Forest Ecology and Biogeography of the Uinta Mountains, U.S.A

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Abstract

The Uinta Mountains form a crossroads of forests and woodlands in the central Rocky Mountains. Although no tree species is endemic to the area, all species characteristic of the central Rocky Mountains are found there, and the ranges of several other species terminate in the Uinta Mountains and the surrounding area. The peninsula-like shape, east-west orientation, and complex terrain of the range create a wide variety of potential forest sites that contrast with other ranges in the central Rockies. As a result, the Uinta Mountains are home to sites of unexpectedly high tree species diversity. Throughout most of the range, vegetation is organized in predictable zones that are characteristic of the Intermountain West; the range exhibits excellent vegetation zonation. However, across much of the northern slope several important species are absent, resulting in unexpectedly low diversity and "missing" vegetation zones. In this paper we provide an overview of the forest ecology and biogeography of the Uinta Mountains and update the local model for vegetation zonation. We also consider some possible explanations for the unexpected vegetation patterns and identify opportunities for future research.

Introduction

In the southwestern Uinta Mountains, near Moon Lake, Nord (1928) described a "natural arboretum" occupying an area of approximately four hectares and spanning an elevation range of a hundred or so meters. Within this area, Nord tallied 14 tree species, representing most of the dominant forest types found in the central and southern Rocky Mountains. What makes the diversity of tree species on the site interesting is the fact that most of the species typically occupy separate elevation zones distributed over an elevation range of more than 2000 m. Although considerable local diversity can be found in the Uinta Mountains, the geographic location and physical characteristics of the range actually facilitate one of the best examples of vegetation zonation in the Rocky Mountains—diverse tree species mixtures are the exception, not the rule.

Given the relatively orderly arrangement of vegetation zones in the Uinta Mountains, it is somewhat surprising that at least four of the species in Nord's (1928) "arboretum"—*Abies concolor*, *Juniperus scopulorum*, *Pinus edulis*, and *P. ponderosa*—are apparently absent or greatly reduced in abundance on the north slope of the range, only 35 km to the north of Moon Lake. These "missing" species are otherwise nearly ubiquitous in the Rocky Mountains within their respective vegetation zones, which makes the gaps in their ranges all the more interesting. Although many ecological studies have been done in the Uinta Mountains (e.g., Graham, 1937; Hayward, 1952), the basic ecology and biogeography of the forests have not been documented in as much detail as have other mountain ranges in the western United States (e.g., Oosting and Reed, 1952; Langenheim, 1962; Reed, 1971, 1976; Kipfmueller and Baker, 2000; Meyer et al., 2005). This lack of documentation may be due, at least in part, to the remoteness of the range and relative inaccessibility of the higher parts of the mountains in the early part of the post-pioneer settlement period (Bent, 1919).

In this paper we analyze broad-scale forest inventory data and present a synthesis of the ecology and biogeography of forests and woodlands of the Uinta Mountains. The discussion will be from two perspectives: (1) the geographic and elevational distributions of individual species, and (2) vegetation zonation, or the patterns of dominant forest types as controlled by elevation, latitude, and other factors. In both perspectives we consider the forests of the Uinta Mountains in the context of the central Rocky Mountains, contrasting characteristics of the Uinta Mountains with selected mountains and plateaus to the north and south.

Area of Analysis

SUBREGIONS OF THE ROCKY MOUNTAINS

To place the Uinta Mountains (40.8°N, 110.3°W) in the context of similar mountains of the western United States, we selected three other geographic areas for comparison: the Bighorn Mountains in northern Wyoming (40.6°N, 107.4°W), the Wind River Range in west-central Wyoming (43.0°N, 109.5°W), and the high plateaus of southern Utah (37.8°N, 112.2°W). The Bighorn Mountains and Wind River Range bear some superficial resemblance to the Uinta Mountains—peninsula-like and with *Artemisia* steppe around most of their periphery. In southern Utah, we aggregated the Aquarius, Paunsaugunt, and Sevier Plateaus, and the Escalante Mountains as well as other minor plateaus and mountains into an area of comparable extent to the Uinta Mountains (hereafter referred to as the southern Utah plateaus).

In our treatment of forest biogeography we place the Uinta Mountains, Bighorn Mountains, Wind River Range, and southern Utah plateaus in the central Rocky Mountains. Various authors have delineated biogeographic subregions in different ways. Our delineation corresponds most closely to Daubenmire's (1943), which he based on "conspicuous" floristic breaks. The boundary

between his northern and central subregions corresponds to an east-west line through the center of Wyoming. The boundary between his southern and central subregions corresponds roughly to the southern Colorado and Utah borders. In other treatments, this central portion of the Rocky Mountains is referred to as the ''middle Rockies'' (Arno and Hammerly, 1984; Habeck, 1987; Long, 1994). This central or middle Rocky Mountain subregion corresponds to what Peet (2000) called the southern Rocky Mountains, while his ''Madrean Rocky Mountains'' subregion corresponds more or less to Daubenmire's (1943) southern subregion.

Although Daubenmire's (1943) break would place the Bighorn Mountains and Wind River Range in the northern subregion, the forest types of the those two ranges more closely resemble the Uinta Mountains because they lack the tree genera (*Larix*, *Taxus*, *Thuja*, and *Tsuga*) characteristic of forests west of the Continental Divide in northern Idaho and western Montana. Hence, we include the Bighorn Mountains and Wind River Range in our discussion only for comparative purposes and do not imply a redefinition of biogeographic boundaries. Likewise, although the plateaus of southern Utah are physiographically and floristically different from the three mountain ranges in many respects, they share most of the major tree species found in the Uinta Mountains. As such, the southern Utah plateaus are useful in our examination of latitude-elevation relationships.

PHYSICAL ENVIRONMENT

Climate

As is the case in much of the western United States, the climate of the Uinta Mountains is controlled by two types of seasonal precipitation patterns—summer dry/winter wet and summer wet/winter dry (Whitlock and Bartlein, 1993). In the former regime, most precipitation comes in the winter as Pacific storms follow the jet stream. Troughs and migration of the jet stream southward bring precipitation to the Uinta Mountains and points farther south. The latter regime is a monsoonal system, bringing moist air northward, as far as southern Idaho and northwestern Wyoming, from the Gulf of California and the Gulf of Mexico during summer (Whitlock and Bartlein, 1993).

After analyzing summer and winter precipitation patterns at SNOTEL stations in the Uinta Mountains, Munroe (2003a) concluded that the eastern Uintas experience the summer wet/winter dry pattern whereas the western part is dominated by the summer dry/winter wet regime. He also found that total precipitation was relatively weakly correlated with elevation, possibly because of varying influence of each system coupled with some rain-shadow effects.

General Geology

The Uinta Mountains are unusual in that the main divide runs east-west. In general, the mountains are formed by an anticline that is somewhat asymmetrical; the 100-km-long crest is closer to the north flank of the mountains than to the south flank (Hansen, 1975). Uplift and erosion have exposed the Precambrian Uinta Mountain Group and Red Creek Quartzite in a broad area surrounding the axis of the anticline. Younger formations that include limestones, sandstones, shales, and conglomerates form concentric bands of varying width; these bands are not continuous at the surface, but are broken and buried by glacial deposits in numerous valleys that extend from the crest of the range into the surrounding lowlands (Atwood, 1909; Hansen, 1975). Many

formations account for a relatively small percentage of the land area. A few strata, such as the Uinta and Bridger Formations, the Bishop Conglomerate, the Precambrian core formations, and Quaternary deposits, occupy the majority of surface area (Hintze, 1980).

Methods

In order to discuss our methods, it is first necessary to clarify some terminology. The three vegetation distribution types that we use here to examine landscape patterns are species range, forest type, and vegetation zone.

Species range refers to the maximum natural geographical distribution of a species. On a map a species' range is typically presented as polygons that may include areas of absence—e.g., areas that are above or below the species elevational limits or where it may be locally limited by unfavorable soil characteristics. Usually, the polygons give no indication of the relative abundance or local dominance by the species and only indicate that it may be present.

Forest type is typically defined by abundance at the stand level, consisting of one or more species that define the type and reflecting current vegetation cover. A forest type may represent any stage of succession, and may or may not be expected to occupy a site indefinitely. This is in contrast to a habitat type (Pfister et al., 1977; Mauk and Henderson, 1984), which represents a potential forest type at climax; a site classified as a particular habitat type may be occupied by a forest type that is the climax type or some seral stage.

Our usage of vegetation (or forest) zone is an extension of Merriam's (1889) life zone concept. A vegetation zone does not refer to a patch of vegetation, but to an area in which a particular vegetation type is expected to dominate over time. Vegetation zones are commonly defined by the expected climax or potential vegetation type. Often they are characterized by types that are usually seral, but are effectively stable because of disturbance patterns, edaphic factors, lack of late-successional associates, or other factors—i.e., they are successionally stable types that differ from the expected climatic climax (Tansley, 1935). Our evaluation of vegetation zones is consistent with Peet's (2000) characterization of the Rocky Mountains, which defined vegetation zones along elevational and topographic-moisture gradients.

