

Article

Topographic Control of Forest Species Distributions in the Interior West from Forest Inventory and Analysis Data

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Abstract

The geographic distribution of forest and woodland ecosystems in the Interior West United States is strongly influenced by topographic factors that, in part, control moisture availability through their effect on insolation, precipitation capture, and retention. Through an empirical approach, we use unique, plot-level data from the Forest Inventory and Analysis Program ($n = 13,437$) over eight ecoregions within eight Interior West states to characterize the distribution of the 12 most abundant tree species with respect to the effects of elevation, slope aspect, and slope steepness. Across species, elevation, and aspect, most forested plots occurred on gentle slopes and the number decreased with increasing slope. Species-specific differences in microenvironmental conditions were evident in the variation between observed (plots containing a subject tree) and expected (all forest plots from the systematic sample) numbers of plots across the gradient combinations. Species groups, broadly defined as woodland, montane, and subalpine, generally exhibited similar responses and revealed more generality than hypothesized. Only Douglas-fir, white fir, subalpine fir, and Engelmann spruce exhibited significant patterns of affinity for particular aspects—most often on north and least often on south—with the relative importance of south aspects decreasing with increasing elevation. Limber pine showed unique, unimodal patterns of affinity for moderately steep slopes, with no consistent patterns by aspect or elevation. Although not significant, at high elevations, woodland species exhibited a tendency to occur more often on south aspects on gentle to intermediate slopes, and less often on north aspects. Unique microenvironments created by interactions between aspect, slope, and elevation create some predictability in the patterns of where species occur. While there were predictable and significant patterns for a few important montane and subalpine species, most species examined lacked any significant relationships to slope, slope aspect, or elevation, suggesting that patterns of occurrence in relation to physiographic factors are much broader than in common generalizations.

Keywords: topography; slope aspect; insolation; elevation; microclimate; forest distributions; forest inventory and analysis; great basin; central and southern Rocky Mountains

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1. Introduction

The distribution of vegetation in the semi-arid, Interior West United States (i.e., Great Basin and central and southern Rocky Mountains, and southwest region) is strongly influenced by topographical factors, such as elevation, slope aspect (hereafter “aspect”), and slope steepness (hereafter “slope”), which directly and indirectly control solar radiation, moisture available to plants, and edaphic characteristics [1]. Forests—clearly associated with mountainous terrain in arid and semi-arid environments [2]—respond to critically important macroclimates created by the topography, such as the presence, juxtaposition, height, and orientation of mountains, which influence the amount and type of precipitation that is delivered. Indeed, previous work has documented the role of elevation on the occurrence of forests, with the view that mountains are “islands” of suitable habitat among a “sea” of hotter and drier valleys [3,4]. However, just as non-forested valleys may not be uniformly unsuitable for trees [5], mountain environments themselves are heterogeneous, providing a range of potentially suitable habitats across interacting microclimatic gradients of aspect and steepness. Assuming relatively consistent propagule pressure, the establishment and survival of tree species in these heterogeneous environments will be influenced by their autoecological traits. In a break with traditional gradient analysis, we make use of a large, systematic random sampling design to document and investigate empirical relationships between elevation, slope, and aspect, and their possible effect on the occurrence of the 12 most abundant tree species in a large area of the Interior West. This basic characterization, heretofore impossible due to required sampling effort, provides a fundamental underpinning to previous work on vegetation distributions.

Gradient analysis [6], whereby groups of sampled species are typically displayed along gradients of elevation, as a proxy for temperature, and topographic characteristics, representing soil moisture, has yielded insight into broad-scale patterns of species composition [7], potential competitive interaction [8], variation in disturbance characteristics [9], and ecological change [10]. However, these non-random sampling approaches across large areas (e.g., elevation, latitude, longitude) are likely to nuance our understanding of natural patterns, as they often seek to maximize variation in gradients. More recent efforts have emphasized that topographic variables are proxies for multiple environmental factors that directly control the establishment and survival of forest tree species [11], and that they interact to amplify or dampen microenvironmental conditions, making their collective influence important, but they are rarely explored directly [12].

