# Distribution Patterns of Great Basin Conifers: Implications of Extinction and Immigration

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## ABSTRACT

Factors influencing the distribution of scattered montane conifers on mountaintops in the Great Basin of North America were investigated. The sources of data were collections and observations on more than 300 mountain ranges in the region. All mountains in the region with at least one montane conifer species and all adjacent source areas were included in the data set. In all, 164 montane island sites and 40 mainland sites were used in the analyses. Physical data for each site were compiled and regression analyses were conducted to test the predictions of three island biogeography models: immigration, extinction, and equilibrium. These models were treated as alternatives to the Random Placement Hypothesis. The Random Placement Hypothesis was refuted. However, none of the island biogeography models explained the observed patterns because mainland species–area slopes were within the expected range of island slopes. The pattern that emerges is one in which both the "mainlands" and islands represent the remnants of a preexisting regional conifer flora. The vertical relief of a site's montane zone is a better estimate of habitat diversity than area, and explains 65% of all variation in species richness on mountain ranges in the region. Although not all predictions of the island biogeography models were supported, it appears that both immigration and extinction of montane and subalpine conifers have occurred in the region during the Late Quaternary. Extinction was more important than immigration in shaping modern conifer distributions because area, not distance to sources, has a stronger influence on species richness.

Key words: conifers, dispersal, extinction, floristics, fragmentation, Great Basin, immigration, island biogeography, mountain islands, species–area relationship.

## INTRODUCTION

The order Pinales (conifers) includes the pines, spruces, firs, cypresses, junipers, redwoods, and yews. Conifers are among the most primitive of modern woody plants, yet they dominate the native vegetation of much of western North America. Conifer forests and woodlands dominate most mountains in the semi-arid Great Basin, and the highest of these mountains possess many montane and subalpine conifer species. High mountain conifer stands in the Great Basin are intriguing due to the large number of sites (Charlet 1996) and the long distances between them (Wells 1983). The existence of these stands invites inquiry into their dispersal (Wells 1983), evolutionary (Critchfield 1984*a*; Kruckeberg 1991; Hamrick et al. 1994), and climatic (Wells 1983; Axelrod 1990) histories, and has profound conservation significance (Brussard et al. 1999).

Desert shrublands dominate most of the Great Basin (Billings 1951; Cronquist et al. 1972). Yet, in the Great Basin's high mountains montane, subalpine, and alpine habitat (MacMahon 1988; Charlet 1991) together comprise about 7.5% of the region (Brussard et al. 1999). Most of these high mountain environments are widely separated by deserts from one another and from the main forest formations of the Rocky Mountains, Colorado Plateau, Columbia Plateau, and Pacific Moun-tains. Nevertheless, most of these Great Basin mountains contain montane and subalpine conifers that also occur in the surrounding regions (Critchfield and Allenbaugh 1969; Little, Jr. 1971; Billings 1990*a*; Charlet 1996).

Equilibrium island biogeography theory (MacArthur and Wilson 1963, 1967) was applied to explain the distribution of organisms in these insular montane habitats (Brown 1978; Harper et al. 1978; Johnson 1978; Reveal 1979; Wells 1983). In those analyses, the following assumptions were made: the Sierra Nevada and Rocky Mountains are biotic sources ("mainlands"), while Great Basin mountains are species-poor habitat fragments ("islands") isolated from the mainlands and from one another by desert habitats ("ocean") unsuitable for the mountain fauna and flora. Workers concluded that the Great Basin biota are depauperate, much more closely affiliated with the Rocky Mountains than with the Sierra Nevada, and that migration from the Rocky Mountains has been important in stocking Great Basin mountains with mammals (Brown 1978), montane plants (Harper et al. 1978), alpine plants (Billings 1978), and montane and subalpine conifers (Wells 1983). Wells (1983) pointed out that Rocky Mountain domination of the Great Basin flora is counterintuitive because prevailing westerly winds should give Sierra Nevada plants a dispersal ad-

vantage to the islands not enjoyed by Rocky Mountain plants. Aside from Kruckeberg (1991) who proposed no source for the Great Basin flora, the consensus is that the Rocky Mountain flora dominates the Great Basin because the continental climate of the Great Basin is more similar to the Rocky Mountains than to the Pacific-influenced climate of the Sierra Nevada. As a result, Rocky Mountain taxa were proposed to be ecologically suited for Great Basin montane environments while Sierran taxa have difficulty establishing in the region (Axelrod 1976, 1990; Harper et al. 1978; Wells 1983; Billings 1990a). The Rocky Mountain domination of the Great Basin flora is so universally accepted that Wells (1983) stated this as fact without citation.

However, recent work has shown that many more vascular plant species occur on individual Great Basin mountains than were previously known. Species distribution data used in previous analyses were independently demonstrated by Charlet (1991) and Morefield (1992) to underreport the number of species present in Great Basin mountain ranges, several of which are now known to have two or more times as many plant species than reported by Harper et al. (1978). When new data for 12 of the larger Great Basin mountain ranges were analyzed, similarities between floras increased and strong Pacific affinities were detected east across the Great Basin to the Nevada–Utah border (Charlet 1991).

Moreover, even our knowledge of the distributions of the most prominent organisms in the region, the conifers, was incomplete. In Nevada, previously unreported occurrences of conifer species on 104 mountain ranges were discovered during a survey (Charlet 1996), and new occurrences on an additional 35 mountain ranges not referred to in the literature were discovered in herbaria (Charlet *in* Ertter 2000). Conifer distributions in the Great Basin need to be reexamined in light of improved data to test whether the patterns are the same as those recognized in previous work. If these patterns are different, reconstruction of the Late Quaternary biogeographic history of conifers in the Great Basin may need to be modified.

### Current Views of Great Basin Conifer Biogeography

Hamrick et al. (1994) concluded that most conifers present at the Tertiary–Quaternary boundary (ca. 2 million years before present) in the central Great Basin went extinct before the Holocene (ca. 10,000 years before present), with only *Juniperus communis, Picea engelmannii, Pinus flexilis,* and *P. longaeva* remaining in lowland pleniglacial forests. *Pinus flexilis* and other Rocky Mountain species may have migrated across central Great Basin lowlands to the Sierra Nevada in the Late Wisconsin (Major and Bamberg 1967; Wells 1983), while pinyon-juniper (*Pinus edulis* or *P. mono-*

*phylla* and *Juniperus osteosperma*) and pinyon-juniper-oak (*Quercus gambelii*) woodlands likely were restricted to refugia in the Mojave and western Sonoran Deserts (Wells 1983). Modern occurrences of other conifers in the Great Basin are explained by Holocene dispersal of five additional montane and subalpine conifer species from the east into the region during the post-Wisconsin warming from ca. 12,000–8000 years before present (Wells 1983; Spaulding 1990; Hamrick et al. 1994). Wells (1983) proposed two highland stepping-stone routes for montane and subalpine conifer migration into the eastern Great Basin during wet intervals during the Holocene. The northern route is from the Middle Rocky Mountains south of the Snake River, at the northeastern border of the region. Wells (1983) proposed that *Abies concolor* and *Pseudotsuga menziesii* var. *glauca* entered the southeastern part of the Great Basin from the Colorado Plateau, with *A. concolor* migrating 500 km northeast to the Ruby Mountains from the Sheep Range. Similarly, Wells (1983) thought that *Pinus albicaulis* colonized mountains of northeastern Nevada from the west in the Holocene. *Pinus ponderosa* is thought to have immigrated into the southern Great Basin (Thompson and Mead 1982; Spaulding 1990; Betancourt et al. 1990b) from source areas perhaps as far as northern Mexico (Wells 1983).

A marked west-east asymmetry in conifer species richness on Great Basin islands was observed by Wells (1983), with longitude negatively correlated with species richness. That is, the farther east the island, the more montane conifer species per area it contains. In the central Great Basin, at longitude 116°W, lies what I call ''Wells' Line:'' the point at which species richness rapidly falls the farther west the island is (Wells 1983). Wells' Line bisects the region into two roughly equal areas. Wells (1983) and later Hamrick et al. (1994) thought that this decrease in richness associated with increasing westerly location was due to more successful dispersal of montane and subalpine conifers from the eastern mainland (Colorado Plateau and Wasatch Mountains) than from the western mainland (Sierra Nevada).

However, Axelrod (1976) doubted that the Great Basin climate in the Pleistocene was as extreme as that proposed by Major and Bamberg (1967), and Thompson (1990) similarly doubted the extreme pleniglacial climate envisioned by Wells (1983). Great Basin subalpine conifers may have been present on rocky outcrops in valleys dominated by cold sagebrush steppe (Thompson and Mead 1982; Thompson 1992), or ''subalpine forest-steppe'' (Thompson 1990). The high topographic diversity in the region may have allowed the existence of many habitats on mountains throughout the Quaternary. Warm sites on south-facing slopes may have allowed local persistence of montane conifer

species at elevations above subalpine conifers on cold valley floors (Axelrod and Raven 1985) during glacio-pluvials, just as cold air drainage prevents modern pin-yon-juniper woodlands from filling most Great Basin valleys today (Billings 1954).

Sierran conifer species were present in the western Lahontan Basin during the Pleistocene (Nowak et al. 1994). Montane and subalpine conifers in the western Great Basin on hydrothermally altered sites today may be relicts from a once more widespread distribution in the Late Pleistocene (Billings 1950; DeLucia et al. 1988). So too, the occurrence of *Pinus washoensis* in the Warner Mountains and on the lee slopes of the Cascades and Sierra Nevada may be relictual (Critch-field 1984*a*; 1984*b*). Further, it is possible that both *Juniperus osteosperma* and *J. scopulorum* were pre-sent at reduced numbers throughout the Pleistocene (Thompson 1992). The mid-Holocene xeric interval likely caused local extinctions of many of these pop-ulations and range-shifts of others into higher eleva-tions of the mountains of the Columbia Plateau, Cas-cades, Rockies, Sierra Nevada, and Great Basin (Critchfield 1984*a*; Charlet 1991; Thompson 1992).

Thus, there are two general views of the Quaternary history of Great Basin conifers that attempt to explain their modern distributions: immigration and extinction. Either montane and subalpine conifers on mountain-tops in the Great Basin are immigrants that arrived during the Holocene or they are relicts from the Pleis-tocene. Fortunately, a theoretical model exists that al-lows examination of modern distributions in terms of the relative contributions of immigration and extinc-tion to the flora: the equilibrium theory of island bio-geography (MacArthur and Wilson 1967).

Many ecological islands with montane and subal-pine conifers occur in the Great Basin. These islands are widely separated from one another and from the main distributions of the species by large areas of un-suitable habitat for conifers. This research examines the factors influencing the modern distribution of Great Basin conifers in order to discern their recent histories. In doing so, I apply the equilibrium theory of island biogeography by assuming mountaintops are islands and neighboring forested regions are mainland source areas.

Did most conifers in the Great Basin go extinct dur-ing the Pleistocene? If so, the modern occurrence of other montane and subalpine conifer taxa in the region represents Holocene colonization success. Alternative-ly, did the montane and subalpine conifers in the Great Basin survive the Pleistocene? If so, these populations are relictual. Or, does the distribution pattern result from a combination of colonization and extinction events during the Quaternary? Does an island bioge-ography model or random placement model best ex-plain the observed distribution? To answer these ques-tions, I determine the current distributions of conifer taxa and the extent of potential montane conifer habitat in the Great Basin and determine the floristic affinities of islands and mainlands based on modern species dis-tributions. I then test the hypotheses of random place-ment and equilibrium island biogeography theory for the distribution pattern of conifers on Great Basin montane islands, and propose an outline of the Late Quaternary history of Great Basin conifers.

### Equilibrium Island Biogeography Theory

MacArthur and Wilson (1963, 1967) developed the equilibrium theory of island biogeography, or Mac-Arthur-Wilson (M-W) model, to explain species rich-ness on oceanic islands. The M-W model has been used since to examine patterns of species richness on insular habitat islands in terrestrial situations (Brown 1971; Wells 1983; Rosenzweig 1995; Lawlor 1986; Newmark 1986; Patterson and Atmar 1986). Habitat islands, whether oceanic or terrestrial, are critically im-portant in our understanding of speciation (Darwin 1859; Wallace 1880; Carlquist 1974; Grant 1986; Kruckeberg 1991), genetic bottlenecks (Wilcox et al. 1986), and extinctions (Brown 1986; Patterson and At-mar 1986). In face of today's ever-increasing human-induced fragmentation of ecosystems, our understand-ing of these processes has important conservation and management implications (Simberloff 1974; Billings 1990*b*; Brussard et al. 1999).

The M-W model posits that an equilibrium number of species ($S$) on an island is caused by equal rates of immigration ($I$) to and extinction ($E$) on the islands. The equation of the resulting species–area curve is:

$$S = CA^z \tag{1}$$

where $S$ = number of species, $A$ = area, $C$ is a constant that modifies the curve, and $z$ = the slope. When the data are log-transformed, this curve becomes linear by the equation:

$$\log S = z * \log A + \log C \tag{2}$$

In the log-linear transformed regression, $\log C$ is the value of $\log S$ at the $Y$ intercept of the regression line.

Direct measurement of $I$ and $E$ of conifers is diffi-cult due to their long lifespan and generation times. Valentine et al. (1991) estimated the general rate of conifer extinction since the Tertiary–Quaternary boundary at 0.2 species per million years. Although direct measurement of $I$ and $E$ in this system is not possible at this time, they can be approximated. Sim-berloff (1974) summarized the control of species rich-ness on islands in the M-W model as an area effect and a distance effect. Area and distance are useful as measurable variables that are surrogates for extinction and immigration rates, respectively. This is applicable

Table 1. Predicted detectable effects of distance (*D*) and area (*A*) of the random placement, MacArthur-Wilson (M-W) immigration, M-W extinction, and M-W equilibrium hypotheses on montane conifer species distributions in the Great Basin.

| Effect | Random placement hypothesis | M-W immigration hypothesis | M-W extinction hypothesis | M-W equilibrium hypothesis |
|---|---|---|---|---|
| Area effect is non-random (species–area slopes are nonrandom) | No, slopes have at least a 5% probability of being derived from a random distribution | Yes, species–area slopes are nonrandom | Yes, species–area slopes are nonrandom | Yes, species–area slopes are nonrandom |
| Mainland species–area slope ($z$) | n/a | Mainlands have low species–area slopes ($z = 0.12$–$0.17$) | Mainlands have low species–area slopes ($z = 0.12$–$0.17$) | Mainlands have low species–area slopes ($z = 0.12$–$0.17$) |
| Island species–area slope ($z$) | n/a | Islands have an immigrant species–area slope ($z < 0.250$) | Islands have a highly insular slope ($z > 0.262$) | Islands have insular, equilibrium slope ($z = 0.250$) |
| Distance effect vs. area effect | $D < A$: there is no distance effect on species richness on islands | $D > A$: distance effect greater than area effect. Descending order of richness in islands: near–large, near–small, far–large, far–small. Recent dispersal, not extinction, controls species richness | $D < A$: distance effect less than area effect. Descending order of richness in islands: near–large, far–large, near–small, far–small. Extinction, not immigration, controls species richness | $D = A$: distance effect about equal to area effect. Descending order of richness in islands: near–large, far–large/ near–small, far–small. Extinction and immigration control species richness equally |

because greater distance from a source pool reduces the probability of immigration, and larger area reduces the probability of extinction on an island (Rosenzweig 1995). The area effect produces a higher intersection of immigration and extinction rate curves (*S*: the predicted equilibrium number of species) on large islands compared to small islands (MacArthur and Wilson 1967; Simberloff 1974; Rosenzweig 1995) and great distance to a source area produces a lower *S* on far islands compared to near islands (Rosenzweig 1995).

Interpretations of species–area relationships and the use of the island biogeography theory have been criticized (Martin 1981; Boecklen and Gotelli 1984; McGuinness 1984*a*; Schoener 1988; Williamson 1988; Hengeveld 1990). Nevertheless, area remains closely related to species richness in most situations (Brown 1986; Rosenzweig 1995). Island biogeography theory has been verified experimentally for invertebrate faunas on oceanic islands by Simberloff and Wilson (1969, 1970) and Simberloff (1976*a,b*). Alternatively, experimental work with faunas on ocean shore boulders (McGuinness 1984*b*), with birds (McCoy 1982) and with plants in forest fragments (Dunn and Loehle 1988) yielded few, if any, of the species–area relationships predicted by the M-W model. However, the problems detected by these workers are avoided here by a large number of samples, by a wide range of sample areas, by testing null hypotheses, and by examining a taxonomic group that has no vagrant species in the study area. That is, all species recorded for a site are residents, and are not simply passing through when the site is sampled.

*Great Basin Conifer Biogeographic Hypotheses*

Three models of conifer responses to Late Quaternary environments that predict testable dispersion patterns are (1) Holocene dispersal (M-W immigration hypothesis), (2) Tertiary relicts (M-W extinction hypothesis), and (3) equilibrium (M-W equilibrium hypothesis). These three hypotheses will be tested as alternatives to the (4) random placement, or null, hypothesis. The hypotheses are examined by testing their predictions regarding three general effects on the number of species on mainlands and islands: area, distance to mainlands, and longitude (Table 1).

*Hypothesis 1: Holocene colonization (M-W immigration).*—Holocene colonization of Great Basin mountains by conifers will be seen in the region today as *I* > *E* on islands. Greater access to islands from mainland sources leads to a low species–area slope (z < 0.25) across the region because island samples resemble mainland samples (Table 1). Distance will be more strongly associated than area with species richness because colonization of mountain ranges frequently occurs. Species richness by island type should be in the following order: near–large > near–small > far–large > far–small, with a wide discontinuity between near–small and far–large islands.

*Hypothesis 2: Holocene extinction (M-W extinction).*—An extinction-driven dispersion pattern will be reflected by *I* < *E*. A steep species–area slope (z > 0.262) will be evident (Table 1). Area will have a greater effect on species richness than distance to mainland sources, because restocking of mountain ranges only rarely occurs and large areas allow more

species to be retained on large islands. Species richness by island type should be in the following order: near–large > far–large > near–small > far–small, with a wide discontinuity between far–large and near–small islands.