The three vegetation distribution types used here constitute a hierarchical arrangement. The species range covers the maximum geographic and elevational extent of a given species. Within a subset of this range the species may be sufficiently abundant that, alone or in conjunction with one or more close associates, it dominates at the stand level. Where a particular forest type is well adapted to certain climatic or edaphic conditions, areas with those conditions represent a vegetation zone which is named for the characteristic forest type. Because it was necessary to classify data to forest type, simple presence-absence data (as indicated by typical range maps) were insufficient. We required data from which relative abundance of species could be calculated and processed through a typing key.

Our primary source of data was the Forest Inventory and Analysis (FIA) program of the USDA Forest Service (Gillespie, 1999). FIA data are collected on all forested lands of the United States on a systematic grid at a density of approximately one plot per 2400 ha. During the last periodic inventory of Utah (O'Brien, 1999), plots were installed at double intensity (i.e., approximately one plot per 1200 ha) on National Forest lands, including the three forests (Ashley, Uinta, and Wasatch-Cache) that encompass
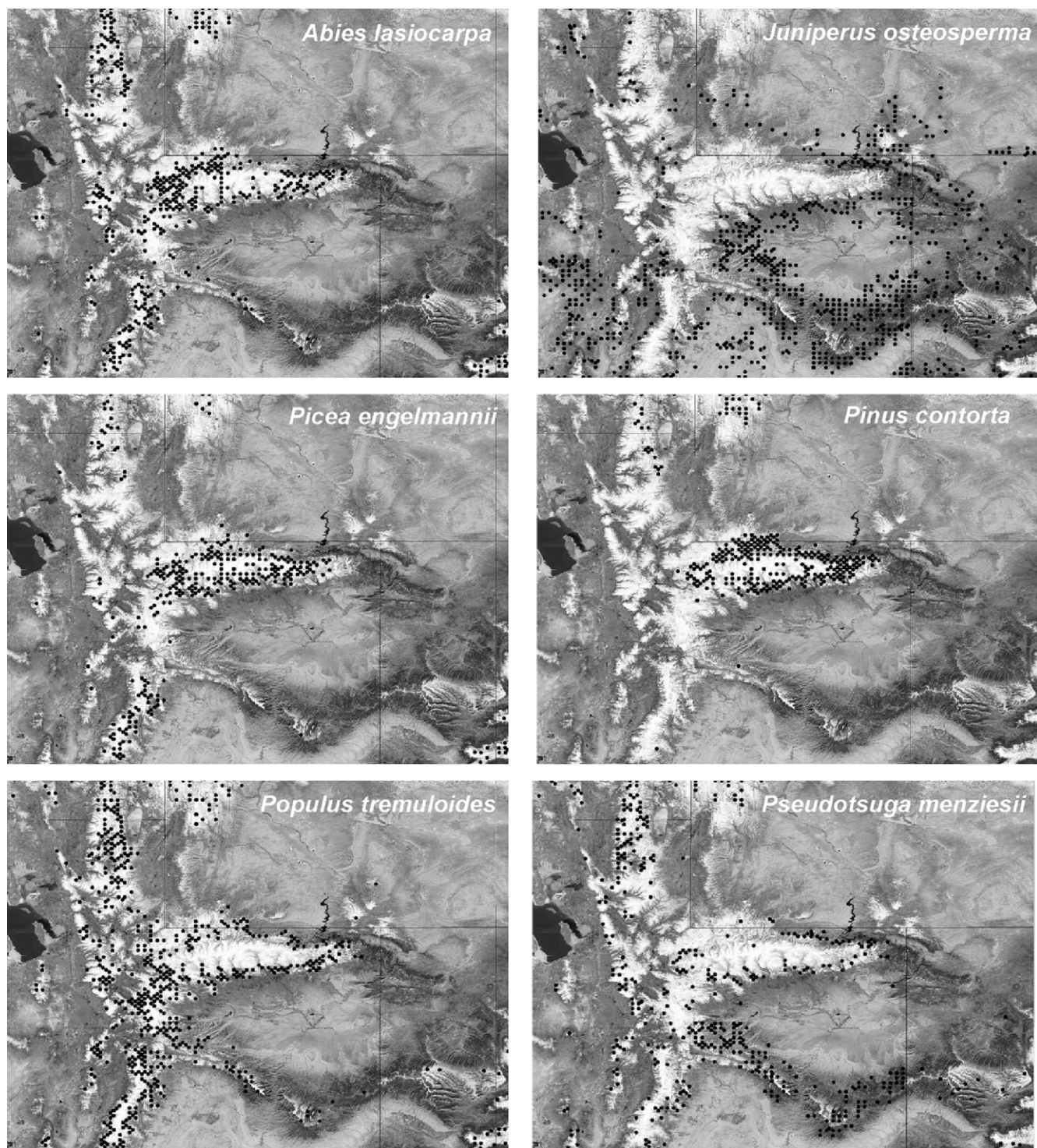
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FIGURE 1. Distribution of selected tree species in the Uinta Mountains and vicinity. The species shown exhibit the four types of distributions that are characteristic of the Uinta Mountains: common (*Abies lasiocarpa*, *Juniperus osteosperma*, *Picea engelmannii*, *Pinus contorta*, *Pseudotsuga menziesii*, and *Populus tremuloides*), well-distributed, but uncommon (*Picea pungens* and *Pinus flexilis* [labeled 5-needle pines]), bypass (*Abies concolor* and *Quercus gambelii*), and the "fishhook" (*Juniperus scopulorum*, *Pinus edulis*, and *Pinus ponderosa*). Ranges of the "fishhook" type extend across the southern slopes, round the eastern end, and terminate near the eastern end of the north slope. As a result, there is asymmetry between the northern and southern vegetation zones in the western Uinta Mountains. The 5-needle pine panel shows the southern limit of *Pinus albicaulis* (square symbols) and the northern limit of *P. longaeva* (round symbols) and are shown with *P. flexilis* (triangle symbols) for comparison. Plot coordinates are approximate to preserve location confidentiality.
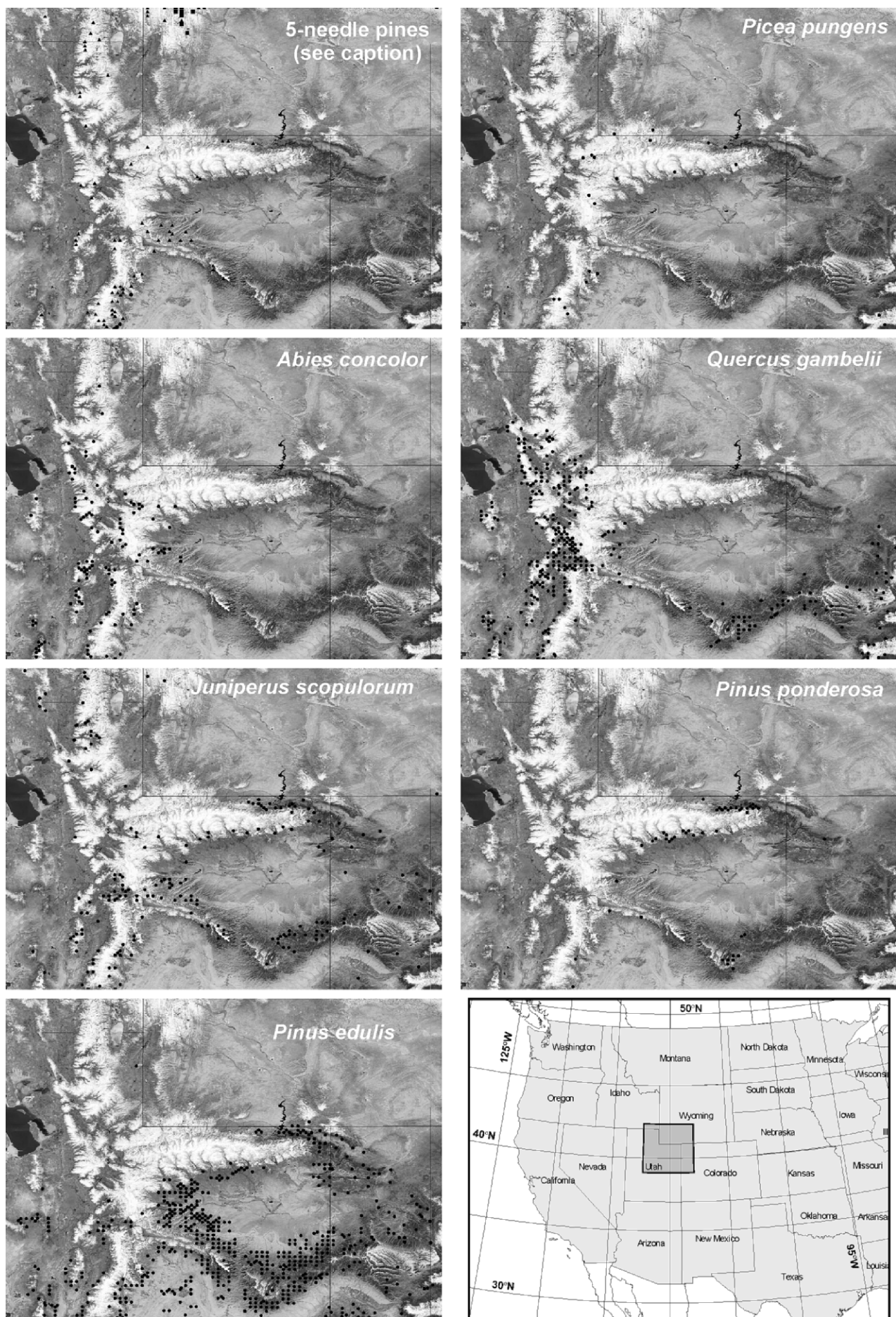
FIGURE 1. Continued.