Temperature control on vegetation occurrence that is associated with elevation is evident from broad-scale analyses of the upper tree line [13], and the relationship between temperature and insolation is reflected in the decreasing elevation of typical vegetation zones with increasing latitude [8]. Elevation also enhances precipitation from storm tracks due to orographic lifting; windward slopes predictably receive much higher moisture than leeward, and this holds regardless of the orientation of the landform. For example, north–south trending Basin and Range mountains clearly exhibit this pattern, but the east–west trending Uinta Mountains in Utah do as well [14]. The apparent affinity of some species to particular elevation bands may be masked, or accentuated, by aspect and slope controls on vegetation occurrence [15], and by temporal variability in low-frequency climatic conditions [16].

Aspect, like elevation, is also a proxy for environmental variables that directly influence forest characteristics [17] and could control the occurrence of particular species. In mid-latitudes of the Northern Hemisphere, aspect controls the influence of insolation on how moisture is retained (primarily in the soil), making NNE aspects the coolest and wettest, while SSW aspects are the most exposed and driest [18,19]. Important for the Interior West United States, most of which receives a majority of its precipitation as wintertime snow from Pacific-origin westerlies [20], is the rain shadow effect exhibited by large

mountains, generally producing wetter west aspects and drier east aspects. However, this difference is at least partially mediated by a reduction in insolation on either the west or east slopes in comparison to the south slopes. Similarly, at both the upper and lower tree lines, the dynamics of species distribution can vary between the north and south slopes [21].

Slope can also directly and indirectly influence the retention of moisture available to plants. Directly, slope affects runoff and infiltration rates [22], and indirectly, it can influence soil development rates [23], loss of soil through mass movement [24], and can amplify or dampen the effect of the aspect on insolation intensity [25]. Depending on latitude and time of year, slope steepness interacts with solar radiation in such a way that perpendicular insolation is possible on southerly aspects, resulting in the highest possible concentration of insolation. In contrast, steep, northerly slopes may rarely, if ever, receive direct insolation, resulting in cooler, moister microclimates. The combined effects of slope and elevation result in north aspects at low elevations having very similar moisture conditions to south aspects at high elevations [12,26].

There is, perhaps, no better region than the U.S. Interior West where the influence of mountains on vegetation via topographical controls is so striking at multiple scales. For example, steep, north-facing slopes dominated by Douglas-fir (DF, *Pseudotsuga menziesii* Franco. Mirb.) directly adjacent to broad, south-facing slopes dominated by Utah juniper (UJ, *Juniperus osteosperma* Torr. Little) are obvious from many mountain valleys. While this observation is partially explained by invoking the autecological traits of each species, e.g., DF's affinity for a moist microclimate [27], versus the ability of UJ to tolerate very dry sites [28,29], a more empirical, broad-scale examination is warranted. Using the U.S. Forest Service, National Forest Inventory and Analysis program data—an extensive, semi-systematic, random sampling grid—we explore the effect of slope, aspect, and elevation on the occurrence of tree species in the semi-arid Interior West. We build upon previous work by explicitly examining the influence of topographical gradients on individual species, using direct observations of site conditions and species presence across the study area. In particular, we address the following research questions. (1) Where are individual species most likely to occur based on aspect and slope in comparison to population-level expectations? (2) Does observed occurrence by aspect and slope change with increased elevation due to lower temperature and increased moisture availability? (3) Do the relationships with topographic variables differ when species are analyzed only where they are dominant (i.e., abundance rather than presence)? (4) Are there important similarities or differences among groups of species? We hypothesized that: (1) regardless of species, most forested plots would be found on gentle slopes and north aspects, representing more mesic conditions with better soil development; (2) shade-tolerant species would be more likely to occur on northerly aspects compared to shade-intolerant species; (3) woodland species would be less aspect-specific than montane or subalpine species; and (4) patterns in the distribution of species where they are more abundant would be markedly different than when considering occurrence only.

2. Materials and Methods

2.1. Study Area

Our study area included the intersection of the eight Interior West states (Idaho, Montana, Wyoming, Nevada, Utah, Colorado, Arizona, and New Mexico) that fall in eight ecoregion provinces [30] where topographical relief has been shown to provide a particularly strong contrast with dry, surrounding valleys [3,4]. The provinces included all seven “semi-desert” provinces, as well as one “steppe” province (southern Rocky Mountains) that contains vegetation similar to that found in the interior mountains (Figure 1). The climate in this region is characterized as seasonally dry with extremely variable

precipitation, dominated by winter precipitation that originates in the Pacific. In the southerly portion of the study area, the North American Monsoon typically brings mid- to late-growing season rain [20].