*Hypothesis 3: equilibrium (M-W equilibrium).*—This model of Great Basin conifer history in the Late Quaternary is simply that $I = E$ in spite of all climatic oscillations. Both immigration and extinction occur on the islands, but species richness on islands across the region is in equilibrium, and species–area slopes have a $z$ value of 0.25 (Table 1). Distance to mainland sources and area will have roughly equivalent influence on species richness on islands. Species richness by island type should be in the following order: near–large > far large/near small > far–small, with near–small and far–large islands having nearly the same number of species.

*Hypothesis 4: Random Placement (null) hypothesis.*—The ''Random Placement'' hypothesis (Arrhenius 1921; Coleman 1981; Coleman et al. 1982) states that species–area slopes are simply a sampling phenomenon with no inherent biological meaning. Therefore, the random placement of species is the null hypothesis for the species–area relationship (Simberloff 1976a,b; Connor and Simberloff 1978, 1979; Connor and McCoy 1979; Simberloff and Connor 1979; McGuinness 1984a; Patterson and Atmar 1986). In this study, Random Placement is the null hypothesis, and the island biogeography explanations are alternative hypotheses for the species–area relationships discovered (Table 1).

<div align="center">MATERIALS AND METHODS</div>

*Study Area*

The Great Basin is an interior province of the Basin and Range physiographic region (Hunt 1967). It occupies more than 500,000 km² and is situated between several mesic physiographic provinces (Brussard et al. 1999). The Great Basin is bounded by the Pacific Mountain System on the west and south, and the Rocky Mountain System on the east and northeast, the Colorado Plateau to the southeast, and the Columbia Plateau to the north (Hunt 1967; Fig. 1). The Great Basin as defined here includes all areas within the Great Basin province of the Basin and Range physiographic region (Hunt 1967), the hydrographic Great Basin (Morrison 1991), the Great Basin floristic province (Holmgren 1972), and the Mojave Desert (Vasek and Barbour 1988). The interior drainage of the Transverse Ranges in the Mojave Desert is the southwestern boundary of the study area. Along the western boundary, I follow Barbour and Major (1988) and Hickman (1993) by including the entire eastern slope of the Sierra Nevada. On the northwestern boundary the ranges

on the Deschutes River-Great Basin divide (e.g., Paulina Mountain), and ranges on the Pit River-Great Basin divide (e.g., Warner Mountains, Gearhart Mountain) are included, all of which are excluded from the Intermountain Region by Holmgren (1972). The northern part of the study area includes the southern Blue Mountains (e.g., Strawberry Mountain) that drain into the Sylvies River (Malheur Basin). Included along the eastern boundary are the Wasatch Mountains and the western front of the Colorado Plateau, components of the hydrographic Great Basin and the Intermountain Region but not the Great Basin floristic division of Holmgren (1972). The southeastern boundary is drawn along the eastern edge of the transition zone between the Mojave and Colorado deserts. As such, the Great Basin as considered here is wider along most of its boundaries than the floristic Great Basin as defined by either Holmgren (1972) or by Cronquist (1982). Of the Rocky Mountain provinces, only the Middle Rocky Mountains have direct contact with the Great Basin, while in the Pacific region, only the Middle and South Cascades, Sierra Nevada, and Transverse Ranges border the Great Basin.

*Great Basin Conifer Flora*

A database was prepared for the analyses that included Great Basin conifer floristic (34 taxa) and physical characteristics (22 variables), plus richness sums for different species categories, of the 206 Great Basin sites. Taxonomic resolution is at the infraspecific level except that I do not separate the varieties of *Juniperus occidentalis* due to the difficulty in distinguishing the varieties in the western Great Basin (Vasek 1966; Cronquist et al. 1972; Charlet 1996) and the hybridization that is occurring in the area (Terry et al. 2000). Nomenclature follows Kartesz (1994).

All mountain ranges in the region that are not part of the Pacific, Rocky Mountains, Colorado Plateau, or Blue Mountains (ca. 450) were considered mountain islands. Collections in 18 herbaria (AUSTIN, BRY, CAS, DUKE, IFGP, NSM, NY, OGDF, OSC, RENO, RSA, UC, UCR, UNLV, US, UT, UTC, and UW) were examined and geographic data from their labels were transcribed and compiled into a presence-absence matrix of vouchered conifer occurrences. The literature was consulted concerning all statements pertaining to conifer distributions on specific physiographic features in the region. I made observations of conifers on more than 315 of the 450 mountain ranges during the past 18 years. In doing so, I verified most of the literature reports and distribution maps for Nevada, California, and Oregon. I collected more than 900 conifer vouchers on about 200 mountain ranges, and entered these data into the matrix. The 900+ collections were divided into 3000+ herbarium sheets and are deposited at

**125°**  **120°**  **115°**  **110°**

OLYMPIC
MOUNTAINS

CASCADE
RANGE

**45°**

PACIFIC COAST

NORTHERN
ROCKY
MOUNTAINS

COLUMBIA
PLATEAU

KLAMATH
MOUNTAINS

MIDDLE
ROCKY
MOUNTAINS

**40°**

SOUTHERN
ROCKY
MOUNTAINS

SIERRA
NEVADA

GREAT BASIN

PACIFIC COAST

**35°**

COLORADO
PLATEAU

TRANSVERSE RANGES

N
W    E
S

50  0   50    100    200 km
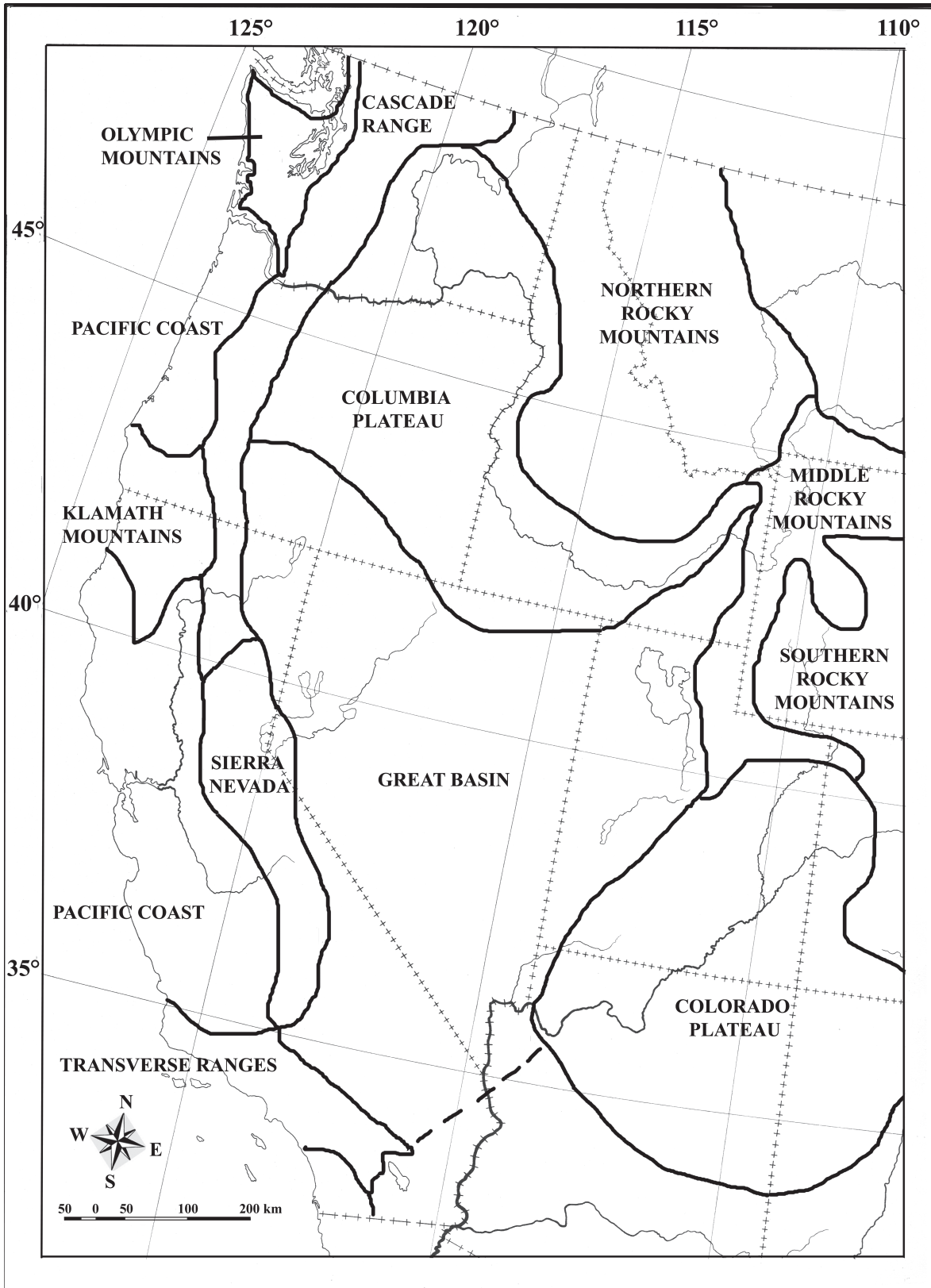
BRY, DUKE, NY, RENO, UC, UCR, UNLV, UTC, and UW. I truncated the samples by eliminating all sites that did not contain at least one montane or subalpine conifer species, leaving 166 montane ''islands.'' I divided ''mainland'' areas along significant physiographic features into 40 smaller samples sufficiently large to resolve conifer distributions from the literature in locations where I did not verify occurrences. The mainland samples are modern source areas within the region. These mainland samples occur in the Blue Mountains, Sierra Nevada, Cascade Range, Colorado Plateau, and Middle Rocky Mountains, and have direct access to Great Basin islands. This set of 206 samples thus represents all known localities of montane and subalpine conifers in the Great Basin, spatially resolved into mountain units (Fig. 2).

### Physical Attributes of Samples

Each sample locality was circumscribed by hand on US Geological Survey 1 : 250,000 topographic maps. Mountain range names and circumscriptions in Nevada follow McLane (1978) and Charlet (1996). Maximum and minimum latitude, longitude, and elevation data were all determined from these maps and compiled. Each locality was individually evaluated to determine the minimum elevation of its montane zone. From these maps and initial data, additional physical attributes and species richness measures (Table 2) for the mountain ranges were assembled into a matrix of mountain ranges by physical and species richness attributes.

*Area.*—The lowest elevation of the montane zone was determined for each range by the elevation of the ecotone between the highest elevations of the pinyon-juniper zone with the upper sagebrush-grass zone or any other zone above the pinyon-juniper zone of Billings (1951). The area data acquired in this way include ecotonal sites that are often occupied by montane conifers. However, most of these ecotones are occupied by pinyon-juniper and other communities, and so I may overestimate the area available to montane and subalpine conifers. In two cases in the western Great Basin (Junction House Range and Kamma Mountains), montane conifers occur on edaphic sites within the pinyon-juniper or lower sagebrush zones (Billings 1950; Charlet 1996) but there is no montane zone in the range. In these cases, the area of this edaphic zone was en-

tered into the data set as the montane zone area. Total area and montane zone area were determined by hand from these maps with a compensating polarimeter (model No. 62005, Keuffel and Esser, New York, USA).

*Distance.*—The distance of an island to other features is the shortest distance between the montane zone boundaries of the samples. These distances were measured from the topographic maps. The shortest distance to each mainland and the shortest distance to any mainland ($DIS_{MAIN}$) were thus determined.

*Mainland and island classification of samples.*—All sample sites within the Great Basin region were classified as either ''mainland'' or ''island'' samples. Mainland samples are located within the Rocky Mountains, Colorado Plateau, Sierra Nevada, Blue Mountains, and Cascade physiographic areas, while islands are the remaining sites on isolated mountain ranges. ''East'' islands are samples whose maximum longitude is less than 116°W, and the remaining island samples are ''west'' islands. Islands were classified as ''near'' or ''far'' by dividing the islands about the median of $DIS_{MAIN}$. Likewise, islands are divided about the median of $AREA_{MON}$ and designated as ''large'' or ''small.'' Additional island categories are created by combination of the size and distance categories, yielding far-large, far-small and near-large and near-small island types.

*Species richness and species categories.*—The total number of conifer taxa on each site ($DIV$) was calculated from the assembled presence–absence matrix and tracked as a variable for the site. Similarly, the numbers of xeric and montane taxa were determined.

Conifer species occurring in the area were evaluated for their presence in broad ecological zones. ''Montane'' is here defined widely, in the terms of Merriam (1898), to include both the arid transition zone upward to the Hudsonian zone (or subalpine), with the upper limits at the Arctic-alpine zone. I set the lower limits of the montane zone at the Sonoran zone, thus excluding the main pinyon-juniper formation throughout the region, consisting of various combinations of *Juniperus californica, J. osteosperma, Pinus edulis,* and *P. monophylla.* Species were classified according to their zonal and regional occurrences.

The number of montane and subalpine taxa on a

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Fig. 1. Physiographic regions, provinces, and sections of the western United States redrawn from Hunt (1967) on a base map by McKnight and McKnight publishers (Bloomington, Illinois). Pacific Mountain System Region: Sierra Nevada Province, Transverse Ranges Province, Cascade Range Province. Pacific Border Province: Klamath Mountains, Olympic Mountains, Pacific Coast. Rocky Mountain System Region: Northern Rocky Mountains Province, Middle Rocky Mountains Province, Southern Rocky Mountains Province. Intermontane Plateaus Region: Columbia Plateau Province, Great Basin Province, Colorado Plateau Province. The Cascade Range, Columbia Plateau, Sierra Nevada, Colorado Plateau, and Middle Rocky Mountains all border the Great Basin. Dashed line indicates approximate boundary between Mojave and western Sonoran deserts.
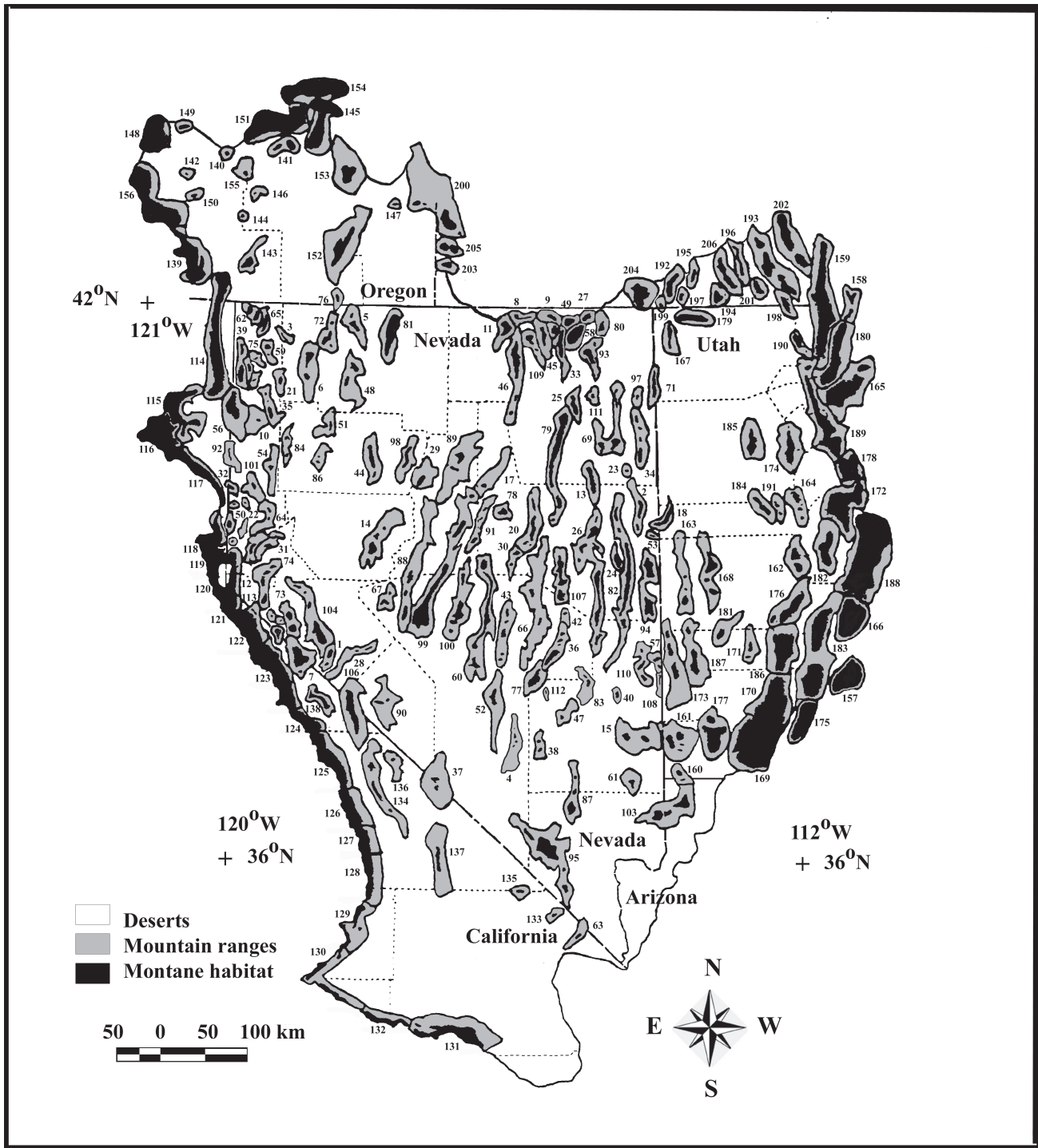
Fig. 2.   Sample sites (irregular polygons) used in the analysis of Great Basin conifers. Sample sites include: Great Basin montane islands with at least one montane conifer species present ($N = 166$), and sample areas used in the Great Basin that occur on adjacent mainlands ($N = 40$). Small numerals indicate sample site location (Appendix 1 for key) except for the following small ranges in Nevada whose numbers are not on the map: Copper Mountains (16), Desert Creek (19), Lost Creek (55), Peavine Mountain (68), Petersen Mountain (70), Seven Lakes (85), Sweetwater Mountains (96), Virginia Range (102), and Wellington Mountains (112). Locations of montane and subalpine areas are portrayed as shaded on Great Basin mountain ranges and adjacent mainlands considered in this study. Note major discontinuities between montane islands and mainlands, and the nearly continuous condition of the montane zone on the eastern and western mainlands. Interglaciopluvial stepping-stone routes available from the east occur north and south of the Bonneville Basin. Stepping stone routes are also available from the west but along smaller islands and over wider low-elevation barriers.