the Uinta Mountains. Elsewhere in the geographic area covered in this study, plots were primarily distributed at approximately one plot per 2400 ha, and the range of plot visitation dates spans 1981 to 2005. In our evaluation of species distributions, we consider all FIA plot data collected in the states of Arizona, Colorado, Idaho, Montana, Nevada, New Mexico, Utah, and Wyoming. In our evaluations of forest type distributions and zonation, our area of interest is confined to the four geographic areas described above.

Each FIA plot samples an area of approximately one hectare, depending on the variable or plot characteristic being measured. The surface area on which individual trees are measured is approximately 0.067 ha. On the standard plot design, up to 120 variables are measured at the plot, subplot, condition (stand), or tree level; these include fundamental variables such as slope, aspect, elevation, species, stem diameter, and height. Additional variables, such as down woody debris and lichen diversity, are measured on a subset of the standard grid. The FIA program uses a nationally standardized algorithm to classify all United States forests into nearly 140 major and minor types (Arner et al., 2001).

Each plot was classified to a forest type using the standard FIA algorithm (Arner et al., 2001). We also created separate presence-absence data sets from the FIA plot data, which included the geographic coordinates of the plots and elevation at the plot center. Using the presence-absence and classified data sets, we mapped the distributions of species and forest types across the area of interest. As additional reference information, we supplemented the FIA plot data using species range information provided by Little (1971) for the central Rocky Mountains and Albee et al. (1988) for Utah, as well as MODIS imagery that was classified to forest type using a combination of geographic data (e.g., climate variables, topographic models) and FIA variables as ground truth data (Blackard et al., in press). We also examined the potential influence of geology on species distributions using Hintze's (1980) geological map of Utah. The digital version of the map used in our analysis was created by Ramsey (1996).

To summarize the elevational distribution of forest types in the four areas selected for comparison, we "clipped" plot data from the FIA master data set to create subsets for each of the geographic areas. Each subset included the entire elevational gradient from lower to upper treeline. Within the Uinta Mountains, we evaluated FIA data from three transect bands approximately 0.42° of longitude in width, oriented north-south, and centered at longitudes 109.67°W, 110.29°W, and 110.87°W to represent the eastern, central, and western Uinta Mountains, respectively. FIA forest type was plotted in a terrain cross section, providing an approximation of the elevation and latitude at which each type was dominant.

Results

TREE SPECIES DISTRIBUTIONS IN THE UINTA MOUNTAINS AND VICINITY

Tree species exhibit several distinct distribution patterns across the Uinta Mountains and adjacent areas (Fig. 1). For some species, their presence in the Uinta Mountains is an important feature of their ranges. For example, the Uinta Mountains have the only extensive *Pinus contorta* forest in Utah. With the exception of a few small, isolated populations, the range is also the southern limit of *P. contorta* in the western Rocky Mountains. In the Colorado portion of the Rocky Mountains, however, the range of *P. contorta* extends much farther south.

Considering species' global and local distributions, we placed the distribution patterns of trees in the Uinta Mountains into four characteristic groups: (1) common—occurring in large numbers within the appropriate habitat (*Abies lasiocarpa, Juniperus osteosperma, Picea engelmannii, Pinus contorta, Pseudotsuga menziesii,* and *Populus tremuloides*), (2) well-distributed, but uncommon—usually species with specific site requirements that occur throughout the Uinta Mountains, but occur sparsely and rarely form a dominant type (*Picea pungens* and *Pinus flexilis*), (3) bypass—species with global ranges that reach the latitude of the Uinta Mountains in the Wasatch Mountains, but do not extend eastward across the Uinta Mountains in any appreciable abundance (*Abies concolor* and *Quercus gambelii*), and (4) the "fishhook" distribution—species' ranges extend across the southern slopes, round the eastern end, and terminate near the eastern end of the north slope (*Juniperus scopulorum, Pinus edulis,* and *P. ponderosa*).

In our evaluation of species distributions we considered elevational distributions of species as well as geographic extent. Our data revealed that the expected negative relationship between latitude and elevation at which a given species is found apparently breaks down across our study area. Upper tree line peaks in elevation at approximately 38°N latitude, with *Picea engelmannii* and *Abies lasiocarpa* reaching nearly 3700 m. Farther north, the data show the expected, nearly linear negative relationship between the latitude and elevation range occupied by a species. Species with ranges that extend south of 38°N appear to occur at lower elevations with decreasing latitude. For some species, their potential upper elevation limits are unknown at lower latitudes because of a lack of high-elevation terrain at those latitudes. This phenomenon appears to hold true for all species for which we have data, and the effect—arch-shaped elevational distributions occurring over nearly 17° of latitude—is quite prominent for species that occupy a broad range of latitude (Fig. 2).

VEGETATION ZONES OF THE UINTA MOUNTAINS AND VICINITY

When we mapped FIA plot locations classified to forest type, the pattern of zonation in the Uinta Mountains was readily apparent (Fig. 3A). However, because vegetation zones are typically defined by potential or climax vegetation, the hierarchy of types must be considered when two or more types occur within the same range of elevation. For example, most associates of *Populus tremuloides* are more shade tolerant and, therefore, later successional. As a result, when the *Populus tremuloides* occurs within a band of elevation dominated by a more tolerant type such as *Pseudotsuga menziesii*, that zone could be designated as a *Pseudotsuga menziesii* zone. This method of designating potential vegetation type is effective in cases where stable or late successional types are common on the landscape. In the Uinta Mountains, the distribution of stand age classes suggests that later successional types are well-represented. Therefore, vegetation zones should be closely related to the distribution of current forest types.

The FIA program recently began development of map products, using FIA plot data in conjunction with current satellite imagery, topographic data, and other auxiliary information (Blackard et al., in press). Figure 3B is a portion of the forest type product that shows modeled dominant vegetation at 250 m resolution for the Uinta Mountains and vicinity. As is evident with FIA plot data, vegetation zones occur in concentric bands around most of the range, except for the northwestern foothills. In this area, there is an abrupt transition from high-elevation conifer types through a narrow, discontinuous *Populus tremuloides* zone, into *Artemisia* steppe with small patches of *Juniperus* woodland. Although *Pseudotsuga menziesii* exists in the area, it apparently
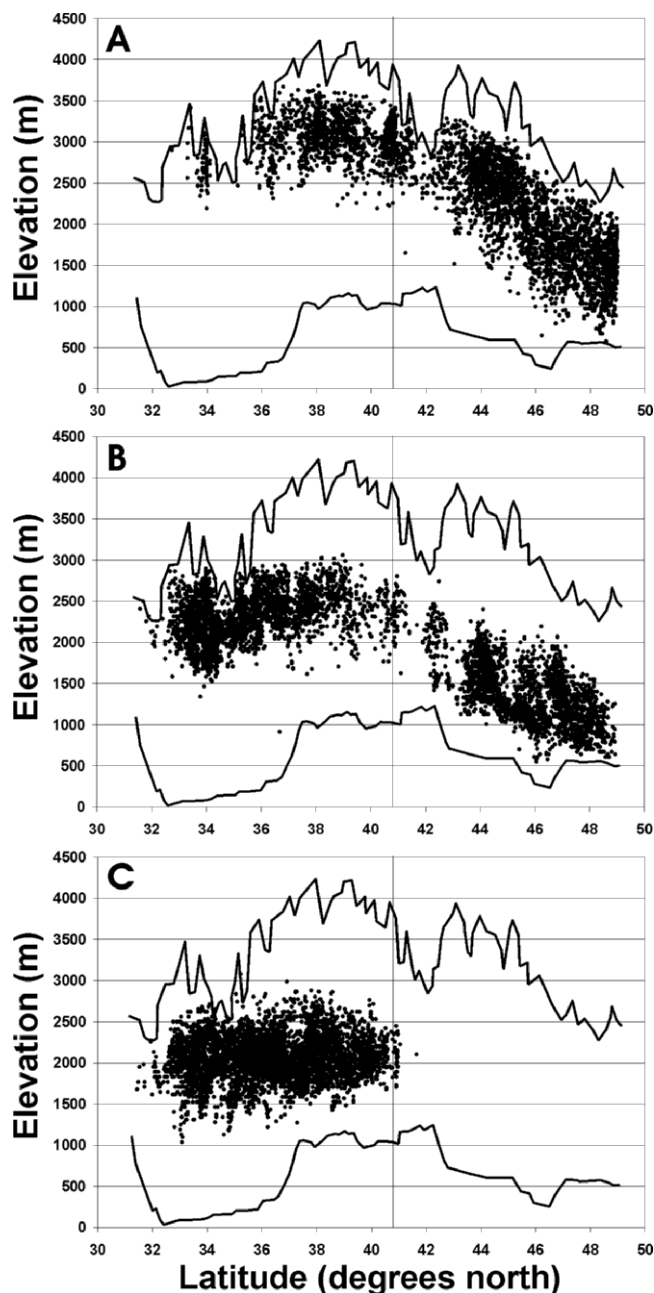
FIGURE 2. Elevation-latitude relationship for *Picea engelmannii* (A), *Pinus ponderosa* (B), and *P. edulis* (C). Dark lines show approximate upper and lower elevational limits of land surface, based on FIA plot grid (point elevations at approximately 5 × 5 km spacing). Vertical line is at the approximate latitude of the main divide of the Uinta Mountains.

