH(1),QUKE(1),ROGY(1)

Plot	Annual Precip. (cm)	Dec.-July Precip. Diff.(cm)	Annual Temp. (°C)	July-Jan. Temp. Diff.(°C)	Soil Depth (cm)	Soil Water Capacity (cm^3/cm^3)	Physical Habitat Type	Species Codes(with abundances)
95	104.7	17.8	9.7	17.8	82.1	0.083	lo_mod	ABCO(1),CACH(1),COCO(1),PSME(2), ROGY(1)
96	141.4	25.8	12.8	16.9	110.4	0.122	lo_wa_mo_f	ARME(1),LIDE(3),PSME(1),RHDI(1), VAOV(1)
97	228.1	38	11.1	6.7	137.9	0.139	co_mo_f_lo	GASH(1),MEFE(1),SESE(4),VAOV(1), VAPA(1)
98	256.7	46.6	11.1	11.5	104.9	0.119	co_cool_mo	ARME(1),GASH(1),LIDE(1),PSME(1), RHMA(1),SESE(1),VAOV(3)