Table 2. Physical variables of mountain ranges and mainland samples used in the analysis of Great Basin conifers.

| Variable | Definition |
|---|---|
| *REGION P, REGION H1, REGION H2, REGION F* | Physiographic region (sensu Hunt 1967), primary hydrographic region, secondary hydrographic region, and floristic region (Holmgren 1972 and/or Hickman 1993) |
| *MAIN, ISLE* | Sample has mainland characteristics (*MAIN* = 1), or sample has island characteristics (*MAIN* = 0) |
| $LAT_{MIN}$, $LAT_{MAX}$, $LAT_X$ | Minimum, maximum, mean latitude |
| $LONG_{MIN}$, $LONG_{MAX}$, $LONG_X$ | Minimum, maximum, mean longitude |
| *EAST, WEST* | Island sample with $LONG_X$ < 116.1°W is *EAST*; island sample with $LONG_X \geq$ 116.1°W is *WEST* |
| $ELE_{MIN}$, $ELE_{MAX}$, $ELE_{VALL}$ | Minimum, maximum elevation, minimum elevation of adjacent valleys |
| *RELIEF* | $ELE_{MAX} - ELE_{MIN}$ |
| *PEAKVAL* | $ELE_{MAX} - ELE_{VALL}$ |
| $RELIEF_{MON}$ | $ELE_{MAX} - ELE_{MON}$ (montane relief) |
| $AREA_{MON}$ | Total area of the montane zone in the sample |
| *AREA* | Total area of the sample |
| *LARGE, SMALL* | Islands with $AREA_{MON}$ > median (*LARGE* = 1), or $AREA_{MON}$ < median (*LARGE* = 0) |
| $DIS_{MAIN}$, $DIS_{PAC}$, $DIS_{BLUE}$, $DIS_{COLU}$, $DIS_{COLO}$, $DIS_{MRM}$, $DIS_{NRM}$ | Minimum distance to the nearest mainland (MAIN), Pacific physiographic provinces (PAC), Blue Mountain (BLUE), Columbia Plateau (COLU), Colorado Plateau (COLO), Middle Rocky Mountains (MRM), Northern Rocky Mountains (NRM), or nearest Rocky Mountain physiographic province (minimum value of $DIS_{MRM}$, $DIS_{NRM}$, $DIS_{COLO}$, $DIS_{RM}$) |
| *NEAR, FAR* | Near Islands: whose distance to a mainland is shorter than the median minimum distance to a mainland (*NEAR* = 1); Far Islands: whose distance to a mainland is greater than the median minimum distance to a mainland (*NEAR* = 0) |
| *DIV* | Number of native conifer species |
| $DIV_{MON}$, $DIV_{ALP}$ | Number of montane conifer species; number of subalpine conifer species that occur in the sample |
| $DIV_{PAC}$, $DIV_{RM}$, $DIV_{WS}$ | Number of conifer species that also occur in Pacific Mountain System physiographic provinces, that also occur in the Rocky Mountain and/or Colorado Plateau physiographic provinces, and the number of the following widespread species that occur in the sample: *Abies grandis, Juniperus communis, Larix occidentalis, Pinus flexilis,* and *P. longaeva* |

mountain range was assigned to the variable $DIV_{MON}$, and the numbers of Rocky Mountain–Colorado Plateau mainland ($DIV_{RM}$), Pacific mainland ($DIV_{PAC}$), or widespread montane or subalpine conifers ($DIV_{WS}$) were compiled. $DIV_{RM}$ is the number of conifer species at a site that are found only in Great Basin islands and/or the Rocky Mountain–Colorado Plateau, $DIV_{PAC}$ is the number of species of a sample that are found only in Great Basin islands and/or the Pacific mainland, and $DIV_{WS}$ is the number of widespread species at a site. In this context, ''widespread'' species are *Pinus longaeva,* whose global distribution is almost restricted to the Great Basin, and 4 species that are shared between all islands and the eastern and western mainlands: *Abies grandis, Juniperus communis, Larix occidentalis,* and *Pinus flexilis. Pinus flexilis* and *J. communis* both occur on the Pacific and Rocky Mountain–Colorado Plateau mainlands and Great Basin islands. *Larix occidentalis* and *Abies grandis* barely enter the Great Basin in the north, do not occur in the Pacific or Rocky Mountain–Colorado Plateau mainlands near the Great Basin, but are in both the Cascades and Northern Rocky Mountains (Charlet 1995). *Pinus albicaulis* and *P. monticola* occur in the Northern Rocky Mountains. However, these populations are widely separated from the Great Basin by the Columbia Plateau, while the species' ranges border the Great Basin in the Sierra Nevada, the Cascade Range, and the Columbia Plateau, and so are here considered Pacific species. *Abies*

*lasiocarpa* and *Picea engelmannii* both occur in the Pacific region, but their range on the mainlands directly contacts the Great Basin only in the Middle Rocky Mountains and Colorado Plateau and so are placed in the Rocky Mountain category.

## Error

All sites in the region known to contain montane or subalpine conifer species are included in the data set. Thus, the sites are not ''samples'' in the sense of representing a portion of the Great Basin; rather, the presence–absence data set presented is all that is known about the distributions of montane and subalpine conifers in the Great Basin. Taylor (1977) pointed out that error is rarely accounted for in whole-flora floristic analyses. However, in this data set errors are minimized due to the low number of taxa, their high visibility, voucher documentation, the intensity of the survey, and the inclusion of all known occurrences of montane and subalpine conifer species in the region. Errors remain in the floristic data, but these will be limited to relatively few errors of omission and fewer of commission.

## Statistical Methods

Data management, processing, descriptive statistics, and correlations were all performed with Microsoft®

Excel for Windows vers. 9 (Microsoft Corporation, Seattle, Washington).

*Regression analyses.*—Data for species–area regression analyses were first log-transformed and then least-squares linear regressions were performed with the transformed data. Dummy variables using the categories near, far, large, small, mainland and island were also used in regressions. Individual sites were assigned values of either 1 if the site was in that category or 0 if it was not. The assumption of a log-linear species–area curve was tested for all regressions reported here by using untransformed data in non-linear regression with SigmaPlot 2002 for Windows vers. 8.0 (SPSS, Inc., Chicago, Illinois, USA). Regression analyses and tests were performed in the computer program JMPin vers. 4.0 (2001; SAS Institute, Inc., Carey, North Carolina, USA). The data set was explored with all-possible-subset multiple regression in the computer program JMPin. The Durbin-Watson test for autocorrelation was used on the significant regressions to test the assumptions of the model (Sokal and Rohlf 1969). Species–area curves were also tested with the Quasi-Newton and Simplex estimation methods. Regression results reported here fit the assumptions of the respective model, and were plotted with SigmaPlot 2002 for Windows vers. 8.0.

*Test of random placement hypothesis.*—I used the Monte Carlo simulation program written by Patterson and Atmar (1986) that, when area is correlated with species richness, randomizes the species richness-by-samples matrix and produces randomly generated species–area slopes to test the Random Placement Hypothesis. I also used a version of this program modified by James Lyons-Weiler (in Charlet 1995) that uses the presence-absence data set rather than species richness by samples, and so randomizes the entire species by sample matrix. All results in which an island had a richness of zero were excluded from consideration, to avoid division by zero. Four hundred simulations were made, for confidence at the 0.95 level ($P < 0.05$; Manly 1992).

## RESULTS

The montane areas of the Great Basin occur throughout the region, and this area is highly fragmented (Fig. 2). Species richness is highly variable, with Great Basin montane islands ranging from 1 (many islands) to 13 (Pine Valley Mountains), and mainland sites ranging from 3 (Bear Lake Plateau) to 15 (Carson Range) species per site (Fig. 3). Of the 34 conifer taxa that occur in the study area, 7 (20.1%) do not reach Great Basin montane islands: *Abies magnifica, Juniperus californica, Larix occidentalis, Pinus balfouriana, P. coulteri, P. sabiniana,* and *Pseudo-tsuga macrocarpa.* The other 27 taxa occur on at least 1 Great Basin island. Of these, 3 are xeric and 24 are montane (Fig. 4). Of the montane taxa, 12 are distributed primarily in the subalpine (Table 3) zones. Almost complete turnover of taxa occurs from east to west across the Great Basin, as only 4 taxa are present in both the Rocky Mountain–Colorado Plateau and the Pacific mainlands adjacent to the Great Basin: 2 subalpine taxa (*J. communis* and *Pinus flexilis*) and 2 xeric, low-elevation taxa (*Juniperus osteosperma* and *P. monophylla*). *Abies concolor* and *Pinus ponderosa* occur on many islands and all mainlands and the varieties are mostly segregated into western (*A. concolor* var. *lowiana* and *P. ponderosa* var. *ponderosa*) and eastern (*A. concolor* var. *concolor* and *P. ponderosa* var. *scopulorum*) parts of the region. The only exception to this east-west segregation is in the Highland, Quinn Canyon, and Wilson Creek ranges of east-central Nevada, where both varieties of *P. ponderosa* occur. The varieties of *Pseudotsuga menziesii* are similarly segregated. However, Pacific Douglas-fir (*P. menziesii* var. *menziesii*) occurs on only 1 montane island in the Great Basin, while Rocky Mountain Douglas-fir (*P. menziesii* var. *glauca*) occurs on 30 islands in the eastern Great Basin (Fig. 4).

The mean distances of all sites to the Rocky Mountains and the Pacific Mountains are nearly the same (249 km and 276 km, respectively), with near islands possessing a mean distance of 133 km and 129 km to the Rockies and Pacific Mountains respectively (Table 4), indicating a roughly symmetrical set of islands.

### Species Richness and Correlates

*Area effect.*—The effect of area on the number of montane conifer species on Great Basin mountain islands numbers was significant in 13 of 16 site combinations analyzed (Table 5). The only exceptions were the Blue Mountains of the Columbia Plateau mainland (where there were only 4 sample sites), small islands, and far-small islands. Regression analysis revealed that less than half of the variation in montane and subalpine species richness on Great Basin montane islands is explained by montane area alone (adj. [adjusted] $R^2 = 0.39$, $N = 166$; Fig. 5). The species–area regression slope for all islands ($z = 0.253$, $N = 166$) is nearly the same as the predicted $z$ value (0.250) for islands at equilibrium (Fig. 5). The species–area slope of east islands ($z = 0.245$) is steeper than that of west islands ($z = 0.223$), near island ($z = 0.251$) and far island ($z = 0.268$) slopes are similar, while large island ($z = 0.303$) and small island ($z = 0.074$) slopes are very different (Table 5).

The mainland sites do not distinguish themselves from island sites except for their higher intercept on the *Y*-axis, indicating their greater number of species
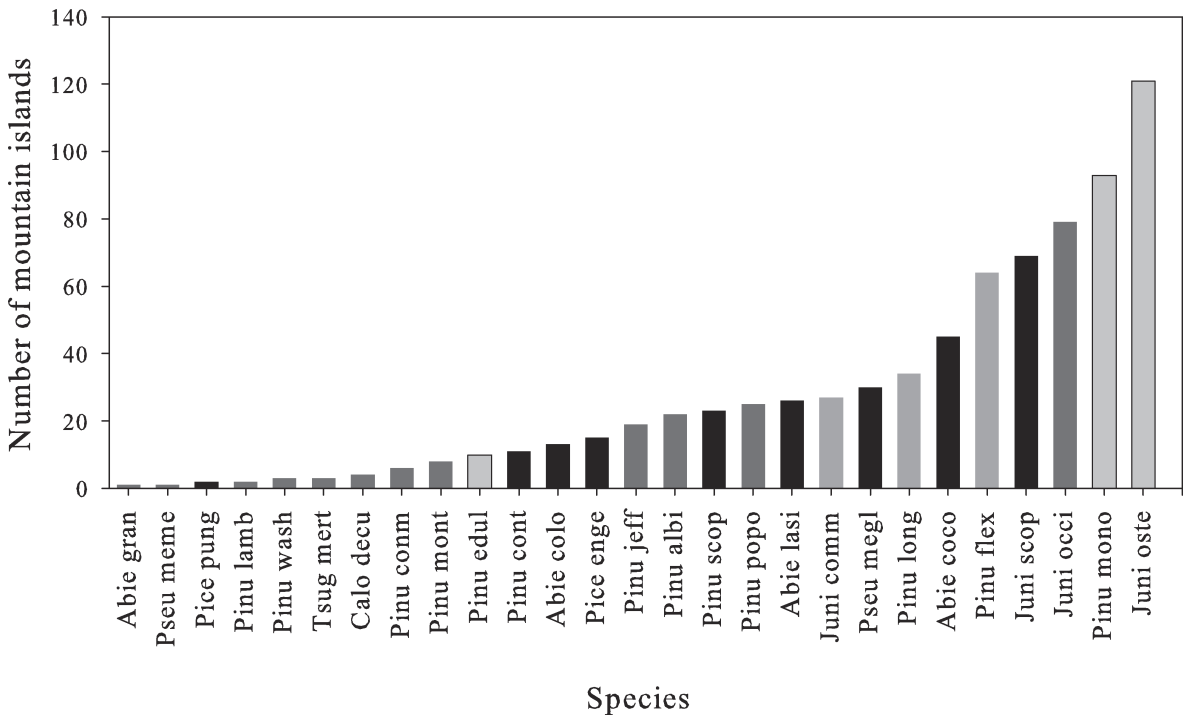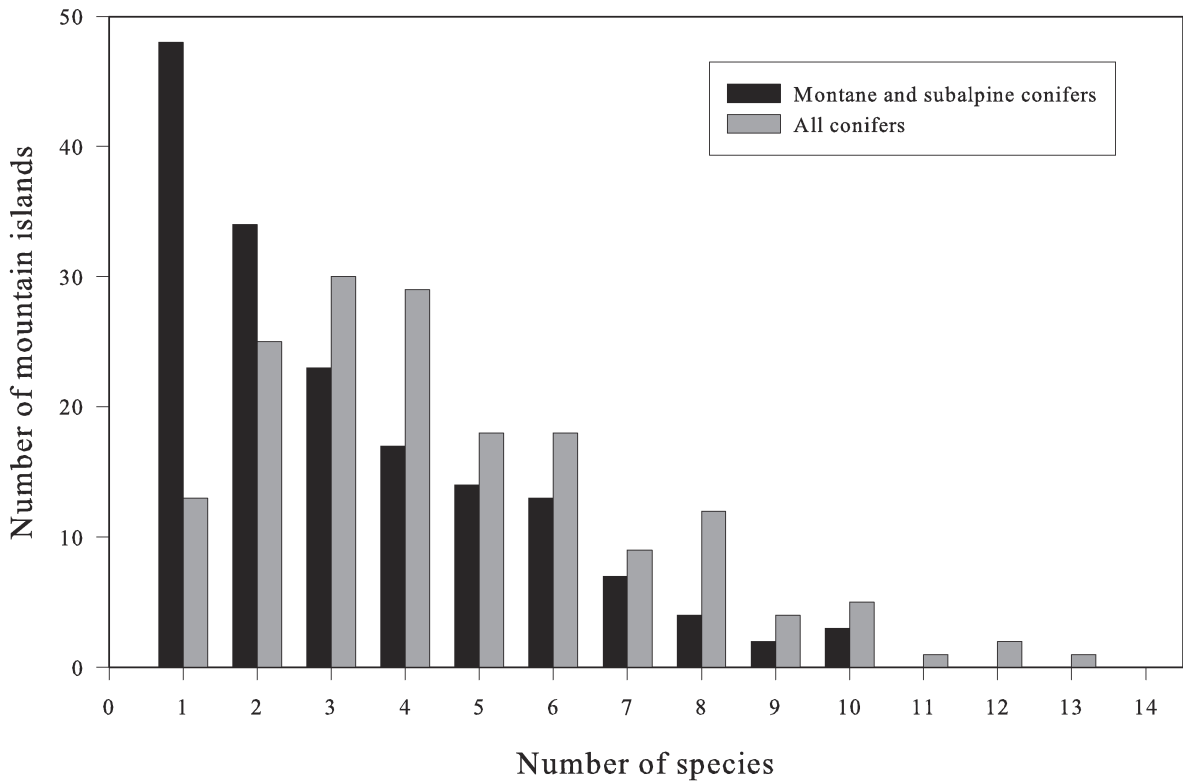
Fig. 3–4. Species richness and distribution of conifers on Great Basin montane islands.—3 (above). Histogram of the number of all conifer taxa ($N = 28$) and all montane and subalpine conifer taxa ($N = 24$) on Great Basin montane islands ($N = 166$). Half of the montane islands have more than 2 montane and subalpine conifer species present.—4 (below). Occurrences of species on Great Basin montane islands. The two species with the widest distributions are the xeric *Juniperus osteosperma* and *Pinus monophylla*. Of the nine most widely distributed species, four are junipers. Xeric conifer bars are outlined in black. Black bars are Rocky Mountain montane species, dark gray bars are Pacific montane species, and light gray bars without black outlines are widespread montane species.