does not dominate in large enough patches to show at the mapped resolution. In contrast, the southern valleys and eastern tip of the range exhibit the full range of forest types.

We developed a set of zone schematics for the Uinta Mountains along eastern, central, and western transects (Fig. 4), using forest type, elevation, latitude, and successional hierarchies. In Figure 4, the upper and lower elevation profiles represent the approximate maximum and minimum surface elevations within each transect, based on point elevations at the center of each FIA plot (including non-forested plots). Each zone is defined and named for the latest successional forest type common in that range of elevation. Some authors have portrayed significant "canting" of

vegetation zones between east and west slopes, as Woodbury (1947) did for the mountains of Utah. In many mountain ranges that are oriented north-south, rain shadow effects cause vegetation zones to differ in elevational distribution on east and west slopes. In the Uinta Mountains we might expect such differences to be caused by differential insolation on north vs. south slopes, as well as rain shadow effects from the two climate systems. However, we separated plots in the Uinta Mountains along the main divide, and found that there was not a substantial difference in elevational distribution in most cases. Exceptions appear to be related to causes other than an actual shift in vegetation zone elevational limits, such as differing species composition or the distribution of land surface elevation within the transect band.

The eastern transect spans just over 2000 m of relief, with the lowest elevations just under 1500 m in the Uinta basin. In the eastern part of the Uinta Mountains there is no upper tree line, and a pure *Picea engelmannii* zone is evident at the highest elevations (approximately 3250–3500 m). The south slope is dissected by deep valleys, such as Ashley Gorge, that facilitate zone "inversion"; here the *Populus tremuloides*, *Pseudotsuga menziesii*, and *Pinus ponderosa* zones are under the control of terrain contour and aspect. Beyond the northern limits of *Pinus edulis*, at least some plots classified as *Juniperus* spp. woodland occur at higher elevation where the *Pinus edulis–Juniperus* spp. type is expected. In effect, the *Juniperus* spp. zone expands by subtraction of *Pinus edulis* from the landscape.

The central transect has the greatest relief, ranging from 1500 m to nearly 4000 m. On this part of the north slope *Pinus edulis* and *Pinus ponderosa* are absent, and *Pseudotsuga menziesii* is less common than to the east. As a result, the *Pinus edulis–Juniperus* spp. and *Pinus ponderosa* zones of the south slope are replaced by a *Populus tremuloides* zone that is bounded at higher elevations by *Pseudotsuga menziesii* or *Pinus contorta* and at lower elevations by *Juniperus* spp. woodland. On the north slope the *Pseudotsuga menziesii* zone is discontinuous, and *Pinus contorta* dominates at somewhat lower elevations than on the south slope. The upper tree line is clearly evident in the central mountains, occurring at approximately 3500 m. A pure *Picea engelmannii* zone is less apparent than to the east. This may be caused by the effects of slope, aspect, or other site factors, or by sampling effects (i.e., *Abies lasiocarpa* locally absent at the plot scale). Whatever the cause, it appears that stands at the upper tree line are primarily of the mixed *Picea engelmannii–Abies lasiocarpa* type.

The western transect exhibits the lowest overall relief of the three transects, with a minimum elevation of approximately 2000 m and highest elevations around 3700 m. Although overall relief is lower, the variation in elevation at any given latitude along the transect is higher in the west—up to 1000 m, as opposed to 500–750 m in the eastern and central regions. Numerous long, deep glacial valleys are primarily responsible for this complex terrain. A clear *Pinus edulis–Juniperus* spp. zone traverses the upper Uinta basin. The *Pinus ponderosa* zone appears to be minor on the western part of the south slope; *P. ponderosa* is mostly found in mixed stands that occupy the bottoms of low-elevation valleys, and these stands are probably inclusions in the *Pseudotsuga menziesii* zone. As elsewhere on the south slope, the *Populus tremuloides*, *Pseudotsuga menziesii*, and *Pinus ponderosa* zones form a mosaic. Above this there also appears to be a complex arrangement of the *Pinus contorta* and *Picea engelmannii–Abies lasiocarpa* zones, with the *Picea engelmannii–Abies lasiocarpa* type dominating the heads of valleys and ridges, and the *Pinus contorta* and *Picea engelmannii–Abies lasiocarpa* types occupying somewhat lower elevations. On the north slope, *Pseudotsuga menziesii* is essentially absent, so there is a distinct *Populus tremuloides* zone of