Table 3. Conifer taxa present in the Great Basin, their abbreviation, common name, ecology of the primary vegetation zones in which they are present, and the physiographic areas in the western United States where they are known (TRA = Transverse Ranges, PAC = Pacific Border Province, SN = Sierra Nevada, CAS = Cascade Range, COLU = Columbia Plateau, COLO = Colorado Plateau, SRM = Southern Rocky Mountains, MRM = Middle Rocky Mountains, NRM = Northern Rocky Mountains). Source categories of the taxa based on the regional analysis of Charlet (1995) and separated into eastern (Rocky Mountain System–Colorado Plateau) or western (Pacific Mountain System) mainland areas that directly border the Great Basin and possess the species. Exceptions to Rocky–Colorado and Pacific categories are Great Basin and widespread categories. The Great Basin is considered the mainland source of *Juniperus osteosperma, Pinus longaeva,* and *P. monophylla*, while *Abies grandis, Larix occidentalis,* and *Pinus flexilis*, whose distributions bordering the Great Basin are not along an eastern or western front, are classified as widespread species. ''*'' indicates taxa that occur in the Great Basin, but not on Great Basin montane islands.

| Taxon | Common name | Ecology | Regions present | Source category of taxon |
|---|---|---|---|---|
| **FAMILY PINACEAE** | | | | |
| *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr. var. *concolor* | Rocky Mountain white fir | Montane | SRM, MRM, COLO | Rocky–Colorado |
| var. *lowiana* (Gord. & Glend.) Lemmon | California white fir | Montane | TRA, PAC, SN, CAS, COLU | Pacific |
| *A. grandis* (Dougl. ex D.Don) Lindl. | Grand fir | Montane | PAC, CAS, COLU | Pacific |
| *A. lasiocarpa* (Hook.) Nutt. var. *lasiocarpa* | Subalpine fir | Subalpine | PAC, CAS, COLU, SRM, MRM, NRM | Rocky–Colorado |
| *A. magnifica* A.Murr.* | California red fir | Subalpine | PAC, SN, CAS | Pacific |
| *Larix occidentalis* Nutt.* | Western larch | Subalpine | CAS, NRM | Widespread |
| *Picea engelmannii* Parry ex Engelm. | Engelmann spruce | Subalpine | PAC, CAS, COLU, COLO, SRM, MRM, NRM | Rocky–Colorado |
| *P. pungens* Engelm. | Colorado blue spruce | Subalpine | MRM, SRM, COLO | Rocky–Colorado |
| *Pinus albicaulis* Engelm. | Whitebark pine | Subalpine | PAC, SN, CAS, COLU, MRM, NRM | Pacific |
| *P. balfouriana* Grev. & Balf. subsp. *austrina* R.J. & J.D.Mastroguiseppe* | Foxtail pine | Subalpine | PAC, SN | Pacific |
| *P. contorta* Dougl. ex Loud. var. *contorta* | Rocky Mountain lodgepole pine | Subalpine | CAS, COLU, SRM, MRM, NRM | Rocky–Colorado |
| var. *murrayana* (Grev. & Balf.) Engelm. | Sierra lodgepole pine | Subalpine | PAC, TRA, SN, CAS, COLU | Pacific |
| *P. coulteri* D.Don* | Coulter pine | Xeric | PAC, TRA | Pacific |
| *P. edulis* Engelm. | Colorado pinyon pine | Xeric | COLO, SRM, MRM | Rocky–Colorado |
| *P. flexilis* James | Limber pine | Subalpine | TRA, SN, COLU, COLO, SRM, MRM, NRM | Widespread |
| *P. jeffreyi* Grev. & Balf. | Jeffrey pine | Montane | TRA, PAC, SN, CAS | Pacific |
| *P. lambertiana* Dougl. | Sugar pine | Montane | TRA, PAC, SN, CAS, COLU | Pacific |
| *P. longaeva* D.K.Bailey | Great Basin bristlecone pine | Subalpine | COLO | Great Basin |
| *P. monophylla* Torr. & Frémont | Singleleaf pinyon pine | Xeric | TRA, SN, COLO | Great Basin |
| *P. monticola* Dougl. ex D.Don | Western white pine | Montane | PAC, SN, CAS, COLU, NRM | Pacific |
| *P. ponderosa* P. & C.Lawson var. *ponderosa* | Pacific ponderosa pine | Montane | TRA, PAC, SN, CAS, COLU | Pacific |
| var. *scopulorum* (Engelm.) E.Murr. | Rocky Mountain ponderosa pine | Montane | COLO, SRM, MRM | Rocky–Colorado |
| *P. sabiniana* Dougl. ex Dougl.* | Gray pine | Xeric | TRA, PAC, SN, CAS | Pacific |
| *P. washoensis* Mason & Stockwell | Washoe pine | Subalpine | SN | Pacific |
| *Pseudotsuga macrocarpa* (Vasey) Mayr* | Bigcone Douglas fir | Montane | TRA | Pacific |
| *P. menziesii* (Mirbel Franco var. *glauca* (Beissn.) Franco | Rocky Mountain Douglas fir | Montane | COLU, COLO, SRM, MRM, NRM | Rocky Mts |
| var. *menziesii* | Pacific Douglas fir | Montane | PAC, SN, CAS, COLU | Pacific |
| *Tsuga mertensiana* (Bong.) Carr. | Mountain hemlock | Subalpine | PAC, SN, CAS, NRM | Pacific |
| **FAMILY CUPRESSACEAE** | | | | |
| *Calocedrus decurrens* (Torr.) Florin | Incense cedar | Montane | TRA, PAC, SN, CAS | Pacific |
| *Juniperus californica* Carr. | California juniper | Xeric | TRA, PAC, SN, COLO | Pacific |
| *J. communis* L. | Common juniper | Subalpine | PAC, SN, CAS, COLU, COLO, SRM, MRM, NRM | Widespread |
| *J. occidentalis* Hook. var. *australis* (Vasek) A. & N.Holmgren | Sierra juniper | Subalpine | TRA, PAC, SN | Pacific |
| var. *occidentalis* | Western juniper | Montane | PAC, CAS, COLU | Pacific |
| *J. osteosperma* (Torr.) Little | Utah juniper | Xeric | TRA, SN, COLO, SRM, MRM, NRM | Great Basin |
| *J. scopulorum* Sarg. | Rocky Mountain juniper | Montane | PAC, CAS, COLU, COLO, SRM, MRM, NRM | Rocky–Colorado |

Table 4. Summary results of conifer species richness, area, and distance to mainland source pools for montane island and mainland sites in the Great Basin. The first data column identifies the set of samples used in the analysis. The other columns present mean numbers of conifer species (columns 3–7), montane surface area (km²; column 8), or distances (km; columns 9–11). MAIN = mainland, PAC = species also in Pacific Mountain System, RM = species also in Rocky Mountains, WS = widespread species.

| 1 Sample set | 2 Number of samples ($n$) | 3 Conifer species | 4 Montane conifer species | 5 RM montane conifer species | 6 PAC montane conifer species | 7 WS montane species | 8 Montane area | 9 Distance to MAIN | 10 Distance to RM | 11 Distance to PAC |
|---|---|---|---|---|---|---|---|---|---|---|
| All sites | 206 | 5.6 | 4.2 | 1.6 | 1.8 | 0.8 | 340 | 60 | 249 | 275 |
| Mainland | 40 | 10.0 | 8.5 | 2.8 | 4.6 | 1.3 | 1006 | 0 | 8 | 1 |
| Pacific | 20 | 10.5 | 9.1 | 0.0 | 8.5 | 0.6 | 598 | 0 | 469 | 15 |
| Rockies | 16 | 10.4 | 8.4 | 6.3 | 0.0 | 2.1 | 1526 | 0 | 0 | 604 |
| Blue Mts | 4 | 5.8 | 5.8 | 2.3 | 3.3 | 1.0 | 966 | 0 | 124 | 208 |
| Islands | 166 | 4.5 | 3.2 | 1.3 | 1.1 | 0.8 | 180 | 119 | 249 | 276 |
| Far | 83 | 4.3 | 3.0 | 1.3 | 0.7 | 1.0 | 166 | 183 | 234 | 302 |
| Near | 83 | 4.8 | 3.4 | 1.3 | 1.6 | 0.5 | 194 | 55 | 264 | 250 |
| Large | 83 | 5.8 | 4.5 | 1.9 | 1.3 | 1.2 | 338 | 123 | 213 | 337 |
| Small | 83 | 3.3 | 1.9 | 0.7 | 1.0 | 0.3 | 22 | 115 | 285 | 219 |
| Near–large | 37 | 6.4 | 5.0 | 2.2 | 2.0 | 0.8 | 411 | 49 | 206 | 337 |
| Near–small | 46 | 3.5 | 2.2 | 0.7 | 1.3 | 0.2 | 19 | 60 | 312 | 180 |
| Far–large | 46 | 5.4 | 4.1 | 1.7 | 0.8 | 1.5 | 279 | 183 | 219 | 331 |
| Far–small | 37 | 3.0 | 1.6 | 0.7 | 0.5 | 0.4 | 25 | 183 | 253 | 267 |
| West | 83 | 3.6 | 2.6 | 0.1 | 2.0 | 0.4 | 164 | 101 | 358 | 122 |
| East | 83 | 5.5 | 3.8 | 2.5 | 0.2 | 1.1 | 195 | 137 | 140 | 430 |

compared to mountain island sites. However, the slopes are much steeper than predicted for mainlands. The species–area slopes of each mainland area (Rocky Mountains–Colorado Plateau, Pacific, and Blue Mountains) are similar ($z$ = 0.286, 0.304, and 0.296, respectively), and steeper than the slope of all islands ($z$ = 0.253). Moreover, each of the mainlands' slopes are steeper than seven of the nine significant ($P < 0.0001$)

species–area slopes found for all island combinations, with only large islands and far-large islands having steeper slopes (Table 5). When the mainland sites are pooled into a mainland species–area plot (Fig. 6), the slope is somewhat lower ($z$ = 0.221, $N$ = 40) than the slope of all islands.

When all island and mainland sites are pooled into a single data set and regressed ($N$ = 206), the slope

Table 5. Summary of regression results for conifer species richness in the Great Basin. The first column (sample set) identifies sample types used in the regression. A complete summary for log–log species–area regressions is presented in columns 2–7. Columns 8–11 report the adjusted (adj.) $R^2$ value of the regression for that sample of species against montane relief (column 8), and three distance measures (columns 9–11). MAIN = Mainland, PAC = Pacific Mountain System, RM = Rocky Mountains; C = Constant, P = Probability, "*" indicates significance at the 0.95 level.

| 1 Sample set | 2 Sample number ($n$) | 3 Formula | 4 $C$ | 5 Slope | 6 $P$ | 7 adj. $R^2$ | 8 adj. $R^2$ of species–montane relief | 9 adj. $R^2$ of RM species–RM distance | 10 adj. $R^2$ of PAC species–PAC distance | 11 adj. $R^2$ of species–distance to MAIN |
|---|---|---|---|---|---|---|---|---|---|---|
| All sites | 206 | $y = 0.304x - 0.095$ | 0.80 | 0.304* | 0.001 | 0.54* | 0.65* | 0.57* | 0.36* | 0.21* |
| Mainland | 40 | $y = 0.221x + 0.274$ | 1.88 | 0.221* | 0.001 | 0.29* | 0.40* | — | — | — |
| Pacific | 20 | $y = 0.304x + 0.125$ | 1.33 | 0.304* | 0.001 | 0.45* | 0.28* | — | — | — |
| Rockies | 16 | $y = 0.286x + 0.028$ | 0.80 | 0.286* | 0.001 | 0.43* | 0.40* | — | — | — |
| Blue Mts | 4 | $y = 0.296x - 0.110$ | 1.07 | 0.296 | 0.25 | 0.33 | 0.97* | — | — | — |
| Islands | 166 | $y = 0.253x - 0.04$ | 0.78 | 0.253* | 0.001 | 0.39* | 0.53* | 0.48* | 0.31* | 0.02* |
| Far | 83 | $y = 0.268x - 0.111$ | 0.92 | 0.268* | 0.001 | 0.38* | 0.59* | 0.31* | 0.12* | −0.01 |
| Near | 83 | $y = 0.251x + 0.012$ | 1.32 | 0.251* | 0.001 | 0.45* | 0.55* | 0.60* | 0.36* | 0.09* |
| Large | 83 | $y = 0.303x - 0.123$ | 1.05 | 0.303* | 0.001 | 0.20* | 0.44* | 0.47* | 0.50* | 0.04* |
| Small | 83 | $y = 0.074x + 0.125$ | 0.70 | 0.074 | 0.15 | 0.03 | 0.11* | 0.521* | 0.25* | 0.06* |
| Near–large | 37 | $y = 0.247x - 0.051$ | 1.33 | 0.247* | 0.001 | 0.20* | 0.49* | 0.61* | 0.68* | 0.03 |
| Near–small | 46 | $y = 0.132x + 0.111$ | 0.91 | 0.132* | 0.001 | 0.05* | 0.11* | 0.62* | 0.22* | 0.12* |
| Far–large | 46 | $y = 0.336x + 0.230$ | 1.28 | 0.336* | 0.001 | 0.17* | 0.46* | 0.29* | 0.15* | −0.02 |
| Far–small | 37 | $y = 0.034x + 0.116$ | 1.56 | 0.034 | 0.632 | −0.02 | 0.16* | 0.29* | 0.18* | −0.02 |
| West | 83 | $y = 0.223x - 0.056$ | 1.35 | 0.223* | 0.001 | 0.33* | 0.41* | 0.22* | 0.19* | 0.14* |
| East | 83 | $y = 0.245x + 0.042$ | 0.87 | 0.245* | 0.001 | 0.39* | 0.58* | 0.20* | 0.04* | −0.01* |
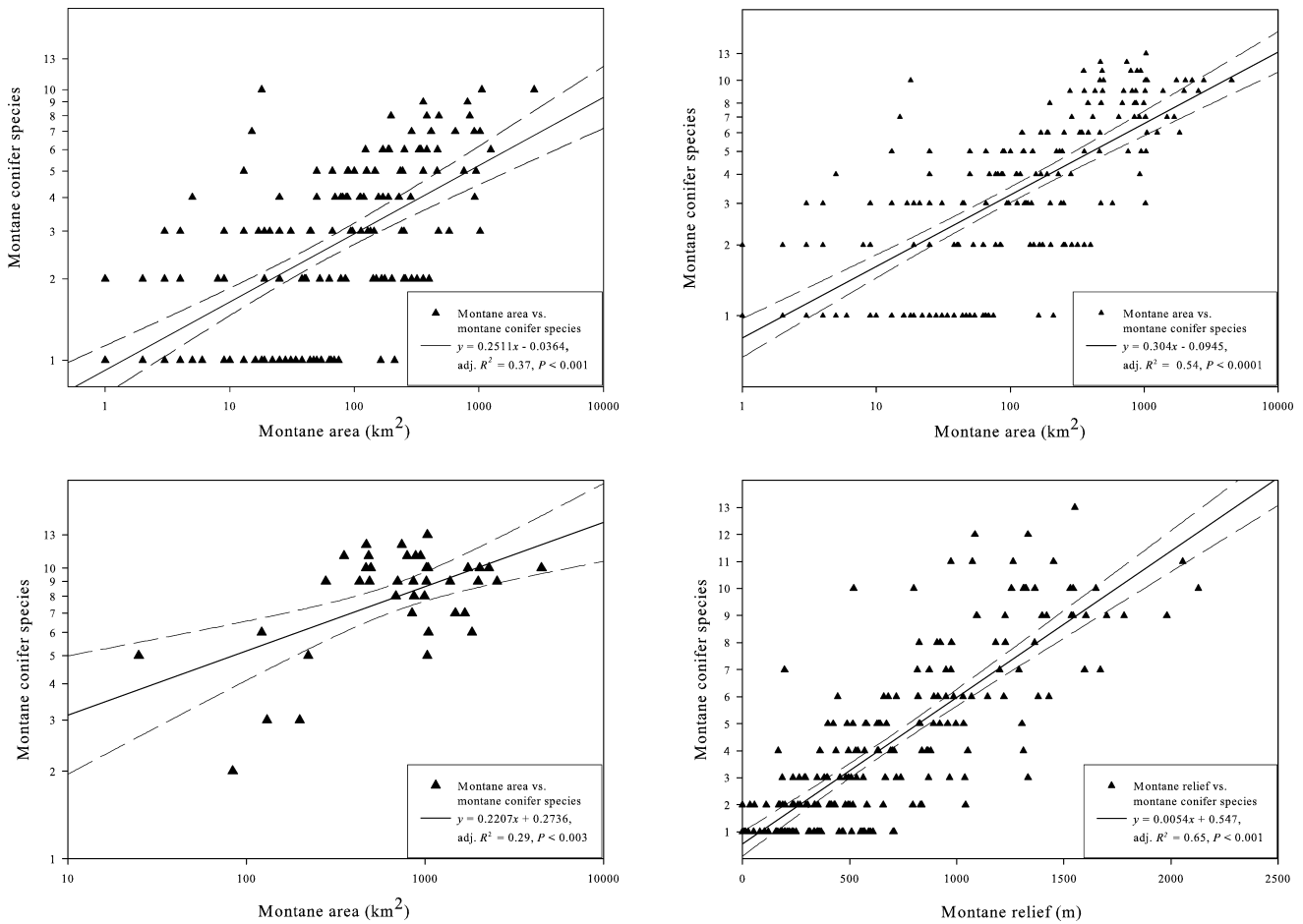
Fig. 5–8. Effect of island area and relief on the number of montane conifer species. Confidence interval (0.95) curves are plotted around the least-squares best-fit line (solid) of the log–log regression.—5 (upper left). Montane and subalpine conifer richness (total pool = 28 taxa) regression on area of all Great Basin montane islands ($N = 166$). Note the relatively steep slope, suggestive of insular islands-in-equilibrium.—6 (lower left). Montane and subalpine conifer richness (total pool = 28 taxa) regressions on area of all mainland sites on the boundary of the Great Basin ($N = 40$). Note the slope ($z = 0.2207$), steeper than expected for a mainland ($z = 0.12–0.17$). Instead, the slope is indicative of islands with relatively good access to mainlands.—7 (upper right). Montane and subalpine conifer richness (total pool = 28 taxa) regressions on area for all sites ($N = 206$). Note the steep slope ($z = 0.304$), indicative of an extinction pattern of isolated islands.—8 (lower right). Montane conifer species ($N = 24$) regressed on montane relief for all sites in the Great Basin ($N = 206$). Of all the physical variables measured, montane relief had the strongest relationship with species number.

increases ($z = 0.304$) as does the explanatory power of the variable. The $R^2$ of the log–log regression indicates that 54% of the variation in species number across sites is explained by area alone ($R^2 = 0.54$, $N = 206$, $P < 0.0001$; Fig. 7, Table 5).

Although area explains more than half of the variation in species number across sites in the region, montane relief ($RELIEF_{MON}$) is more closely related in every case (Fig. 8), with all 12 species–area regressions having a significant ($P < 0.01$) relationship between $RELIEF_{MON}$ and species number, and an $R^2$ value of 0.65 in the entire data set ($N = 206$).

*Distance effect.*—The minimum distance of a Great Basin island to a mainland ($DIS_{MAIN}$) showed a significant relationship to conifer species richness in seven of eleven (7/11) log–log regressions (distance to mainland regressions were not run for mainlands). The non-significant $DIS_{MAIN}$ regressions were for far, near-large, far-large, and far-small islands (Table 5). However, the explanatory power of the relationships was far less than that found for area, as adjusted $R^2$ values ranged from 0.02 (all islands, $N = 166$) to 0.14 (west islands, $N = 83$) in the significant regressions of $DIV_{MON}$ as a response to $DIS_{MAIN}$.

When species are separated into either Pacific ($PAC_{DIV}$) or Rocky Mountain–Colorado Plateau ($RM_{DIV}$) source pool classes and the richness of these pools are used, distance to the specific mainland is negatively correlated with species richness. That is, the closer to the specific mainland, the more species the mountain island possessed also in that source pool. When the island types are examined separately with regression, all of the combinations are significant, with adjusted $R^2$ values ranging from 0.12 ($PAC_{DIV}$ vs. $DIS_{PAC}$ on far
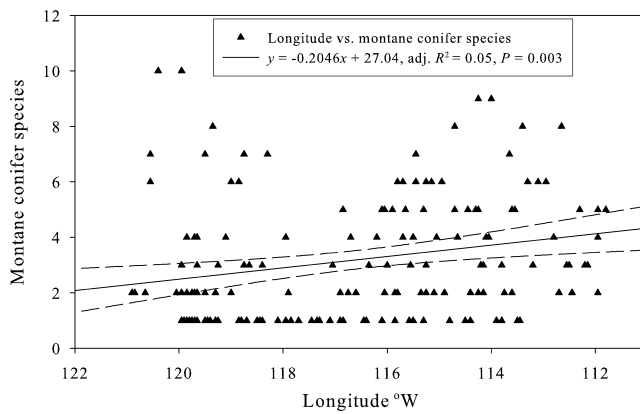
Fig. 9. Montane and subalpine conifer richness (total pool = 28 taxa) regressions on longitude of montane islands ($N = 166$). Confidence interval (0.95) curves bound the least-squares best-fit line (solid) of the regression. Note the asymmetrical, bimodal distribution with maximum richness of 4 taxa per sample at about 117°W, and maxima at 10 taxa per sample at both 120°W and 113°W.

islands) to 0.68 ($PAC_{DIV}$ species vs. $DIS_{PAC}$ on near-large islands), values comparable to those found in the log–log species–area regressions (Table 5). However, the distance effect is weakened because there was no significant distance relationship that related to the number of widespread species ($DIV_{WS}$) a mountain island possessed ($P = 0.47$ for $DIV_{WS}$ vs. $DIS_{MAIN}$).

*Latitude and longitude effects.*— Latitude did not have a significant relationship to the number of montane conifer species on Great Basin islands (adj. $R^2 = 0.006$, $P = 0.31$). Longitude is significantly related to $DIV_{MON}$, but explains only 5% of the variation of species richness on mountain islands (adj. $R^2 = 0.05$, $P = 0.003$; Fig. 9). However, when $DIV_{PAC}$ (adj. $R^2 = 0.37$, $P < 0.0001$; Fig. 10) or $DIV_{RM}$ (adj. $R^2 = 0.56$, $P < 0.0001$; Fig. 11) are considered separately, the relationship of longitude to species richness is strong.

*Multiple regressions.*—The best predictive model obtained for montane species richness on Great Basin islands was distance to mainland and montane relief ($DIS_{MAIN}$ and $RELIEF_{MON}$) regressed on montane conifer diversity (adj. $R^2 = 0.715$, $P < 0.0001$, $N = 206$). A multiple regression model of the island biogeography terms *MAIN, NEAR,* and *LARGE* (as dummy variables, values of 1 or 0) showed a strong linear relationship of these variables as predictors of montane species richness (adj. $R^2 = 0.591$, $P < 0.001$, $N = 206$). The addition of the dummy variable *EAST* did not improve the model.

A multiple regression model of all distance measures ($DIS_{MAIN}$, $DIS_{RM}$, $DIS_{COLO}$, $DIS_{BLUE}$, $DIS_{PAC}$, and $DIS_{NRM}$) for all sites in the region as predictors of montane conifer species number yielded an adjusted $R^2$ value of 0.32 ($P < 0.001$, $N = 206$). A multiple regression model using the physical measures of latitude
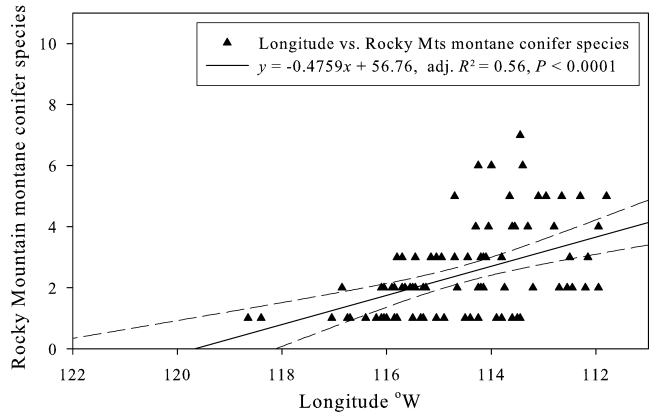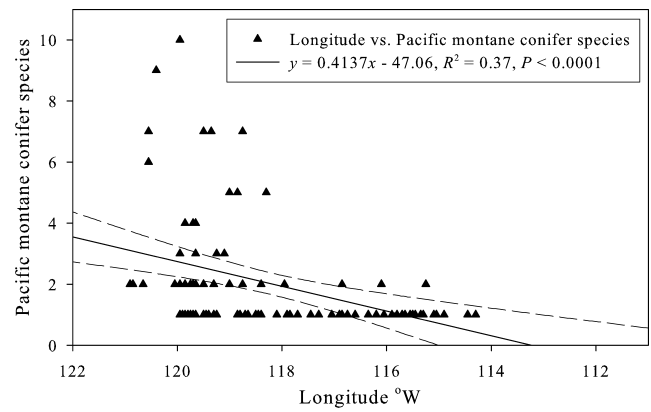




Fig. 10–11. Regressions on island longitude as for Fig. 9, but with conifer species subdivided by region of origin. Confidence interval (0.95) curves bound the least-squares best-fit line (solid) of the regression.—10 (above). Pacific montane and subalpine conifer species richness (12 taxa). Pacific species are found as far east as 114°W. Note the stronger linear relationship than that found for the complete species pool.—11 (below). Rocky Mountain–Colorado Plateau montane and subalpine conifer richness (8 taxa). Rocky Mountain species extend west to slightly more than 118°W. Note the much stronger linear relationship than that found for the complete species pool.

(mean only), longitude (mean only), elevation, distance, and montane relief (13 variables) explained 76% of the variation in montane conifer species number (adj. $R^2 = 0.76$, $P < 0.0001$, $N = 206$).

*Comparison of effects on species richness.*—When the adjusted $R^2$ values of species–area regressions on mountain islands and species-distance from mainland on montane island categories are compared, measures of distance are significant in 64% (7/11) of the categories, while 82% (9/11) of island categories were significant in the species–area regressions. However, in all cases the $R^2$ values are much lower for distance compared to area. Only when separated into species pools and mainland sources are the $R^2$ values comparable, but no distance measure accounts for the widespread species group (Table 5).

The distance effect is weaker than the area effect.

This fact is verified by examining the predicted versus the observed order of species richness by island type (Fig. 12). The descending order of species richness by island type predicted by the M-W equilibrium model is near-large, near-small, far-large, and far-small, with near-small and far-large nearly the same. For conifers on Great Basin montane islands, the observed rank order is: near-large (5.0 species/island), far-large (4.1 species/island), near-small (2.2 species/island), and far-small (1.6 species/island). Large island, not near island, combinations rank first and second. The main discontinuity exists between large and small islands, with far–large islands possessing nearly twice as many species as near-small islands. The stronger relationship of area to species number than distance to species number can be visualized by displaying the numbers of species on small and large islands together and those of far and near islands together (Fig. 13–14). Both distance and area have an effect, but the distance effect is much less than the area effect ($D < A$).

### Refutation of the Hypotheses

The mainland and island species–area regression slopes are not reproduced by randomized permutations ($P < 0.05$), regardless of whether only the richness totals are replaced or the whole matrix of occurrences is randomized. The conifers in the Great Basin are nonrandomly distributed, and on this basis, the random placement hypothesis is refuted.

Island slopes are expected to be shallow (i.e., $<$ 0.250) in the M-W immigration hypothesis, reflecting high immigration rates to near islands from mainlands, thereby forcing the left side of the plot upward. Slopes are predicted to be steeper ($z > 0.262$) in the M-W extinction hypothesis, reflecting the stronger effect that area has in controlling the extinction rate. Instead, island slopes are at a nearly equilibrium pitch ($z = 0.253$), with near-large islands ($z = 0.247$) the only island type on the immigration side of equilibrium. On this test, both the M-W extinction and M-W immigration hypotheses fail, and the M-W equilibrium hypothesis still stands.

However, the distance effect is dwarfed by the area effect in the rank order of island types by number of conifer montane species (Fig. 12–14). Further, all distance measures combined into a multiple regression model explained only 32% (adj. $R^2 = 0.32$) of the variation in species number on islands. Distance thus performs poorly when compared with area as montane area alone explains 54% ($R^2 = 0.54$) of this variation. In this test, the M-W extinction hypothesis correctly predicts the pattern while both the M-W immigration and M-W equilibrium overestimate the effect of distance on the number of montane conifer species on

Great Basin montane islands, as the distance effect is less than the area effect ($D < A$).

All mainland species–area regression slopes are much steeper than the range predicted by any of the M-W models. This is the case whether considered separately ($z$ ranging from 0.286 to 0.304) or combined ($z = 0.221$; Table 5), and are outside the predicted range of mainland $z$ (0.12–0.17). All M-W models fail in this test.

In summary, the random placement hypothesis made 1/2 correct predictions while M-W immigration made 1/4, the M-W extinction 2/4, and the M-W equilibrium model made 2/4 correct predictions (Table 6), and so all the hypotheses are refuted.

### DISCUSSION

The distribution of montane and subalpine conifers in the Great Basin remains enigmatic. The random placement hypothesis and all of the M-W models were refuted. This may mean that island biogeography theory applied to Great Basin conifers is inappropriate. However, I contend that it informs us about the dynamics of these conifer distributions, and challenges us to reexamine our assumptions.

### Effects on Conifer Species Richness in the Great Basin

*Area effect.*—Species–area slopes for all islands ($z = 0.253$, $N = 166$; Table 5, Fig. 5–7) fit the islands-in-equilibrium pattern. These results are far from those that Wells (1983) observed ($z = 0.212$, $N = 54$). The species–area slopes I report here suggest that Great Basin montane islands are currently on the extinction side of equilibrium.

Often the value of $C$ is not reported in island biogeography analyses (Gould 1979). Interpretation of $C$ is difficult because in the original form of the equation (equation 1), $C$ modifies the slope of the curve, but when the transformed equation (equation 2) is used to perform log–log linear regression, $C$ is the intercept of the regression line with the $Y$-axis at $X = 1$ (Gould 1979; Rosenzweig 1995). Virtually all $C$-values observed here are near 1. This means that these regressions predict that when a square km of montane area is selected from the region at random, a single montane or subalpine conifer species will be found in that square km. This seems to be a reasonable prediction for Great Basin montane islands.

*Distance effect.*—The results imply that immigration from mainlands is not the primary factor governing the presence of montane conifers on Great Basin islands. The distance effect is significant, but weak for all islands and island type combinations, and fades to insignificant in far, near–large, and far–small islands.
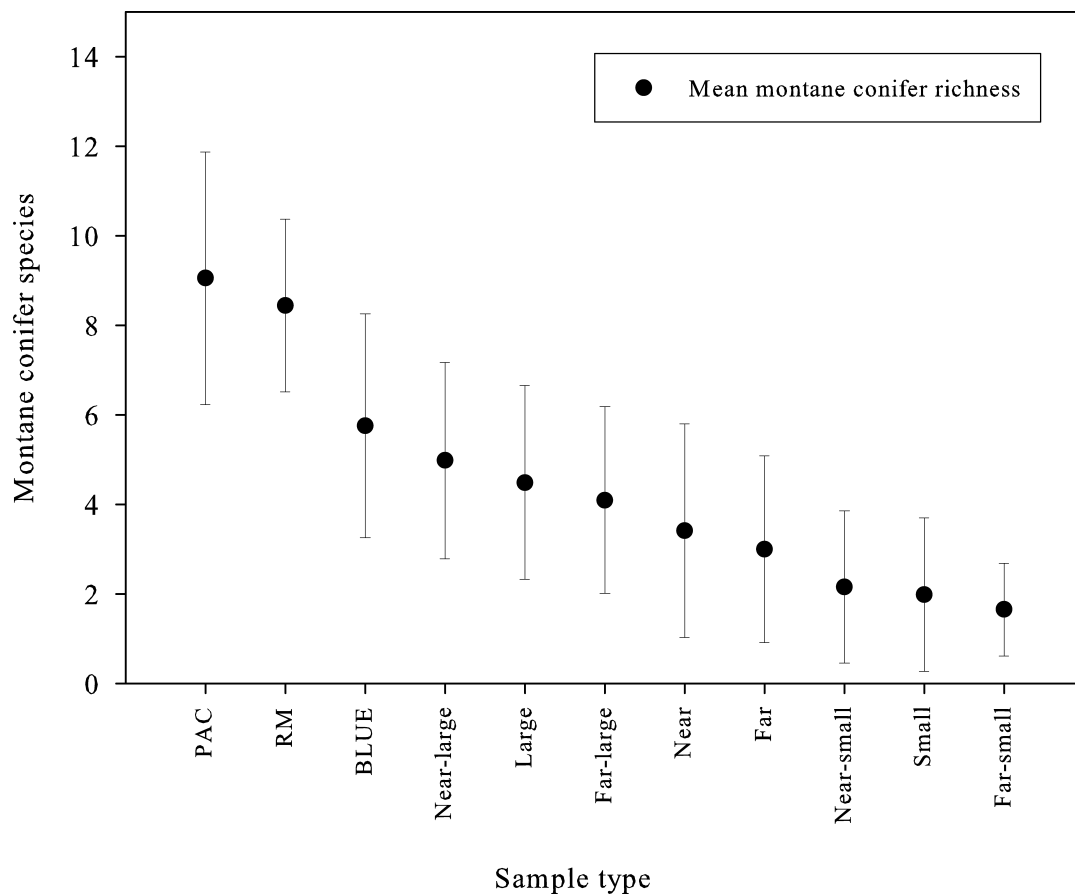
Fig. 12. Montane conifer richness by sample type. Sample types arranged from left to right by descending order of mean montane conifer species number. Vertical bars represent the standard deviation about the mean. PAC = Pacific Mountain System samples, RM = Rocky Mountain samples, BLUE = Blue Mountains mainland of the Columbia Plateau. Remaining sample types are island categories according to size (large-small) and distance (near-far). All mainlands reside on the high richness side of the figure, while island categories are ordered consistently with an extinction-driven island biogeography model.

The distance effect is overwhelmed by the area effect; clearly a sign of an extinction-driven pattern.

Examination of the relationship between longitude and species richness allows a view of the relative contributions of the eastern and western source pools of the Great Basin. Longitude explains little about how many species are on a mountain, but does explain what set of species is most likely to be there. Longitude is the single most important variable associated with species turnover in the region. A key to understanding the effect of longitude in the Great Basin is to examine source pools separately. Longitude is strongly associated with both Pacific and Rocky Mountain–Colorado Plateau montane conifer species richness on Great Basin islands, and so reflects the effects of distance to both the Pacific and Rocky Mountain–Colorado Plateau mainlands. As longitude decreases, islands have more species that are also in the Rocky Mountains (Fig. 11) and fewer species shared with Pacific mountains (Fig. 10). As longitude increases, the number of Pacific species on islands increases while species also in the Rocky Mountains are less likely to be found

(Fig. 10, 11). These patterns are asymmetric because Rocky Mountain taxa extend deeper into the Great Basin than Pacific taxa, but a greater number of Pacific taxa occur on Great Basin islands than Rocky Mountain taxa. When these two distance effect patterns are overlaid, the two patterns are hidden within the bimodal distribution in the plot of species richness on islands versus longitude (Fig. 9).