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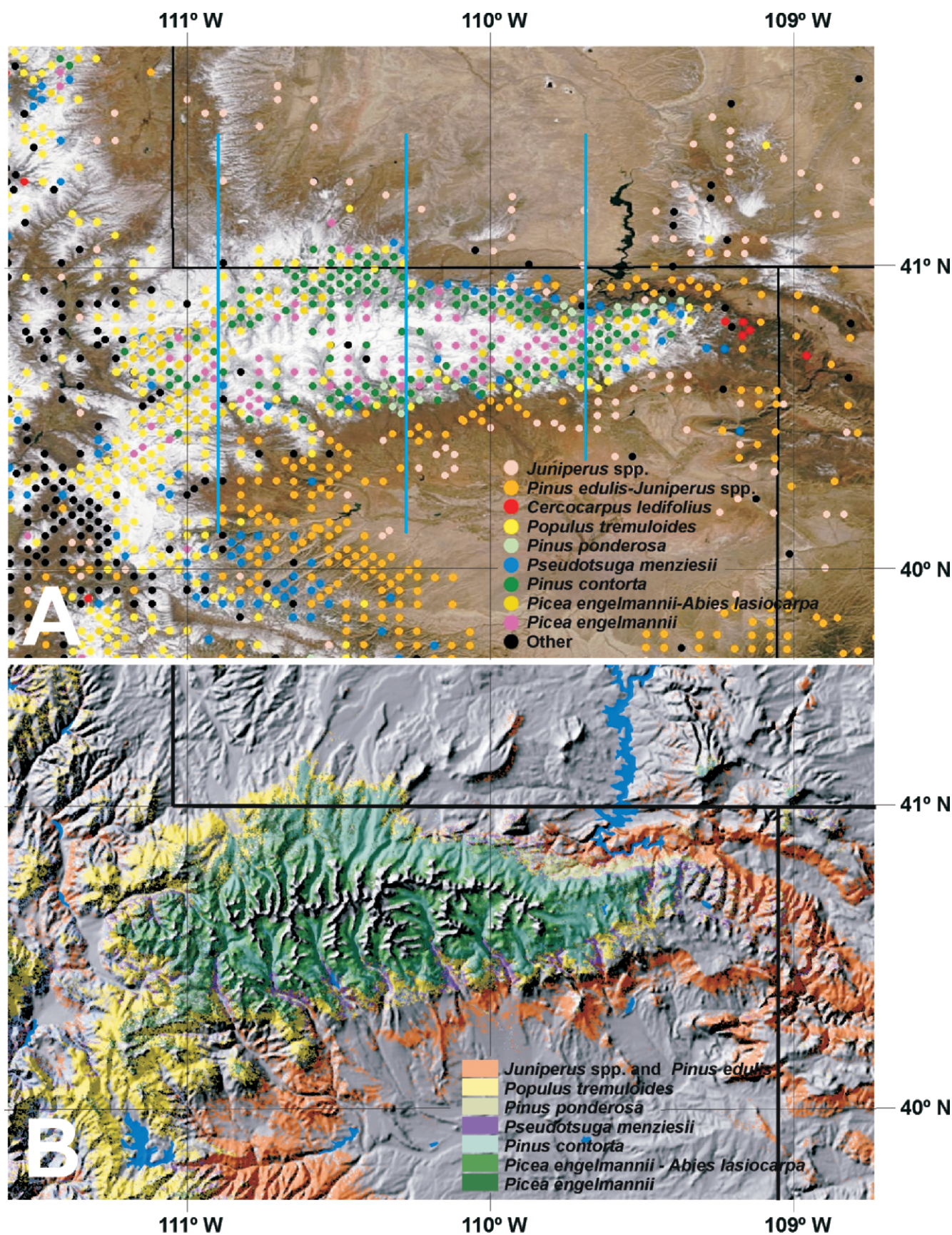**FIGURE 3.** Forest types at Forest Inventory and Analysis (FIA) plot locations (A) and modeled forest types (B) for the Uinta Mountains and vicinity. Some forest types mapped in (B) are combined or omitted from the legend for clarity. Blue lines in (A) are the midlines of forest zone transect bands (see Figure 4); bands are approximately 0.42° wide. Plot coordinates in (A) are approximate to preserve location confidentiality.
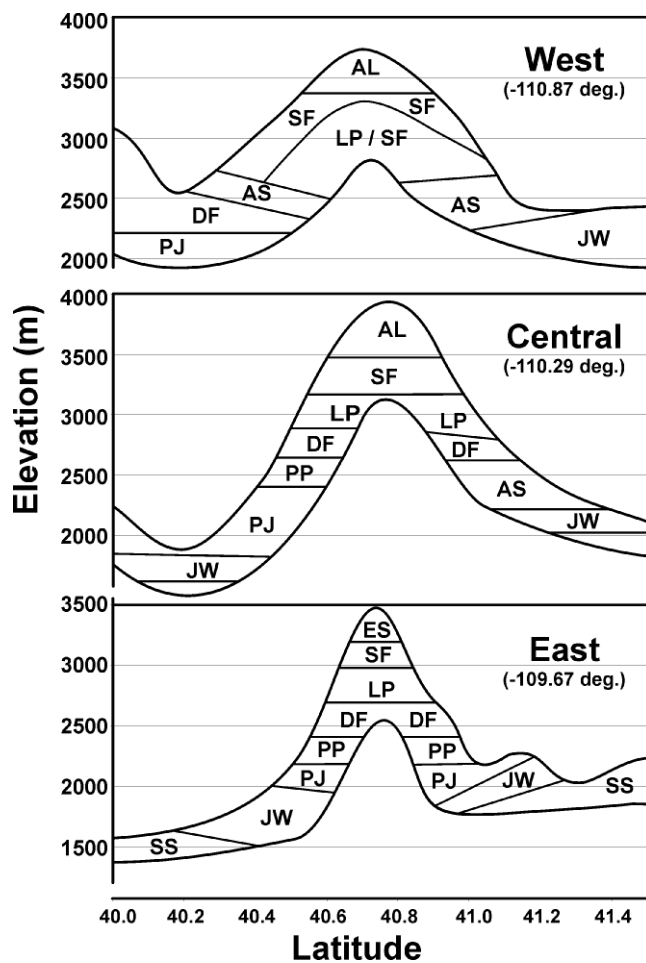
FIGURE 4. **Vegetation zones of the Uinta Mountains based on FIA data. Upper and lower lines represent approximate maximum and minimum elevations occurring in transect bands. Longitudes are midlines of transect bands. Angled zones indicate potential mixing of zones due to aspect. AL = alpine, AS = aspen (*Populus tremuloides*), DF = Douglas fir (*Pseudotsuga menziesii*), ES = Engelmann spruce (*Picea engelmannii*), JW = juniper (*Juniperus* spp.) woodland, LP = lodgepole pine (*Pinus contorta*), PJ = pinyon-juniper (*Pinus edulis–Juniperus* spp.), PP = ponderosa pine (*Pinus ponderosa*), SF = spruce-fir (*Picea engelmannii–Abies lasiocarpa*), SS = sagebrush (*Artemisia*) steppe.**

varying width and continuity (see Fig. 3B). Below the *P. tremuloides* zone is sparse *Juniperus* spp. woodland, barely constituting a zone because of its fragmented nature. The resulting effect on the western part of the north slope is a relatively abrupt transition from *Picea engelmannii–Abies lasiocarpa* and *Pinus contorta* forest types into non-forest (primarily *Artemisia* steppe), sometimes with a narrow *Populus tremuloides* zone.

The four geographic areas we selected for comparison show similar arrangements of forest types with elevation—i.e., types tend to maintain their order in each location (Fig. 5). An important feature revealed by this comparison is the effect of latitude on the elevation at which each type occurs.

GEOLOGY AND FOREST TYPE DISTRIBUTION

Overlaying FIA plot locations on Hintze's (1980) geologic map did not reveal any strong associations between geologic formation and forest type. However, a cross-tabulation of

elevation by forest type and geologic formation (Table 1) reveals some important relationships. First, the most common forest types found in the Uinta Mountains, *Pinus edulis–Juniperus* spp., *Picea engelmannii–Abies lasiocarpa*, *Pinus contorta*, and *Populus tremuloides*, occur on a broad range of formations. Second, each forest type tends to be confined to an elevation range of 500 to 1000 m, regardless of the formation on which it is found. In contrast, the geologic formations tend to span broader ranges of elevation than forest types; the portion of any given formation that supports any forest type typically spans 900 to 1500 m.

Discussion

FACTORS AFFECTING TREE SPECIES DISTRIBUTIONS

Daubenmire (1943) observed that, unlike the northern and southern Rockies, the central Rockies have no large woody plant species that are peculiar to the region. There are, however, a number of northern and southern Rocky Mountain species that have their latitudinal limits in the central Rockies. In some ways the central Rockies can be thought of as an ecotone between the northern and southern Rocky Mountains, and this may be particularly true of the Uinta Mountains. The Uinta Mountains appear to lie in a band of latitude where species turnover is especially high, resulting in relatively high tree species diversity. Although there are examples of high local (alpha) tree species diversity (Nord, 1928; Cottam, 1930; Graham, 1937), the uniqueness of the Uinta Mountains and surroundings may be better characterized by beta diversity, or species turnover that occurs across the landscape.

There is the general assumption that the limits of species at upper elevations and northern latitudes are controlled by temperature and that lower elevational and southern limits are associated with water stress (e.g., Daubenmire, 1943; Neilson and Wullstein, 1983). However, as Goodrich (2005) noted, many factors affect the distribution of vegetation in the Uinta Mountains and the relative importance of factors appears to vary locally. Two species distributions of interest in the Uinta Mountains—the bypass and fishhook types—are exhibited mostly by lower-elevation species that are near the absolute northern limits of their ranges or, in the case of *Pinus ponderosa*, its northern limit in the western central Rocky Mountains. This suggests that both precipitation and temperature limits may affect species distributions.

Arno and Hammerly (1984) attributed the differences in Uinta and Wasatch vegetation to summer rains vs. summer drought, differences in geology and topography, and the Wasatch Front as a "barrier" to plant migration. *Quercus gambelii*, a bypass species, is well represented in the Wasatch Mountains but nearly absent in the Uinta Mountains. Neilson and Wullstein (1983) suggested that the northern ecotone of *Q. gambelii* results from the elevational convergence of the "tolerable thermal and moisture zones" (i.e., spring freezing and summer drought). The ranges of bypass species, therefore, may be explained primarily by climatic and geologic differences between the Wasatch Range and the Uinta Mountains.