Wells (1983) examined mainly the eastern component of the Great Basin conifer flora (38/54 mountain islands occurring east of 116°W) and concluded that longitude was negatively associated with species richness, reflecting the domination of the region by Rocky Mountain conifers. However, the region is not simply dominated by Rocky Mountain conifers. Now it is clear that a countercurrent of affinities exists between both the Pacific and Rocky Mountains and the Great Basin. Wells (1983) followed 11 montane conifer species on 54 islands, but there are 24 species dispersed across at least 166 islands. Twelve of these species reaching islands also occur in the Pacific Mountains but not the Rockies, 8 occur in the Rockies but not
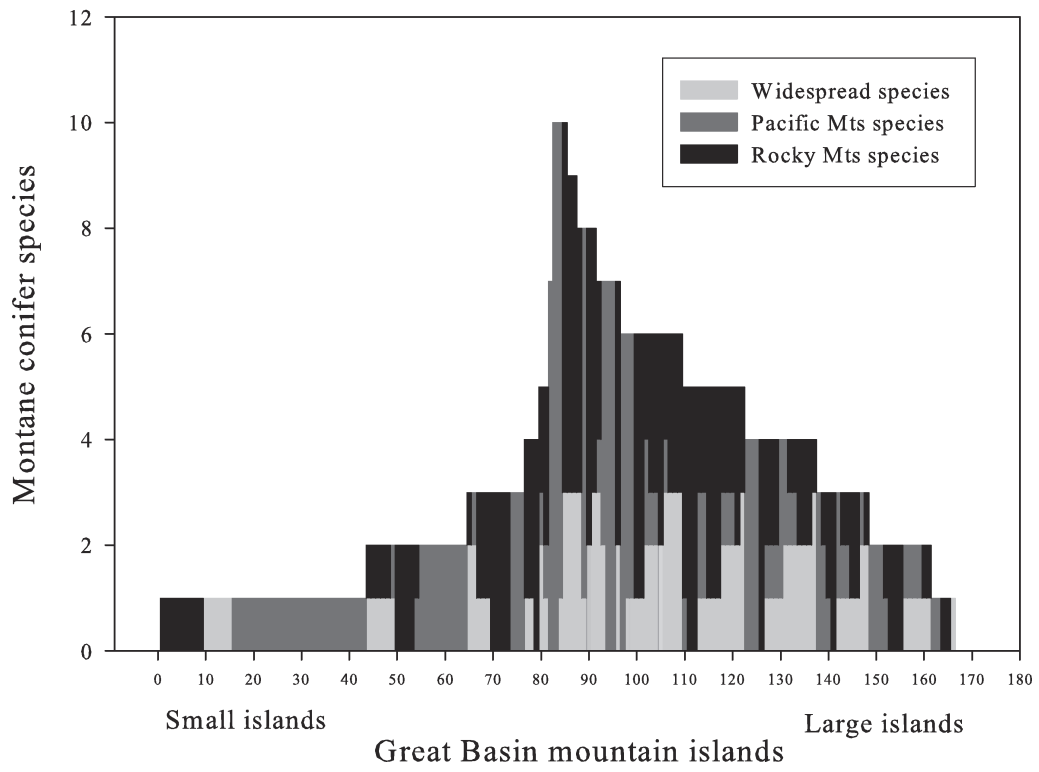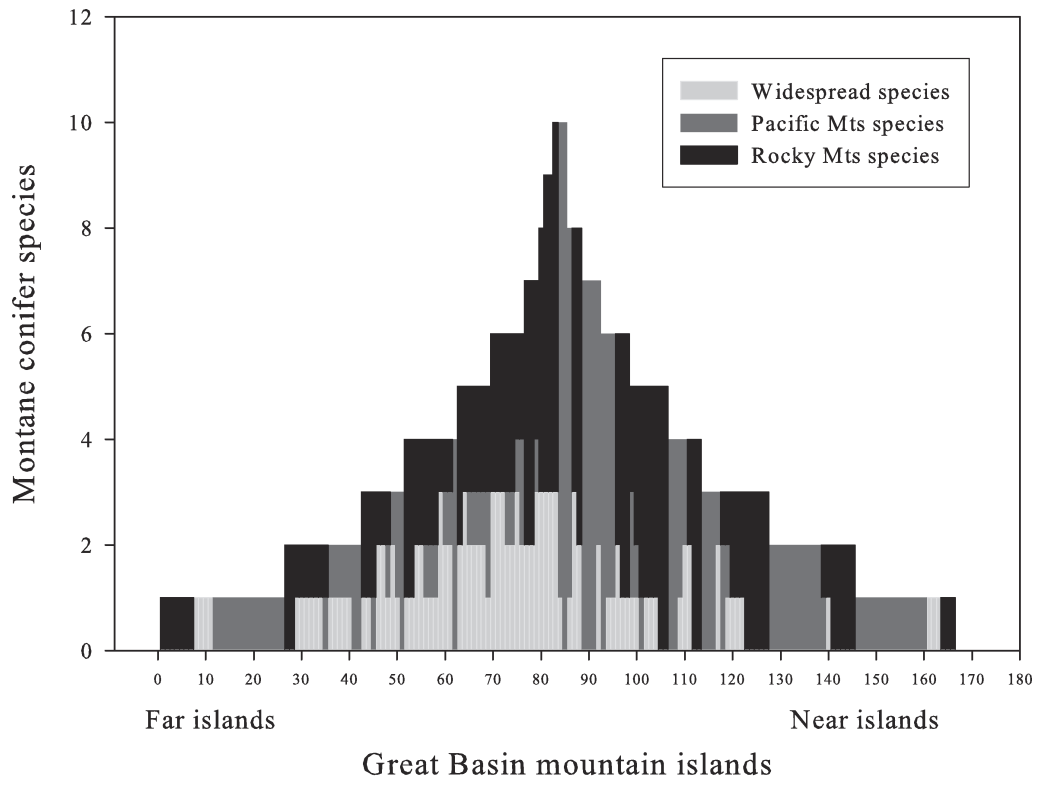
Table 6. Summary of results and conclusions concerning the predicted and detected effects of distance, area, and habitat diversity on conifer species richness of Great Basin mountains and number of occurrences of species for hypotheses considered. "*" indicates a successful prediction of the hypothesis.

| Effect | Random placement hypothesis predictions | M-W immigration hypothesis predictions | M-W extinction hypothesis predictions | M-W equilibrium hypothesis predictions | Results |
|---|---|---|---|---|---|
| Area effect on species–area slopes | Nonrandom | Nonrandom* | Nonrandom* | Nonrandom* | Species–area slopes are nonrandom |
| Mainland slope ($z$) | n/a | 0.15 | 0.15 | 0.15 | Separate: $z = 0.286$–$0.304$ Combined: $z = 0.221$ |
| Island slope ($z$) | n/a | $<0.250$ | $>0.262$ | $0.250*$ | $z = 0.253$ |
| Distance effect vs. area effect | $D < A*$ | $D > A$ | $D < A*$ | $D = A$ | $D < A$ Distance effect weaker than area effect |
| Conclusion | 1/2 successful predictions: Refuted | 1/4 successful predictions: Refuted | 2/4 successful predictions: Refuted | 2/4 successful predictions: Refuted | Extinction model performs best, but tending toward equilibrium |

the Pacific Mountains, and 4 additional widespread montane species are not associated with distance whatsoever. These results contradict Well's (1983) idea of an overwhelming domination of the Great Basin conifer flora by the Rocky Mountains.

### Ecological Controls on Conifer Distributions

Most workers interpreted the apparent absence of Pacific taxa in the Great Basin as an ecophysiological phenomenon, due primarily to inadequate summer precipitation in the western Great Basin (Harper et al. 1978; Reveal 1979; Wells 1983; Axelrod and Raven 1985). Unfortunately, upland precipitation data, especially seasonal precipitation data in the western Great Basin, are lacking. A short record at montane elevations exists that allows comparison between western and eastern ranges at the same latitude. Here, there was no difference in total or seasonal distribution of precipitation between stations over 2150 m in the Warner Mountains (41°N 120.4°W) and the Jarbidge Mountains (41°N 115.3°W; Charlet 1991).

If Sierran taxa have adaptations for summer drought that distinguish them from Rocky Mountain taxa (Axelrod 1976; Axelrod and Raven 1985), this should provide the Sierran taxa with an advantage in the colonization of Great Basin mountains. Such drought adaptations are advantageous, even in climate regimes that have summer rain. These adaptations should promote the competitive ability of Sierran taxa on the western and central montane islands free of Rocky

Mountain conifers and dominated by aggressive Great Basin shrubs and grasses. Alternatively, Lahontan and other western basins may have been important areas for the selection of summer-drought adaptations during the glaciopluvials and their intervening periods. The mountains of these basins may have been staging areas for conifer populations to return to the eastern Sierra Nevada during the interglaciopluvials.

Of the 15 Pacific montane taxa that occur on the lee slopes of the Sierra-Cascade axis, 12 occur on Great Basin montane islands, while eight Rocky Mountain taxa also occur on Great Basin islands. Pacific montane conifers occur on 93/166 (56%) of the Great Basin montane islands, while 88/166 (53%) of the islands possess at least one Rocky Mountain-Colorado Plateau montane conifer species (Fig. 4). This implies that Pacific montane conifers are tolerant of environments in the western Great Basin.

Although western Great Basin islands are not as species-poor as once thought, why do Pacific taxa not range as deeply in the Great Basin as Rocky Mountain taxa? Wells (1983) suggested that a lack of stepping stones in the West contributed to the poor representation of Pacific taxa in the Great Basin. However, there are at least two highland stepping stone routes available for dispersal of conifers into the Great Basin from the west (Fig. 2; cf. Wells 1983: Fig. 5b). The first route is from the Walker River Basin through the archipelago of the Sweetwater, Bodie, Pine Grove, Wassuk, and Excelsior Mountains across the Lahontan

←

Fig. 13–14. Montane conifer species richness by island type in the Great Basin, with richness divided into number of species (y-axis) affiliated with one of three regional categories, Rocky Mountain, Pacific, or Widespread. The x-axis represents all 166 islands, each individually depicted by a single needle-thin richness column, within which different regional categories are illustrated by different shades of gray and black.—13 (upper graph). Far islands (left of center, arranged with fewest species on left and most species on right) and near islands (right, arranged with most species on left and fewest on right) are almost perfectly symmetrical, indicating the small effect of distance on determining species numbers on islands.—14 (lower graph). Small islands (left of center, arranged with fewest species on left and most on right) and large islands (right, arranged with most species on left and fewest on right) are asymmetrical, with small islands impoverished compared to large islands, revealing the strong association between area and species numbers on islands.

Trough to the Paradise Range and thence to the central Great Basin ranges (Bell and Johnson 1980; Lavin 1981). The second route is north of the Lahontan Basin along the Great Basin–Columbia Basin hydrographic divide (Charlet 1991). These potential stepping-stone routes have lower elevations and wider gaps than the two routes in the east proposed for the central Great Basin by Wells (1983). Zonal depression during glaciopluvials could have made these western routes (particularly along the Columbia Plateau divide) highly suitable for range-expansion of subalpine conifers. However, during interglaciopluvials, dispersal along these routes is unlikely, and extinction is likely because the generally low relief of these mountain ranges prevents upslope range-contractions.

Comparison of the physical data of the sample sites east and west of 116°W is informative. Although the number of islands on both sides of Wells' Line is the same (83), there are many more large islands east of the line (52) than west of the line (32). Further, western islands contain nearly 20% less montane area than eastern islands (Table 4). Rocky Mountain and Pacific taxa only rarely occur on the same mountain range and thus rarely, if ever, compete. Even when related Pacific and Rocky Mountain taxa are on the same mountain, the taxa are usually segregated. For example, *Juniperus occidentalis* and *J. scopulorum* in the Bull Run Mountains, and *Pinus ponderosa* var. *ponderosa* and var. *scopulorum* in three central Great Basin mountain ranges (Charlet 1996).

*The Problem of Mainland Slopes*

All M-W models predicted values of mainland slopes ($z = 0.12–0.17$) well below the observed slopes ($z = 0.286–0.304$; Table 6). Does this indicate a flaw with island biogeography theory as applied to Great Basin montane islands? Possibly, but there is a more likely explanation: a ''mainland source'' for the islands was not sampled. When species–area data from two biogeographic provinces are combined in a single plot, the resultant slope increases dramatically (Rosenzweig 1995). For instance, Rosenzweig never found an interprovincial species–area slope with $z < 0.610$ (Rosenzweig 1995). However, in this data set, when all mainland samples are combined into a single species–area plot, the slope decreases ($z = 0.221$), and well below that predicted by Rosenzweig (1995). Moreover, the slope is well above the range expected for a single mainland curve ($z = 0.12–0.17$), looking instead more like a set of large islands, well connected to a mainland. When mainland samples are included with island samples, $z$-values still exhibit an insular slope well within the range observed for individual island sets ($z = 0.304$). These results suggest that sampling has occurred within one biogeographic province and that the

mainland has not been sampled, or it does not exist at this time. Wells (1983) obtained a flat slope ($z = 0.04$) for the Rocky Mountain–Colorado Plateau mainland, but used only 5 samples with very large areas as opposed to the 16 Rocky Mountain–Colorado Plateau samples of various sizes used in this study.

In spite of the high dissimilarity between the eastern and western borders and the rapid species turnover between 114–118°W longitude, complete species turnover in the region does not occur. The lack of complete species turnover and the overlapping countercurrent of species affinity across the 206 sites (Fig. 9–11) are consistent with the pattern of a single biogeographic province. This pattern is nearly symmetrical, with taxa affiliated with the Rocky Mountains represented more strongly on Great Basin mountain islands than Pacific taxa, but more Pacific species than Rocky Mountain species in the Great Basin. The asymmetry in the pattern occurs near the northern and southern boundaries of the region. In the north, Pacific affinities spread farther east than elsewhere in the region, whereas in the south the Mojave Desert mountains are mainly affiliated with the Rockies and are connected with the Pacific mainland to a lesser degree. The strongest floristic discontinuity occurs in the south, and this discontinuity softens considerably in the northern Great Basin.

Further validation for the idea that the Great Basin as considered here is a single biogeographic region is seen when the Wasatch Mountains on the eastern boundary of the Great Basin are compared to the Middle Rocky Mountains, the physiographic province to which the Wasatch belongs. *Juniperus horizontalis, Pinus albicaulis,* and *P. aristata* all occur in the Middle Rocky Mountains (Charlet 1995) but not in the Wasatch Mountains. Of these, only *P. albicaulis* occurs on Great Basin islands, but these populations are closer to western mainland samples than to Middle Rocky Mountain sources. Further, all conifer taxa in the Wasatch Mountains occur on Great Basin islands. Thus, the conifer flora of the Wasatch Mountains more closely resembles Great Basin islands than it resembles the Middle Rocky Mountains.

*Great Basin Conifer Endemism*

Although no conifer taxon is strictly endemic to the Great Basin physiographic province, 5 species in 3 genera are nearly so: *Juniperus osteosperma, Pinus longaeva, P. monophylla, P. washoensis,* and *Pseudotsuga macrocarpa.* Of these, only *P. longaeva* and *P. monophylla* (section *Parryae*) are somewhat closely related (Strauss and Doerksen 1990). The distribution pattern of these near-endemics is symmetrical, with two species widespread throughout, one endemic to the northwestern border, another to the center and the southeastern border, and a single species endemic to

the southern border. *Juniperus osteosperma* is endemic to the Great Basin and its borders with all surrounding regions except the Cascade Range. *Pinus monophylla* has a similar distribution except that it approaches the Columbia Plateau only from the east. *Pinus longaeva* is endemic to Great Basin islands and the extreme western Colorado Plateau, while *P. washoensis* is endemic to the northwestern boundary. *Pseudotsuga macrocarpa* is endemic to the Transverse Ranges, and its occurrence at the headwaters of the Mojave River places it within the hydrographic Great Basin. The distributional ranges of all these species overlap, except that *P. longaeva, P. macrocarpa,* and *P. washoensis* never occur with one another. Rosenzweig (1995) defined biological islands and mainlands as two ends of a continuum that are only rarely realized: mainlands only possess species that originate on the mainland, while islands contain only immigrant species. The distribution of these 5 near-endemic taxa suggests that the Great Basin as defined here is a single area of endemism, or a biogeographic province.

### Extinctions since the Tertiary–Quaternary Boundary

The island biogeography multiple regression models are good predictors of species richness, but what are the extinction and immigration rates? That is, how often does conifer extinction and immigration occur in the region? *Neotoma* nest contents are the best direct measure of species occurrences at a site over time, but the method has limitations.

The crowning achievement of *Neotoma* nest content evidence to date is the documentation of *Pinus monophylla* colonization in the Great Basin. The Holocene *Neotoma* midden record is relatively complete temporally for pinyon and/or juniper woodlands, and it is clear that *P. monophylla* was a Holocene invader of the central Great Basin from refugia in the southern part of the region. Further, the record documents its rapid spread north during the last 4000 years (e.g., Wells 1983; Thompson 1990, 1992; Wigand and Nowak 1992).

It is difficult to securely document colonization events unless records are as complete as they are for *Pinus monophylla,* but documentation of extinctions with macrofossils is unequivocal (Betancourt et al. 1990*a*). There are many such examples in the Great Basin (Charlet 1995). While woodrat midden data can definitively document conifer extinctions, it is much more speculative to propose montane or subalpine colonizations based on *Neotoma* midden evidence. Paleorecords document significant vegetation changes at a site, but species are not necessarily absent from the mountain every time they are absent from a stratigraphic sample. Pleistocene materials, if any exist, are usually much rarer than Holocene materials at the site.

It is therefore difficult to ascertain when a species arrived at a mountain: there simply may be no record of the species there at that time. Subalpine conifers are also poorly represented in the *Neotoma* midden record because subalpine environments in the Great Basin offer poor conditions for the long-term preservation of middens. The most complete *Neotoma* records are of low-elevation conifers found primarily in the modern Mojavean, pinyon-juniper, lower sagebrush-grass, and shadscale zones, and it is in these Great Basin environments that most woodrats reside (Vaughan 1990).

*Disturbance.*—The intermediate disturbance hypothesis (Connell 1978; Sousa 1979; McGuinness 1984*b*) posits that very low and very high levels of disturbance cause a reduction in species richness, while intermediate levels of disturbance allow the most species to occur. Although this explanation for the species–area relationship appeared in the literature 30 years ago, it is rarely examined as an alternative to M-W models (McGuinness 1984*a*), and has not been used to explain the modern distribution of Great Basin conifers.

The disturbance regime for the Great Basin at the time scale that would affect conifers is unknown, but likely is important. Miocene volcanism was extensive in the Great Basin (Stewart 1980), and major climatic disturbances occurred throughout the Quaternary. During interglaciopluvials, fire is probably the greatest single disturbance affecting conifers. The phenomenon of montane balds (Billings and Mark 1957), common throughout the Great Basin, provides a hint to the effect that fires have on the distribution of Great Basin conifers. Montane balds are the tops of high mountains that are truly montane as far as temperature regime and precipitation is concerned, but have no conifers. Fires in the 20th century created new balds or near-balds (e.g., Fort Sage Mountain, Petersen Mountain; Charlet 1996). Fires can quickly extinguish a relict population, many conifer populations in the Great Basin are tiny, and conifers require the ground to be inoculated with appropriate mycorrhizal cultures (Hansen 1947; Axelrod 1986; Perry et al. 1989). It is thus unlikely that conifers could jump-disperse to balds following fires. In the past 20 years, I visited at least 50 such balds at many degrees of isolation and never observed a tree seedling of a species that was not already present on that mountain. Future studies should explore means of quantifying the disturbance regime of the region.

### CONCLUSIONS

The modern Great Basin conifer flora is much richer than was previously known in terms of (a) the number of species present, (b) the number of mountain ranges in which the species occur, and (c) the number of spe-

cies present in individual mountain ranges. Longitude is poorly related to overall species richness, but it represents the gradient along which species turnover is the most rapid, with *Juniperus communis* and *Pinus flexilis* the only montane conifers occurring on both sides of the Great Basin. Likewise, latitude is not related to species richness, but is also related to species turnover, as many taxa occur only at the northern or southern limits of the region.

Rocky Mountain taxa are well represented in the Great Basin but do not dominate it floristically. Pacific conifers do not range as deep into the Great Basin as Rocky Mountain conifers because fewer large, high-relief mountain ranges permitting upslope range-contraction are present in the western Great Basin compared to the eastern Great Basin. However, there is plenty of relief on the eastern slopes of the Sierra Nevada to allow upslope contraction of taxa that may have ranged into the Lahontan Basin during the Pleistocene. The modern distribution data suggest that high-elevation Pacific conifers are ecophysiologically tolerant of the Great Basin montane zone. They were more widespread in the western Great Basin in the Late Quaternary, but went extinct on small, low-relief islands. Potential access for montane and subalpine taxa to the central Great Basin, whether from the east or the west, was maximized during glaciopluvials.

All M-W island biogeography models (immigration, extinction, and equilibrium) fail to explain species richness in the Great Basin because mainland species–area slopes are much steeper than predicted. When the Pacific, Rocky Mountains, Colorado Plateau, and Blue Mountains mainland samples are combined into a single species–area plot, the resulting slope is lower than the individual mainland slopes, but not as low as slopes expected for mainlands. However, if these mainland samples are part of separate biogeographic provinces, the expected species–area slope of the pooled mainland sites should increase dramatically. Therefore, I conclude that the lee slope of the Sierra Nevada, the Columbia Plateau, the western front of the Middle Rocky Mountains and Colorado Plateau, and the interior Great Basin mountains are all part of a single biogeographic province. Instead of indicating a failure of the M-W models, application of the model provides insight into the system. The island-like slope of the mainlands may mean that ''mainland'' source areas were not sampled. That is, all samples included here are part of a single biogeographic region that is a ''breaking up of biotas of large islands into semi-isolated communities'' (MacArthur and Wilson 1967: 18).

In addition to the problem of mainland slopes, the M-W models do not entirely explain the observed patterns of island species richness. The M-W immigration model fails on every prediction except for that of non-random species–area slopes. Island slopes are closer to equilibrium than the M-W extinction model predicts. A conspicuous failure of the equilibrium model is that the observed distance effect is much weaker than the area effect on species richness of montane islands.

Although each model fails in at least 2 predictions, the M-W models explain most of the variation in species richness. It appears that island biogeography theory is necessary but insufficient to explain all of the observed patterns of conifer species richness in the Great Basin. These patterns and the history of the region are so complex that the complete solution likely will not be found in any idealized model. Instead, when I consider all of the effects on species richness together, I conclude that the answer to the Great Basin conifer conundrum—extinction or immigration?—is both extinction and immigration with the following caveats. Extinction is more important than immigration, and extinction drives the richness patterns not only on the islands, but also on the so-called mainlands.

Montane relief is a powerful predictor of species richness because it is strongly associated with habitat diversity. Montane relief consistently outperforms area as a predictor of species richness, and inclusion of additional habitat diversity measures will be fruitful. Kruckeberg (1991) was keen on emphasizing the importance of special edaphic sites to understand the patterns of biodiversity in a region. While this study addresses the influence of landforms (Kruckeberg 2002a) in a rudimentary way, it does not account for the heterogeneity of the region's lithology (Kruckeberg 1991, 2002b). Future studies will be well served by including measures of the region's geology as an additional physical feature controlling the biodiversity of conifers within the region. It is reasonable to assume that disturbance regimes are critically important in the region, and I recommend the pursuit of means whereby disturbance can be quantified. By including a disturbance factor in the M-W model, future analyses are likely to explain more variation of conifer species richness in the Great Basin.

Based on the success of montane relief alone to predict species richness in the Great Basin and on the other results in this study, I deduce a generalized response of Great Basin conifers to the climatic oscillations of the Quaternary as follows. The Tertiary conifer flora throughout western North America was very diverse and relatively homogeneous. Increasing aridity and continentality accompanied the Sierra Nevada and Rocky Mountain orogenies, causing the extinction of many taxa from the present-day Great Basin, and selection for drought- and cold-tolerant adaptations in the taxa that remained. Most taxa present today in the Great Basin were present at the Tertiary–Quaternary boundary.

In the Quaternary, attrition of taxa continued

through two million years of long glaciopluvials followed by short, intense interglaciopluvial episodes. North–south and south–north movements of taxa were heavily favored over east–west and west–east movements. Contacts with source pools outside the region mainly are with species-rich northern pools and species-poor southern pools rather than with eastern and western pools. Boreal conifers shift their ranges south toward the Great Basin during each glaciopluvial episode, while interglaciopluvials force conifer populations in the Great Basin to range-shift north or upslope on high-relief mountains (if available). The north–south orientation of the hundreds of mountain ranges in the Great Basin, Pacific Mountain System, and Rocky Mountain System are well-suited to act as conduits for these latitudinal range-shifts.

Populations stranded on high-relief mountains during interglaciopluvials may persist until the ensuing glaciopluvial. Alternatively, drought and fire may remove them. Regardless of the fates of these montane and subalpine conifers, xeric conifers range-shift into the Great Basin from the south. The southern contribution to the conifer flora is small in number of species, but floods the region with individuals during interglacials. Replacement of lost taxa through speciation has possibly occurred in the cases of *Pinus longaeva* and *P. washoensis*. However, the overall effect on species richness of individual mountains through these climatic oscillations is higher richness during glaciopluvials and reduced richness during interglaciopluvials because of the difference in northern and southern source pool diversities.

The effect of these source pools on Great Basin conifer richness in the terms of island biogeography theory is as follows. The immigration rate of species from northern source pools is greater than the extinction rate of conifers in glaciopluvials ($I > E$), and the immigration rate of species from southern source pools is lower than the extinction rate of conifers in interglaciopluvials ($I < E$). This creates a modern interglaciopluvial pattern of conifer richness in which the most area is occupied by the fewest taxa (the xeric conifers), while most taxa occupy the smallest of the ecological zones available to conifers (the subalpine).

It seems that the Great Basin was a montane-subalpine mainland for conifers in the Tertiary, but is no longer. Throughout the climatic oscillations of the Quaternary, and in the interglacial episodes in particular, the montane and subalpine area of the Great Basin broke up, becoming island-like. Therefore, both the ''mainlands'' and ''islands'' I have considered in this study are the remnants of this ancient mainland. In glacial episodes, the Great Basin is a sink for these species to which they retreat. During interglacial events, the Great Basin is a source for these species to restock the periphery of the Sierra Nevada, Cascades, and Rocky Mountains while they are slowly removed locally in the Great Basin.

ri, Therese, and Dene Charlet demonstrated unbeliev-
able patience and support.

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Appendix I. Presence/absence matrix of conifer occurrences on Great Basin mountains. Sample numbers correspond to sites on the regional map (Fig. 2). The sample name includes the name of the mountain range and a two-letter code for the county (if the sample site is in Nevada). If a sample extends from Nevada into another state, that state two-letter code is indicated following the Nevada county codes: Carson City (CC), Churchill (CH), Clark (CL), Douglas (DO), Elko (EL), Esmeralda (ES), Eureka (EU), Humboldt (HU), Lander (LA), Lincoln (LI), Lyon (LY), Mineral (MI), Nye (NY), Pershing (PE), Storey (ST), Washoe (WA), White Pine (WP). Conifer occurrences are indicated by a "1" and absence by a dash. Mainland (M) or island (I) status of each sample is indicated in the final column. Columns a–ah denote conifer taxa[a].

| | a | b | c | d | e | f | g | h | i | j | k | l | m | n | o | p | q | r | s | t | u | v | w | x | y | z | aa | ab | ac | ad | ae | af | ag | ah | ai | aj | ak |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 Anchorite Hills MI | - | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | 3 | 3 | I |
| 2 Antelope Range WP EL | - | - | - | 1 | 1 | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | 1 | - | - | - | - | - | - | - | - | - | 4 | 2 | I |
| 3 Badger Mts WA HU | - | - | - | 1 | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | I |
| 4 Belted Range NY | - | - | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | 3 | 3 | I |
| 5 Bilk Creek Mts HU OR | - | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | I |
| 6 Black Rock Range HU PE | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | 2 | I |
| 7 Bodie Mts MI LY CA | - | - | 1 | - | - | 1 | - | - | - | - | - | - | - | - | 1 | 1 | - | - | - | - | 1 | - | - | - | - | - | - | 1 | - | - | - | - | - | - | 8 | 6 | I |
| 8 Bruneau Range EL | - | - | - | - | - | 1 | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 5 | 5 | I |
| 9 Buck Creek Mts EL | - | - | - | - | - | 1 | - | - | - | 1 | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 4 | 4 | I |
| 10 Buffalo Hills WA | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | 1 | I |
| 11 Bull Run Mts EL | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 5 | 5 | I |
| 12 Carson Range WA DO CA | 1 | - | - | 1 | 1 | 1 | 1 | - | - | - | 1 | - | - | - | - | - | - | 1 | - | - | 1 | - | 1 | 1 | - | 1 | 1 | 1 | - | - | - | 1 | 1 | - | 15 | 13 | M |
| 13 Cherry Creek Range WP | - | - | - | 1 | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 6 | 4 | I |
| 14 Clan Alpine Mts CH | - | - | - | 1 | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 3 | 1 | I |
| 15 Clover Mts LI | - | - | - | 1 | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | 4 | 2 | I |
| 16 Copper Mts EL | - | - | 1 | 1 | - | 1 | - | - | - | 1 | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 5 | 5 | I |
| 17 Cortez Mts EU LA | - | - | 1 | 1 | - | 1 | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 3 | 1 | I |
| 18 Deep Creek Mts WP UT | - | - | 1 | 1 | - | 1 | 1 | - | - | 1 | - | - | 1 | - | 1 | - | - | 1 | - | - | - | - | - | 1 | - | 1 | - | - | - | - | - | 1 | - | - | 11 | 9 | I |
| 19 Desert Creek Mts LY | - | - | - | - | 1 | 1 | 1 | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 5 | 3 | I |
| 20 Diamond Mts EU WP | - | - | - | 1 | - | 1 | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | 4 | 2 | I |
| 21 Division Range WA HU | - | - | - | 1 | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | I |
| 22 Dogskin Mtn WA | - | - | - | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | 3 | 2 | I |
| 23 Dolly Varden Mts EL | - | - | - | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 3 | 1 | I |
| 24 Duck Creek Range WP | - | - | - | - | - | 1 | 1 | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | 6 | 4 | I |
| 25 East Humboldt Range EL | - | - | - | - | - | 1 | 1 | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | 6 | 4 | I |
| 26 Egan Range WP LI | - | - | - | - | - | 1 | 1 | - | - | 1 | - | - | 1 | - | 1 | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | 8 | 6 | I |
| 27 Elk Mts EL | - | - | - | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 3 | 3 | I |
| 28 Excelsior Mts MI | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | 3 | 1 | I |
| 29 Fish Creek Mts LA PE | - | - | - | 1 | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | 1 | I |
| 30 Fish Creek Range EU NY | - | - | - | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | 5 | 3 | I |
| 31 Flowery Range ST | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | 4 | 2 | I |
| 32 Fort Sage Mts WA CA | - | - | - | 1 | 1 | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | 4 | 3 | I |
| 33 Fox Creek Range EL | - | - | - | 1 | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 4 | 4 | I |
| 34 Goshute Mts EL | - | - | 1 | 1 | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | 7 | 5 | I |
| 35 Granite Range WA PE | - | - | - | 1 | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | 1 | I |
| 36 Grant Range NY | - | - | - | 1 | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | 8 | 6 | I |
| 37 Grapevine Mts ES NY CA | - | - | - | 1 | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | 3 | 1 | I |
| 38 Groom Range LI | - | - | - | 1 | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 4 | 2 | I |
| 39 Hays Canyon Range WA | - | - | - | 1 | - | 1 | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 3 | 2 | I |
| 40 Highland Range LI | - | - | - | - | 1 | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | 1 | 1 | - | 1 | 1 | - | - | - | - | - | - | 7 | 5 | I |
| 41 Home Camp Range WA | - | - | - | 1 | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | I |

Appendix I. Continued.

| | a | b | c | d | e | f | g | h | i | j | k | l | m | n | o | p | q | r | s | t | u | v | w | x | y | z | aa | ab | ac | ad | ae | af | ag | ah | ai | aj | ak |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 42 Horse Range NY | - | - | - | 1 | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | 4 | 2 | 1 |
| 43 Hot Creek Range NY | - | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | 1 | - | - | - | - | - | - | - | - | - | - | 5 | 3 | 1 |
| 44 Humboldt Range PE | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 3 | 1 | 1 |
| 45 Ichabod Range EL | - | - | - | - | 1 | 1 | - | - | - | 1 | - | - | - | - | 1 | - | - | - | - | - | 1 | - | - | 1 | - | - | - | - | - | - | - | - | - | - | 4 | 4 | 1 |
| 46 Independence Mts EL | - | - | 1 | - | 1 | 1 | - | - | - | 1 | - | - | - | - | 1 | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 6 | 5 | 1 |
| 47 Irish Mtn LI | - | - | - | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | - | 1 | - | - | - | - | - | - | - | 5 | 3 | 1 |
| 48 Jackson Mts HU | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | 1 | 1 |
| 49 Jarbidge Mts EL | - | - | 1 | - | 1 | 1 | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 5 | 5 | 1 |
| 50 Junction House Range WA | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | 1 | - | - | - | - | - | - | 4 | 2 | 1 |
| 51 Kamma Mts PE HU | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | 1 | 1 |
| 52 Kawich Range NY | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 3 | 1 | 1 |
| 53 Kern Mts WP UT | - | - | 1 | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 5 | 3 | 1 |
| 54 Lake Range WA | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | 1 | 1 |
| 55 Lost Creek Hills WA | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | 1 |
| 56 Madelin Mesa WA CA | - | - | 1 | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | 2 | 2 | 1 |
| 57 Mahogany Mts LI UT | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | 4 | 2 | 1 |
| 58 Marys River Range EL ID | - | - | 1 | - | 1 | 1 | - | - | - | 1 | - | - | - | - | 1 | - | - | - | - | - | 1 | - | - | - | 1 | - | - | - | - | - | - | - | - | - | 6 | 6 | 1 |
| 59 Massacre Range WA | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | 1 |
| 60 Monitor Range NY EU LA | - | - | 1 | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | 1 | 1 | 1 | - | 1 | - | - | - | - | - | - | - | 6 | 4 | 1 |
| 61 Mormon Mts LI CL | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | 3 | 1 | 1 |
| 62 Mosquito Mts WA | - | - | - | 1 | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | 1 | - | - | - | - | 4 | 4 | 1 |
| 63 New York Mts CL CA | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 3 | 1 | 1 |
| 64 Pah Rah Range WA | - | - | - | 1 | - | - | - | 1 | - | - | - | - | - | - | - | - | - | 1 | - | - | 1 | 1 | - | 1 | 1 | - | 1 | 1 | - | - | - | - | - | - | 4 | 2 | 1 |
| 65 Painted Point Range WA | - | - | - | 1 | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | 2 | 2 | 1 |
| 66 Pancake Range NY WP | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | 1 | 1 | 1 | - | - | 1 | - | - | - | - | - | - | - | 4 | 2 | 1 |
| 67 Paradise Range NY | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | 4 | 2 | 1 |
| 68 Peavine Mtn WA CA | 1 | - | - | - | - | - | - | 1 | - | 1 | - | - | - | - | - | - | - | 1 | - | - | - | 1 | - | - | 1 | - | 1 | - | - | - | - | - | - | 1 | 12 | 10 | 1 |
| 69 Pequop Mts EL | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | 1 | - | - | 1 | - | - | - | - | - | - | - | 7 | 5 | 1 |
| 70 Petersen Mtn WA CA | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 4 | 3 | 1 |
| 71 Pilot Range EL UT | - | - | 1 | - | - | 1 | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 6 | 4 | 1 |
| 72 Pine Forest Range HU | - | - | - | - | 1 | 1 | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 4 | 3 | 1 |
| 73 Pine Grove Hills LY | - | - | - | 1 | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | 1 | - | 1 | - | - | - | - | - | - | - | - | 6 | 4 | 1 |
| 74 Pine Nut Mts LY DO | - | - | - | - | - | - | 1 | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | 1 | - | - | 6 | 4 | 1 |
| 75 Pinto Peak Range WA | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | 1 |
| 76 Pueblo Mts HU OR | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | 1 |
| 77 Quinn Canyon Range NY LI | - | - | - | 1 | 1 | 1 | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | 1 | - | - | 1 | - | - | 1 | - | - | - | - | - | - | - | 8 | 6 | 1 |
| 78 Roberts Mts EU | - | - | 1 | 1 | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 6 | 4 | 1 |
| 79 Ruby Mts EL WP | - | - | 1 | - | 1 | 1 | 1 | - | - | - | - | - | 1 | - | 1 | - | - | - | - | - | 1 | - | - | 1 | - | - | - | - | - | - | - | - | - | - | 9 | 7 | 1 |
| 80 Salmon River Range EL ID | - | - | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | 2 | 1 |
| 81 Santa Rosa Range HU | - | - | - | 1 | - | - | 1 | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | 2 | 1 |
| 82 Schell Creek Range LI WP | - | - | 1 | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | 1 | 1 | - | 1 | - | - | - | - | 1 | - | 1 | 10 | 8 | 1 |
| 83 Seaman Range LI NY | - | - | - | 1 | 1 | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 6 | 4 | 1 |
| 84 Selenite Range PE | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | 1 |
| 85 Seven Lakes Mtn WA CA | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | 2 | 1 | 1 |
| 86 Seven Troughs Range PE | - | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | 1 | 1 |

Appendix I. Continued.