The fishhook distributions, however, may be most strongly controlled by climatic conditions that are influenced by the Uinta Mountains themselves. The topography of the Uinta Mountains appears to affect the strength of the monsoon climate regime. Munroe (2003a) showed that the summer wet/winter dry precipitation pattern appears to wrap around the Uinta Mountains on the eastern flank, reaching its western limit on the north slope at approximately 110.56°W. Just east of this longitude, the main
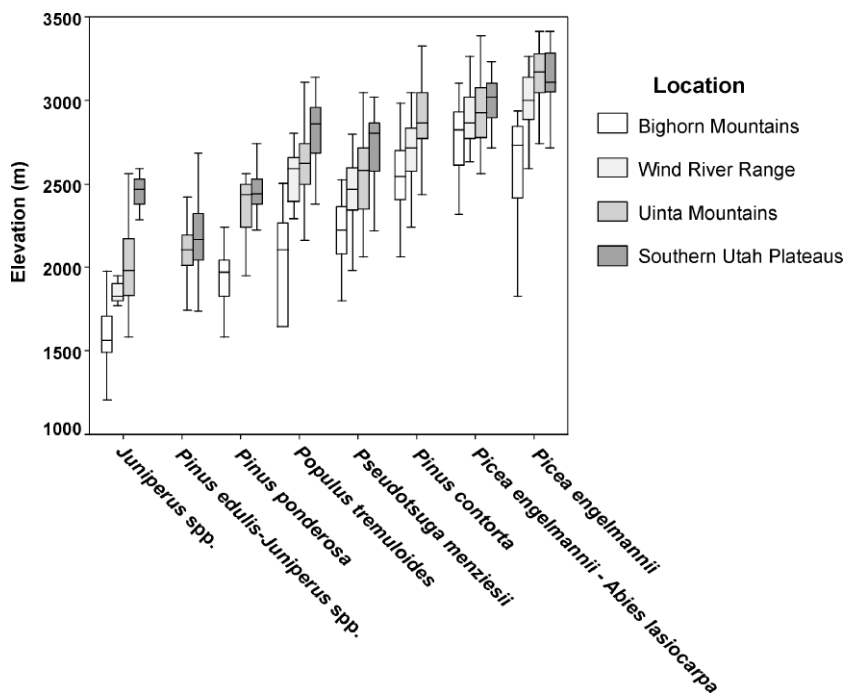
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FIGURE 5. Elevational distributions of forest types common in the central and northern Rocky Mountains. Trends among regions within types show latitude-elevation relationship. Some forest types do not occur in all four regions. Wide spread in the juniper woodland type is partly due to different species that define the type in different regions. Horizontal bars represent median elevation; vertical bars and whiskers represent quartiles. Elevations of outlying observations are omitted for clarity.

divide of the Uinta Mountains is at its highest elevation (>4000 m). Following the divide eastward, maximum elevations continue to decrease and the mountains present a lessening barrier to monsoonal moisture.

On the north slope the western limits of the three fishhook species—*Juniperus scopulorum*, *Pinus ponderosa*, and *P. edulis*—are nearly coincident at approximately 109.90°W, or about 50 km east of where Munroe's (2003a) analysis located the western limit of the summer wet/winter dry precipitation pattern. At this longitude, the maximum elevations of the Uinta Mountains are less than 3100 m and the hydrologic divide approaches 2900 m. Given the coincidence of species distributions, limits of the monsoon pattern, and lowering of topography, it may be reasonable to assume that there is a barrier effect.

Although the range of *Pseudotsuga menziesii* was not characterized as a fishhook distribution, this species becomes more dominant moving eastward along the north slope, and the western extent of the north slope is coincident with the transition between summer dry/winter wet (Monroe, 2003a). One may argue that this pattern is influenced by the presence of geologic and topographic features in the eastern part of the north slope that are not present in the western part; *Pseudotsuga menziesii* forms some of its best stands on limestone hogbacks that are prominent in the eastern parts, but absent to the west.

The negative relationship between latitude and the elevation at which a species exists is a relatively well-known concept in plant ecology. However, less well-understood are the local effects of relative relief and climatic effects. We noted earlier that upper tree lines tend to be limited by temperature, whereas lower tree lines are typically limited by precipitation. Therefore, where elevation fails to be an effective proxy for temperature or precipitation, knowing the local climatic regime should be a better predictor of vegetation distribution. Gannett (1882) recognized this and noted dramatically different tree lines at similar latitudes. He attributed an apparent breakdown in the elevation-latitude relationship below 41° in the Rocky Mountains to an "accident of topography," meaning that the abruptness of elevation change over the local landscape was more important than absolute elevation.

FOREST TYPES AND ZONES

Comprehensive descriptions of Rocky Mountain forest and woodland biogeography have been provided by West and Young (2000) and Peet (2000). Peet's (2000) treatment of the distribution and structure of Rocky Mountain forests included generalizations concerning the distribution of the major zones with respect to elevation and topographic-moisture gradients. Our local adaptation of Peet's (2000) schematic (Fig. 6), in conjunction with our cross-section descriptions (Fig. 4), provides a generalized zonation model for the Uinta Mountains that is finer in resolution and more comprehensive (for forest vegetation) than the descriptions by Svihla (1932) and Graham (1937), but is somewhat coarser in resolution than the site-specific relationships described by Mauk and Henderson (1984) and Goodrich (2005). As such, our model fills in the middle ground and provides a useful template for comparing and contrasting the distribution of major vegetation zones in the Uinta Mountains with zones in other mountain ranges.

EFFECTS OF SUBSTRATE ON VEGETATION DISTRIBUTION

Peet (2000) argued that for most vegetation studies in the Rocky Mountains, the "conspicuous" importance of elevation and moisture tends to obscure the influence of substrate variation. Graham (1937) noted a lack of correlation between substrate and vegetation zones in the Uinta Mountains, stating that environmental factors such as precipitation, temperature, and length of growing season were more influential on vegetation than variations in substrate. Peet (2000) cited Despain's (1973) study of the Bighorn Mountains as a counter-example which highlights the influence of substrate.

We will not settle the question here, but it may be that the relative influence of substrate depends on the scale of the analysis. We conducted our analysis at the scale of the formations and found no obvious associations. However, many of the geologic formations include members of varying lithology and texture; any

sensitivity of vegetation to this variation is lost at the scale of our analysis.

Goodrich (2005) provided several examples of microscale zonation, especially in the alpine zones. Likewise, Mauk and Henderson (1984) distinguished their habitat types on the basis of site quality and understory associates, both of which are sensitive to substrate as well as climate. A significant portion of silvicultural and ecological research is dedicated to understanding these sensitivities, so to say that there is no correlation between forest zones and substrate would be misleading. Rather, at the scale of the Uinta Mountains these local variations tend to appear as noise when compared to the dominant effects of elevation, moisture, temperature, and other factors such as disturbance.

ROLE OF DISTURBANCE IN VEGETATION ZONES

Disturbance Regimes in the Interior West

Disturbance regimes play a key role in the ecology and biogeography of western United States forests and can greatly alter successional trends and vegetation zonation. Although humans may have influenced these forests for millennia (Kay, 1994), we are especially interested in the alteration of disturbance regimes following pioneer settlement of the western United States. Natural and human-caused disturbance interact and modify patterns developed by climate and topography.

Bark beetles are extremely important ''agents of change'' in Rocky Mountain coniferous forests (Samman and Logan, 2000). In the Uinta Mountains the principal bark beetles are *Dendroctonus ponderosae*, *D. pseudotsugae*, and *D. rufipennis*. *Dendroctonus ponderosae* attacks *Pinus contorta*, *P. ponderosa*, and *P. flexilis*. *D. pseudotsugae* and *D. rufipennis* are restricted to *Pseudotsuga menziesii* and *Picea engelmannii*, respectively. At endemic levels, attacks by these bark beetles are focused on isolated individuals and small groups of the host trees. Outbreaks, such as the *Dendroctonus ponderosae* outbreak that occurred in the Uinta Mountains in the early 1980s, can occur when locally high populations of beetles are coupled with large numbers of susceptible host trees and environmental conditions favorable for beetle survival (Samman and Logan, 2000). For each of these important bark beetle species, host susceptibility is exacerbated by an abundance of large, less vigorous trees, conditions typically found in dense mature stands dominated by the host species.

The legacies of fire are ubiquitous in the forests of the Uinta Mountains and there are important differences in fire regimes with respect to temperature, moisture, and elevation associated with zonation. For example, fires are exceedingly infrequent in the high-elevation *Picea engelmannii–Abies lasiocarpa* zone where fuels are typically too wet to burn (Bradley et al., 1992). In an unpublished report of north slope fire history, Wadleigh (1997) suggested fire frequencies of 300 years in the *Picea engelmannii– Abies lasiocarpa* zone; nevertheless, she observes that evidence of these infrequent fires is ubiquitous. In contrast, on warm, dry sites at lower elevations, e.g., within the *Pinus ponderosa* zone, fine fuels accumulate rapidly and fires were frequent in the absence of fire exclusion. There is an inverse relationship between fire frequency and severity in these forested ecosystems (Long, 2003). Within the *Picea engelmannii–Abies lasiocarpa* zone the heavy accumulation of fuels during the long period between fires often results in a high-severity, stand-replacing disturbance when a fire does occur. In contrast, in the absence of fire exclusion, the frequent fires in low elevation forests would have been low-severity, understory fires.

The implications of fire exclusion vary by zone, forest type, and the natural fire regime. In the *Picea engelmannii–Abies lasiocarpa* zone where fires were naturally uncommon, fire exclusion has had limited impact. In the *Pinus ponderosa* zone where fires were naturally frequent, fire exclusion is associated with the development of dense stands with continuous canopies and abundant ladder fuels; such stands are at increased risk of stand-replacing fire (Agee and Skinner, 2005). The implications of fire exclusion in forests that would have had intermediate fire frequencies (e.g., 100–200 years) are most apparent at the landscape level (Long, 2003). This is illustrated by shifts in the age-class distribution of *Populus tremuloides* and *Pinus contorta* stands.