| | a | b | c | d | e | f | g | h | i | j | k | l | m | n | o | p | q | r | s | t | u | v | w | x | y | z | aa | ab | ac | ad | ae | af | ag | ah | ai | aj | ak |
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| 87 Sheep Range CL LI | - | - | 1 | - | 1 | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | 1 | 1 | - | 1 | - | - | - | - | - | - | - | 8 | 6 | 1 |
| 88 Shoshone Mts NY LA | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 3 | 1 | 1 |
| 89 Shoshone Range LA EU | - | - | - | 1 | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 3 | 1 | 1 |
| 90 Silver Peak Range ES | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | 3 | 1 | 1 |
| 91 Simpson Park Range LA EU | - | - | - | 1 | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 4 | 2 | 1 |
| 92 Smoke Creek Mts WA CA | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 0 | 1 | 1 |
| 93 Snake Mts EL | - | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 3 | 2 | 1 |
| 94 Snake Range WP | - | - | 1 | - | 1 | 1 | 1 | - | - | - | - | - | 1 | - | - | - | - | - | - | - | 1 | - | - | 1 | 1 | - | 1 | - | - | - | - | 1 | - | - | 12 | 9 | 1 |
| 95 Spring Mts CL NY | - | - | 1 | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | - | 1 | - | - | - | - | - | - | - | 8 | 6 | 1 |
| 96 Sweetwater Mtns LY DO CA | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | 1 | 10 | 8 | 1 |
| 97 Toano Range EL | - | - | - | 1 | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 4 | 2 | 1 |
| 98 Tobin Range PE | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | 1 | 1 |
| 99 Toiyabe Range NY LA | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 5 | 3 | 1 |
| 100 Toquima Range NY | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 4 | 2 | 1 |
| 101 Virginia Mts WA | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 3 | 1 | 1 |
| 102 Virginia Range WA CC LY ST | - | - | - | 1 | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | 1 | 1 | 1 | 1 | - | - | - | - | 1 | - | - | 9 | 7 | 1 |
| 103 Virgin Mts CL AZ | - | - | - | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 6 | 4 | 1 |
| 104 Wassuk Range MI LY | - | - | 1 | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 8 | 6 | 1 |
| 105 Wellington Hills DO | - | - | - | 1 | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 4 | 2 | 1 |
| 106 White Mts ES MI CA | - | - | 1 | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | 9 | 7 | 1 |
| 107 White Pine Range WP NY | - | - | 1 | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | 1 | - | - | 1 | - | - | - | - | - | - | - | 8 | 6 | 1 |
| 108 White Rock Mts LI UT | - | - | - | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | 5 | 3 | 1 |
| 109 Wild Horse Range EL | - | - | - | - | - | 1 | 1 | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | 2 | 1 |
| 110 Wilson Creek Range LI | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | 1 | 1 | - | - | - | - | 1 | - | - | 7 | 5 | 1 |
| 111 Wood Hills EL | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 3 | 1 | 1 |
| 112 Worthington Mts LI | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | 1 | - | - | - | - | - | - | - | - | - | - | 3 | 1 | 1 |
| 113 Zunnamed Mts DO CA | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 6 | 4 | 1 |
| 114 Warner Range CA OR | 1 | - | 1 | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 10 | 10 | 1 |
| 115 Eagle Lake CA | 1 | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | 1 | - | - | - | - | 7 | 7 | 1 |
| 116 Red Cinder CA | 1 | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | 12 | 12 | M |
| 117 Diamond Mts CA | 1 | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | 1 | - | 13 | 11 | M |
| 118 Bald-Verdi Ranges CA | 1 | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 9 | 9 | M |
| 119 Donner Pass CA | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 11 | 11 | M |
| 120 Tahoe-West CA | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 12 | 12 | M |
| 121 Ebbetts Pass CA | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 12 | 11 | M |
| 122 Sonora Pass CA | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 11 | 10 | M |
| 123 Tioga Pass CA | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 11 | 9 | M |
| 124 Mammoth Mtn CA | 1 | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 12 | 11 | M |
| 125 Mount Sill CA | 1 | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 12 | 11 | M |
| 126 Mount Whitney CA | 1 | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 11 | 10 | M |
| 127 Olancha Peak CA | - | - | 1 | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | 1 | - | - | - | - | - | 7 | 6 | M |
| 128 Owens Peak CA | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | 1 | - | - | - | - | - | 7 | 5 | M |
| 129 Pinyon Mts CA | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | 1 | - | - | - | - | - | 5 | 2 | M |
| 130 Tehachapi Pass CA | 1 | 1 | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | 1 | - | - | - | - | - | - | - | 1 | - | 1 | - | - | - | 8 | 5 | M |
| 131 San Bernardino Mts CA | 1 | 1 | 1 | 1 | 1 | - | - | 1 | - | - | - | - | - | - | - | - | - | - | 1 | - | 1 | - | - | - | - | - | - | 1 | - | - | - | - | - | - | 13 | 9 | M |

Appendix I. Continued.

| | a | b | c | d | e | f | g | h | i | j | k | l | m | n | o | p | q | r | s | t | u | v | w | x | y | z | aa | ab | ac | ad | ae | af | ag | ah | ai | aj | ak |
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| 132 San Gabriel Mts CA | 1 | 1 | - | 1 | 1 | - | - | 1 | - | - | - | - | - | - | - | - | - | - | 1 | - | 1 | 1 | 1 | - | - | - | - | 1 | - | - | 1 | - | - | - | 13 | 9 | M |
| 133 Clark Mts CA | - | - | - | 1 | 1 | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 3 | 1 | 1 |
| 134 Inyo Mts CA | - | - | - | 1 | 1 | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | 1 | 1 | - | - | - | 1 | - | - | - | - | - | - | 6 | 4 | 1 |
| 135 Kingston Range CA | - | - | - | 1 | 1 | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 3 | 1 | 1 |
| 136 Last Chance Mts CA | - | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | 3 | 1 | 1 |
| 137 Panamint Mts CA | 1 | - | - | 1 | 1 | - | - | 1 | - | - | - | - | - | - | 1 | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 5 | 3 | 1 |
| 138 Glass Mtn CA | - | - | - | 1 | 1 | - | - | 1 | - | - | - | - | - | - | 1 | - | - | - | - | - | 1 | 1 | - | - | 1 | 1 | - | - | - | - | - | - | - | 1 | 8 | 7 | 1 |
| 139 Gearhart Mtn OR | - | - | - | 1 | 1 | - | 1 | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | 1 | - | - | - | - | - | - | - | - | 6 | 6 | 1 |
| 140 Glass Buttes OR | - | - | - | 1 | 1 | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | 2 | 1 |
| 141 Green Butte OR | - | - | - | 1 | 1 | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | 3 | 3 | M |
| 142 Green Mtn OR | - | - | - | 1 | 1 | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | 2 | 1 |
| 143 Hart Mtn OR | - | - | - | 1 | 1 | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 3 | 3 | 1 |
| 144 Juniper Mtn OR | - | - | - | 1 | 1 | - | 1 | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | 1 |
| 145 King Mtn OR | - | - | - | 1 | 1 | - | 1 | - | - | - | - | 1 | - | - | - | - | - | - | - | - | 1 | 1 | - | 1 | - | - | - | 1 | - | - | 1 | - | - | - | 5 | 5 | M |
| 146 Little Juniper Mtn OR | - | - | - | 1 | 1 | - | 1 | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | 1 |
| 147 Cedar Mtn OR | - | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | 1 |
| 148 Paulina Mtn OR | - | - | - | 1 | 1 | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | 1 | 8 | 8 | M |
| 149 Pine Mtn OR | - | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | 2 | 1 |
| 150 Saint Patrick Mtn OR | - | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | 2 | 1 |
| 151 Snow Mtn OR | - | - | - | 1 | 1 | - | - | 1 | 1 | - | - | 1 | - | - | - | - | 1 | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 6 | 6 | M |
| 152 Steens Mtn OR | - | - | 1 | 1 | 1 | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 3 | 3 | 1 |
| 153 Stinkingwater Mts OR | - | - | - | 1 | 1 | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 3 | 3 | 1 |
| 154 Strawberry Mtn OR | - | - | - | 1 | 1 | - | - | - | 1 | - | - | - | - | - | 1 | - | 1 | - | - | - | 1 | - | - | - | - | 1 | - | - | - | - | - | - | - | - | 9 | 9 | M |
| 155 Wagontire Mtn OR | - | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | 1 |
| 156 Yamsay Mtn OR | - | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | - | - | 1 | 1 | - | - | - | - | - | - | - | 1 | 7 | 7 | M |
| 157 Aquarius Plateau UT | - | 1 | 1 | 1 | 1 | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | 1 | - | - | - | - | - | - | 12 | 10 | M |
| 158 Bear Lake Plateau UT ID | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 3 | 3 | M |
| 159 Bear River Range UT ID | - | 1 | 1 | 1 | 1 | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | - | 1 | 1 | - | - | - | - | - | 1 | - | - | - | 12 | 9 | M |
| 160 Beaver Dam Mts UT | - | - | - | - | - | 1 | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | 1 | - | - | - | 1 | - | - | - | - | - | - | - | - | - | 6 | 3 | 1 |
| 161 Bull Valley Mts UT | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 4 | 1 | 1 |
| 162 Canyon Range UT | - | 1 | 1 | 1 | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | 1 | - | - | - | - | - | - | - | 7 | 5 | 1 |
| 163 Confusion Range UT | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 4 | 2 | 1 |
| 164 East Tintic Mts UT | - | - | - | 1 | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | - | 1 | - | - | - | - | - | - | - | - | - | - | 5 | 2 | 1 |
| 165 Echo Canyon UT | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 7 | 6 | M |
| 166 Fish Lake Plateau UT | - | 1 | 1 | 1 | 1 | 1 | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 11 | 9 | M |
| 167 Grouse Creek Mts UT | - | - | - | 1 | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | 1 | - | - | - | 4 | 2 | 1 |
| 168 House Range UT | - | - | - | 1 | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 8 | 6 | 1 |
| 169 Kolob Plateau UT | - | 1 | 1 | 1 | 1 | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 13 | 10 | M |
| 170 Markagunt Plateau UT | - | 1 | 1 | 1 | 1 | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | 1 | - | - | - | - | - | - | - | 12 | 10 | M |
| 171 Mineral Mts UT | - | - | - | 1 | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 7 | 4 | 1 |
| 172 Mount Nebo UT | - | 1 | 1 | 1 | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 9 | 7 | M |
| 173 Needle Range UT | - | 1 | - | 1 | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 5 | 3 | 1 |
| 174 Oquirrh Mts UT | - | - | 1 | - | 1 | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 5 | 3 | 1 |
| 175 Paunsaugunt Plateau UT | - | 1 | 1 | 1 | 1 | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | - | - | 1 | - | - | 1 | - | - | - | - | - | - | 1 | 12 | 10 | M |
| 176 Pavant Range UT | - | 1 | 1 | 1 | 1 | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | 1 | - | - | - | - | - | - | - | - | - | - | 10 | 8 | M |

Appendix I.  Continued.

| | a | b | c | d | e | f | g | h | i | j | k | l | m | n | o | p | q | r | s | t | u | v | w | x | y | z | aa | ab | ac | ad | ae | af | ag | ah | ai | aj | ak |
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| 177 Pine Valley Mts UT | - | - | 1 | - | 1 | 1 | 1 | - | - | 1 | - | 1 | 1 | 1 | - | - | 1 | - | - | 1 | 1 | - | - | 1 | 1 | - | 1 | - | - | - | - | 1 | - | - | 13 | 10 | I |
| 178 Provo UT | - | - | 1 | - | 1 | 1 | 1 | - | - | 1 | - | 1 | 1 | 1 | - | - | 1 | - | - | 1 | 1 | - | - | 1 | 1 | - | 1 | - | - | - | - | 1 | - | - | 12 | 10 | M |
| 179 Raft River Range UT | - | - | 1 | - | 1 | 1 | 1 | - | - | 1 | - | 1 | 1 | 1 | - | - | 1 | - | - | 1 | 1 | - | - | 1 | 1 | - | 1 | - | - | - | - | 1 | - | - | 10 | 8 | I |
| 180 Red Spur Mtn UT | - | - | 1 | - | 1 | 1 | 1 | - | - | 1 | - | 1 | 1 | 1 | - | - | 1 | - | - | 1 | 1 | - | - | 1 | 1 | - | 1 | - | - | - | - | 1 | - | - | 10 | 7 | M |
| 181 San Francisco Mts UT | - | - | - | - | 1 | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | 1 | - | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | 4 | 3 | I |
| 182 San Pitch Mts UT | - | - | 1 | - | 1 | 1 | - | - | - | 1 | - | 1 | 1 | - | - | - | 1 | - | - | 1 | 1 | - | - | 1 | 1 | - | 1 | - | - | - | - | - | - | - | 8 | 5 | I |
| 183 Sevier Plateau UT | - | - | 1 | - | 1 | 1 | 1 | - | - | 1 | - | 1 | 1 | 1 | - | - | 1 | - | - | 1 | 1 | - | - | 1 | 1 | - | 1 | - | - | - | - | - | - | - | 10 | 8 | M |
| 184 Sheeprock Mts UT | - | - | 1 | - | 1 | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | 1 | - | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | 4 | 3 | I |
| 185 Stansbury Mts UT | - | - | 1 | - | 1 | 1 | 1 | - | - | 1 | - | 1 | 1 | 1 | - | - | 1 | - | - | 1 | 1 | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | 10 | 8 | I |
| 186 Tushar Mts UT | - | - | 1 | - | 1 | 1 | 1 | - | - | 1 | - | 1 | 1 | 1 | - | - | 1 | - | - | 1 | 1 | - | - | 1 | 1 | - | 1 | - | - | - | - | - | - | - | 11 | 9 | M |
| 187 Wah Wah Mts UT | - | - | 1 | - | 1 | 1 | 1 | - | - | 1 | - | 1 | 1 | 1 | - | - | 1 | - | - | 1 | 1 | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | 8 | 5 | I |
| 188 Wasatch Plateau UT | - | - | 1 | - | 1 | 1 | 1 | - | - | 1 | - | 1 | 1 | 1 | - | - | 1 | - | 1 | 1 | 1 | - | - | 1 | 1 | - | 1 | - | - | - | - | - | - | - | 13 | 10 | M |
| 189 Wasatch Mts UT | - | - | 1 | - | 1 | 1 | 1 | - | - | 1 | - | 1 | 1 | 1 | - | - | 1 | - | - | 1 | 1 | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | 10 | 9 | M |
| 190 Wellsville Mts UT | - | - | 1 | - | 1 | 1 | 1 | - | - | 1 | - | - | 1 | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 5 | 4 | I |
| 191 West Tintic Mts UT | - | - | 1 | - | 1 | 1 | 1 | - | - | 1 | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 5 | 3 | I |
| 192 Albion Mts ID | - | - | 1 | - | 1 | - | 1 | - | - | 1 | - | 1 | 1 | 1 | - | - | 1 | - | - | - | 1 | - | - | 1 | - | - | - | - | - | - | - | - | - | - | 9 | 7 | I |
| 193 Bannock Range ID | - | - | 1 | - | 1 | - | - | - | - | 1 | - | 1 | 1 | 1 | - | - | 1 | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 6 | 5 | I |
| 194 Black Pine Mtn ID | - | - | 1 | - | 1 | - | - | - | - | 1 | - | 1 | 1 | 1 | - | - | 1 | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 7 | 6 | I |
| 195 Cotterel Mts ID | - | - | 1 | - | 1 | - | - | - | - | 1 | - | - | 1 | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 3 | 1 | I |
| 196 Deep Creek Mts ID | - | - | 1 | - | 1 | - | - | - | - | 1 | - | - | 1 | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 3 | 2 | I |
| 197 Jim Sage Mts ID | - | - | 1 | - | 1 | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | 1 | I |
| 198 Malad Range ID UT | - | - | 1 | - | 1 | 1 | 1 | - | - | 1 | - | 1 | 1 | 1 | - | - | 1 | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 4 | 3 | I |
| 199 Middle Mtn ID UT | - | - | 1 | - | 1 | 1 | - | - | - | 1 | - | - | 1 | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | 1 | I |
| 200 Owyhee Mts ID OR | - | - | 1 | 1 | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | 5 | 5 | I |
| 201 Pleasantview Hills ID | - | - | 1 | - | 1 | 1 | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | 1 | I |
| 202 Portneuf Range ID | - | - | 1 | - | 1 | 1 | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 6 | 5 | I |
| 203 Red Canyon Mts ID | - | - | 1 | - | - | 1 | - | - | - | 1 | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | I |
| 204 South Hills ID NV | - | - | 1 | - | 1 | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 4 | 3 | I |
| 205 South Mtn ID | - | - | 1 | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | 2 | I |
| 206 Sublett Range ID | - | - | - | - | 1 | 1 | - | - | - | 1 | - | - | 1 | - | - | - | 1 | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 7 | 6 | I |

[a]Legend for conifer taxa occurring in the sampled areas: (a) *Calocedrus decurrens*, (b) *Juniperus californica*, (c) *J. communis*, (d) *J. occidentalis*, (e) *J. osteosperma*, (f) *J. scopulorum*, (g) *Abies concolor concolor*, (h) *A. concolor lowiana*, (i) *A. grandis*, (j) *A. lasiocarpa*, (k) *A. magnifica*, (l) *Larix occidentalis*, (m) *Picea engelmannii*, (n) *P. pungens*, (o) *Pinus albicaulis*, (p) *P. balfouriana*, (q) *P. contorta latifolia*, (r) *P. contorta murrayana*, (s) *P. coulteri*, (t) *P. edulis*, (u) *P. flexilis*, (v) *P. jeffreyi*, (w) *P. lambertiana*, (x) *P. longaeva*, (y) *P. monophylla*, (z) *P. monticola*, (aa) *P. ponderosa scopulorum*, (ab) *P. ponderosa ponderosa*, (ac) *P. sabiniana*, (ad) *P. washoensis*, (ae) *Pseudotsuga macrocarpa*, (af) *Pseudotsuga menziesii menziesii*, (ag) *P. menziesii glauca*, (ah) *Tsuga mertensiana*, (ai) conifer diversity, (aj) montane conifer diversity, (ak) mainland (M)/island (I).