Pioneer-era and subsequent logging has also influenced the age-class distribution of stands, primarily in the lower zones. This effect is particularly apparent in the *Pinus contorta* zone on the north slope. The route of the original transcontinental railroad was just to the north of the Uinta Mountains, and tie-hacking for railroad construction began in 1867 (Ayres, 1983). Logging for charcoal production and tie replacement for the Union Pacific Railroad continued for decades.

Resulting Vegetation Patterns

Disturbance tends to produce characteristic patterns on the landscape with respect to forest composition and stand age class distribution. For our discussion of age class distribution, we will place the Uinta Mountains in the context of neighboring mountain ranges. As with the characterization of forest type, the FIA program uses an algorithm to calculate stand age class. While the calculation of stand age in even-aged stands is elementary, the age of uneven-aged stands is subject to a user's definition. The stand age calculated by FIA is designed to reflect the age of the dominant size class occurring on a plot, thereby avoiding overstatement of age in cases where a few relict individuals from a previous stand may remain after a stand-replacing disturbance.

The age class distribution in the Uinta Mountains is a legacy of disturbance history (Fig. 7A). The forested landscape consists of a complex mosaic of patches of different ages reflecting time since the last major disturbance. The age distribution of boreal and subalpine forested landscapes can be effectively characterized by a negative exponential model, the details of which depend on disturbance frequency (Johnson et al., 1995). While we do not have sufficient information on the disturbance ecology of Uinta forests to specify the model precisely, it is clear that in general, age class distribution is consistent with expectations for a landscape with a stand-replacement fire regime. However, this distribution is only evident in stands of pre-settlement age (Fig. 7A). The modal age class is 80–100 years, reflecting the beginning of settlement-era logging and a period of increased fire frequency (Wadleigh, 1997). During the last 70 years or so both logging and fires have been greatly reduced. As a result, there is an ''excess'' of the 80–100 year age class (analogous to the human ''baby boom'' demographic) and a substantial ''deficit'' in the <70 year age classes.

This pattern has significant implications for future disturbance regimes and current management planning. As this cohort ages, it becomes more susceptible to stand-replacing fire and insects because of fuel accumulation over time and movement of trees into size and age classes more susceptible to bark beetles (Samman and Logan, 2000). This age class would have been represented during the natural disturbance regime, of course, but by occupying a larger proportion of the landscape than usual there is an increased possibility of contagion between susceptible patches. This can open the way for unusually large disturbance

TABLE 1

Occurrence of major Forest Inventory and Analysis (FIA) forest types on geologic formations of the Uinta Mountains and vicinity. Main body cell values are mean elevations for plots occurring on the formation, with number of plots in parentheses. Bottom row shows mean, maximum, and minimum elevations, and total number of plots for each forest type on all formations. Right column shows mean, maximum, and minimum elevations, and total number of plots for each geologic formation. Formation figures also include plots for minor types that have been omitted from the type list for clarity. As a result, some plot totals in the right column are greater than the sum of the major forest types. Geologic units are based on Ramsey's (1996) digital conversion of the Geologic Map of Utah (Hintze 1980).

Geologic formation†	184	185	201	221	265	266	268	281	901	925	Formation, all forest types Mean (Min, Max, n)
C1		1951 (1)				2804 (2)	2828 (1)		2773 (1)		2632 (1951, 2835, 5)
J1	1707 (1)	2073 (1)	2347 (1)			2713 (1)			2489 (3)		2329 (1707, 2713, 7)
J2	1878 (3)							2499 (1)	2722 (3)		2300 (1832, 2774, 6)
Jg	1771 (7)	2027 (2)							2781 (5)		2202 (1646, 3128, 16)
K1										2188 (1)	2188 (*, *, 1)
K2		2048 (4)							2506 (4)	2101 (2)	2242 (1951, 2652, 10)
K3			2743 (1)		3231 (1)	2865 (1)			2536 (10)	2211 (2)	2449 (1756, 2804, 14)
M2									2879 (3)	2286 (2)	2758 (2286, 3231, 7)
M3					3091 (1)	3033 (2)					3052 (2957, 3109, 3)
P2	2042 (1)	2266 (3)	2621 (1)			2911 (4)	2860 (1)		2468 (3)		2548 (2042, 3109, 14)
PCm		2134 (1)									2134 (*, *, 1)
PCs	2316 (2)	2096 (11)	2578 (25)	2320 (13)	3213 (32)	2971 (25)	2948 (4)	2938 (41)	2666 (20)	2562 (2)	2772 (1829, 3439, 190)
P		2111 (4)	2575 (4)			2865 (2)	2989 (1)	2682 (1)	2581 (4)		2533 (1951, 2989, 17)
PP		2054 (2)	2499 (2)			2865 (3)		2806 (4)	2604 (12)	2499 (1)	2633 (2054, 3048, 24)
Qa	1853 (2)	2015 (6)			2965 (3)	2687 (6)		2784 (10)	2526 (1)		2526 (1744, 3078, 29)
Qao	1868 (3)	1846 (3)						2965 (3)			2360 (1707, 3109, 11)
Qg	2015 (5)	2053 (4)	2617 (7)	2541 (4)	3144 (38)	3048 (24)	3078 (2)	2920 (68)	2660 (17)		2901 (1890, 3453, 177)
Qls	1962 (1)	2103 (2)				2713 (3)		2454 (2)	2547 (2)		2388 (1951, 2865, 11)
T1									2526 (5)		2627 (2164, 3134, 6)
T3	1760 (12)	2152 (29)	2483 (4)		3138 (3)			2798 (7)	2720 (7)	2387 (2)	2285 (1585, 3200, 67)
T4		2057 (2)	2286 (1)		2995 (7)	2869 (9)	3056 (1)	2943 (26)	2678 (11)		2815 (2042, 3231, 60)
TK									2302 (3)	2157 (2)	2244 (2058, 2560, 5)
Tov			2560 (1)		2926 (1)	2560 (1)			2770 (7)		2744 (2560, 2926, 10)
TR1	1952 (5)	1895 (4)							2713 (1)		2049 (1676, 2713, 11)
TR2	1848 (4)	2210 (2)							2835 (1)		2104 (1676, 2835, 8)
Forest type, all formations mean (min, max, n)	1870 (1584, 2560, 46)	2092 (1676, 2422, 80)	2565 (2063, 3048, 47)	2372 (1951, 2560, 17)	3149 (2530, 3414, 86)	2931 (2256, 3385, 83)	2968 (2649, 3145, 10)	2904 (2438, 3322, 165)	2638 (2090, 3170, 123)	2293 (1981, 2743, 14)	2664 (1585, 3453, 710)

Key to geologic formation codes

C1 – Lodore Sandstone
J1 – Curtis Formation, Entrada Sandstone, Carmel Formation
J2 – Morrison Formation
Jg – Nugget (Navajo) Sandstone
K1 – Dakota and Cedar Mountain Formations
K2 – Mancos Shale (Hilliard Shale & Blair Formation north of Uinta Mountains), Frontier Sandstone, Mowry Shale
K3 – Mesaverde Group
M2 – Humbug Formation, Deseret Limestone

Key to forest types

184 – *Juniperus* spp.
185 – *Pinus edulis-Juniperus* spp.
201 – *Pseudotsuga menziesii*
221 – *Pinus ponderosa*
265 – *Picea engelmannii*
266 – *Picea engelmannii / Abies lasiocarpa*
268 – *Abies lasiocarpa*
281 – *Pinus contorta*

(continued)

TABLE 1
(continued)

Key to forest types

901 – *Populus tremuloides*
925 – *Quercus* spp.

Key to geologic formation codes

M3 – Doughnut Shale
P2 – Park City Formation
PCm – Red Creek Quartzite
PCs – Uinta Mountain Group
P – Morgan Formation and Round Valley Limestone
PP – Weber Sandstone
Qa – Alluvium and coluvium
Qao – Older alluvium
Qg – Glacial deposits
Qls – Landslides
T1 – Wasatch/Cotton Formation, Flagstaff Limestone
T3 – Duschesne River Formation, Uinta Formation - south of Uinta Mountains, Bridger Formation - north of Uinta Mountains
T4 – Bishop Conglomerate
TK – North Horn and Currant Creek Formations
Tov – Oligocene volcanic rocks
TR1 – Moenkopi Formation, Dinwoody Formation
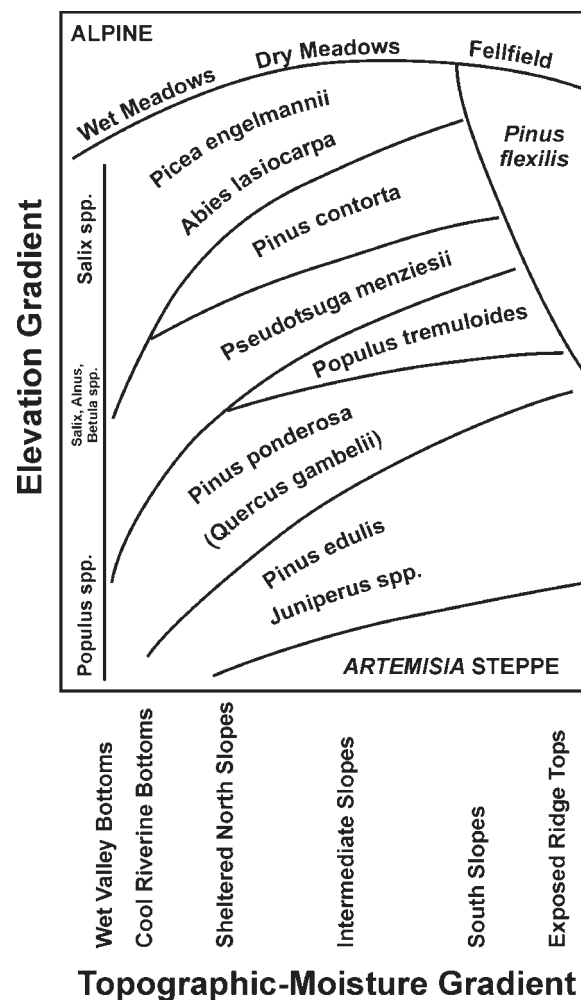TR2 – Chinle Shale, Gartra Sandstone Member

FIGURE 6. Generalized vegetation zonation in northern Utah along elevation and moisture gradients (after Peet, 2000).

events, especially when a large acreage of susceptible stands is combined with stress events such as drought.

This scenario is already under way. The second mode in the graph (Fig. 7A), which occurs in the youngest age classes, is caused, at least in part, by stand-replacing disturbances in the increasingly susceptible age classes. In some cases, forest managers have recognized the age class imbalance and are regenerating stands in order to restore the historical age class distribution. However, the rate of replacement generally lags behind the graduation of stands into a susceptible condition. As a result, large acreages will remain at risk for some time.

This pattern is not unique to the Uinta Mountains. The Bighorn Mountains, Wind River Range, and southern Utah plateaus all exhibit similar patterns (Figs. 7B–7D). This makes synchronized, large-scale disturbance a possibility. Such an event occurred recently in the southwestern United States, when prolonged drought facilitated a bark beetle epidemic over much of the range of *Pinus edulis* (Shaw et al., 2005). Synchrony of such events appears to occur when stressful environmental conditions coincide with large acreages of forest in a susceptible condition, as has been shown for the climate-fire relationship in the Southwest (Baisan and Swetnam, 1990; Swetnam and Betancourt, 1990). Under such circumstances, disturbance appears at multiple points on the landscape and spreads locally through contagion. As a result, the overabundance of susceptible conditions may not
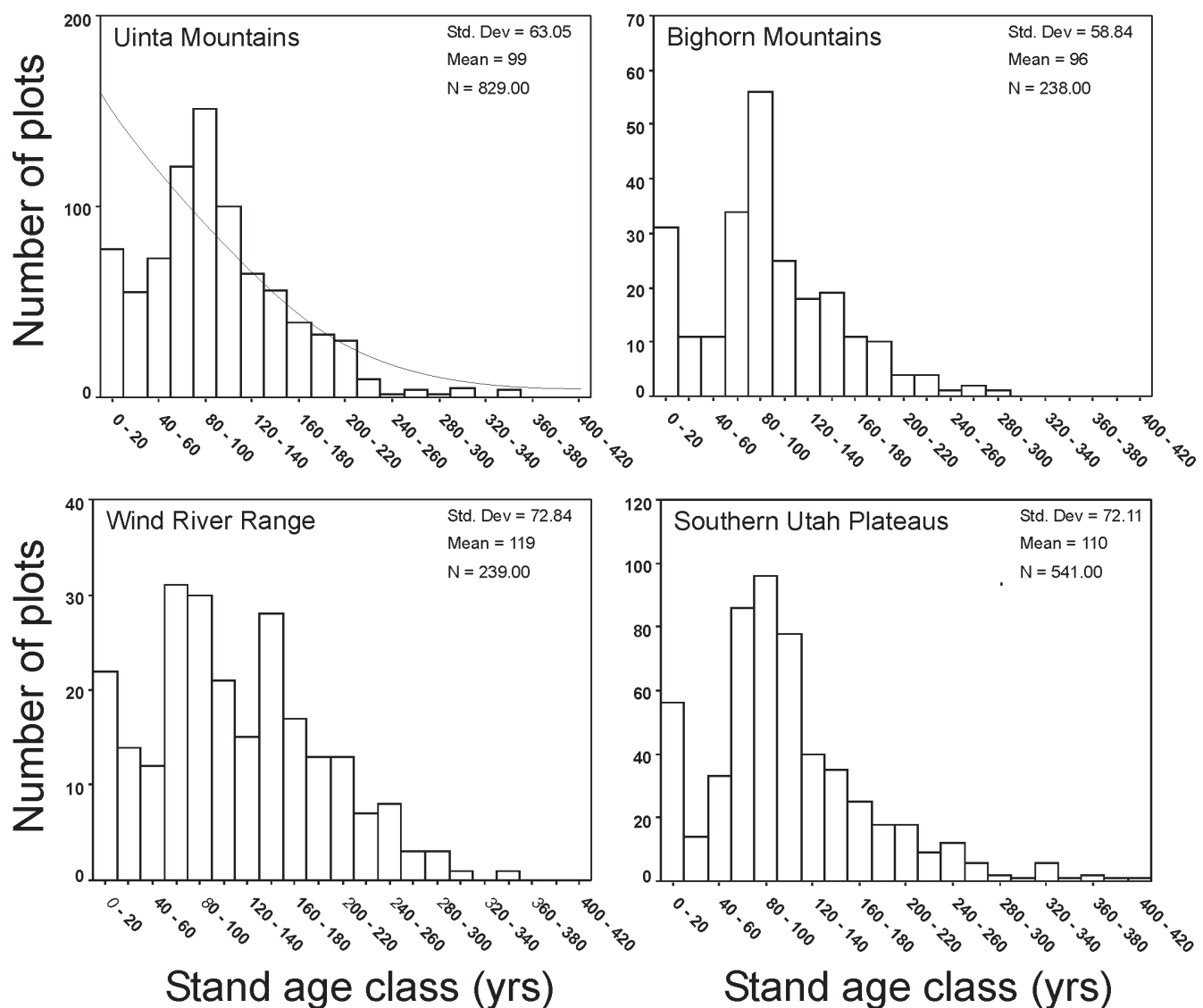
FIGURE 7. Age class histograms for the Uinta Mountains, Bighorn Mountains (Wyoming), Wind River Range (Wyoming), and southern Utah Plateaus. Curve on Uinta Mountains graph approximates expected age class distribution under a historical disturbance regime.

necessarily cause the start of disturbance, but it can affect its severity and rate of spread.

Conclusions and Recommendations for Future Research

Our investigation into the state of knowledge about forest ecology and biogeography in the Uinta Mountains has revealed some gaps. Some of these gaps relate to the current condition of the forest and historical processes and events that created it. Other gaps are more basic in nature, such as the definition of species-specific climatic envelopes. Although it is likely that the forest types and zones found in the Uinta Mountains share much of their general ecology with similar types elsewhere, there are undoubtedly important differences at local scales. For example, the relationships between forest type, substrate, and landform observed by Goodrich (2005) are unique to the Uinta Mountains and must be characterized locally. It is possible that some of the unique characteristics of Uinta Mountains forests have gone unnoticed or have not been addressed because of assumptions about the characteristics of species and environments in the Uinta Mountains as compared with other western mountains.

Perhaps the most important differences are those related to individual species distributions, the effect of range limits on the local distribution of forest types and zones, and the distribution of types and zones on the greater landscape. The arrangement of vegetation zones in the Uinta Mountains is relatively predictable, but there is a lack of understanding with regard to the discontinuity of these zones across the range. The role of substrate has not been adequately addressed, nor has the role of the mountains themselves as a barrier to plant migration and an influence on local climate. Once the basic ecological processes are understood, the effects of environmental change on the future forests of the Uinta Mountains can be projected more accurately.

Of course, there is research being conducted in some of the topic areas that we mention here. However, the applicability of results is a function of scale. Some efforts approach species distribution and projected response to climate change at the regional scale (e.g., Bartlein et al., 1997; Shafer et al., 2001; Cole and Arundel, 2007). In studies such as these, the subtleties of vegetation distribution that we illustrate in this paper tend to be lost due to issues of scale, especially in areas where modeled results

are uncertain. At the other end of the spectrum, localized studies (e.g., Munroe, 2003a, 2003b) reveal detailed local histories of vegetation change but may lack potential for inference to the greater landscape. Therefore, we advocate a meso-scale approach that encompasses the greater Uinta Mountains ecosystem.

Acknowledgments

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