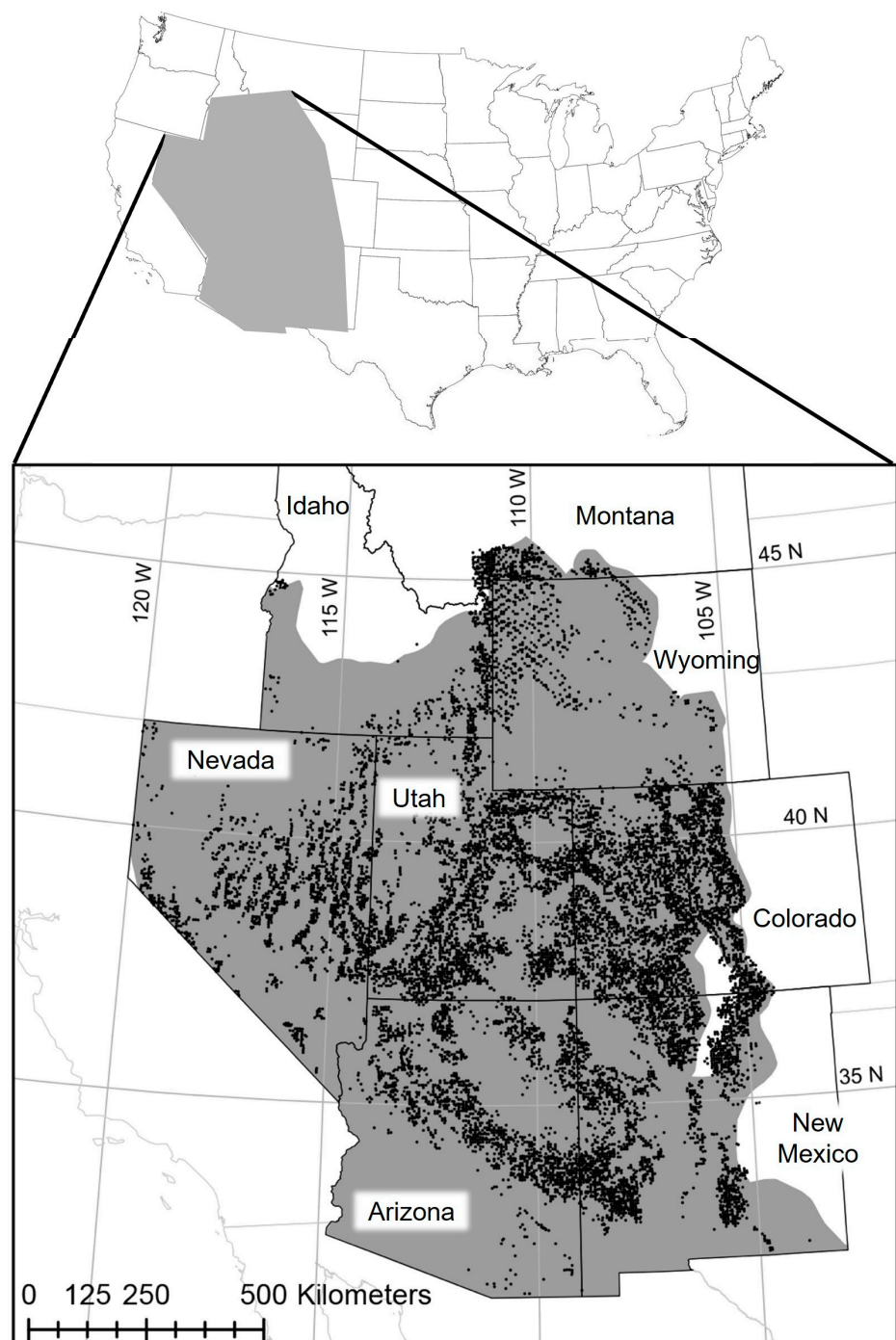


Figure 1. Study area, showing the intersection of eight Interior West states of the conterminous U.S. and eight ecoregion provinces (Table 1) with locations of plots on which the twelve tree species occur. Some plots appear outside of the study area because plot locations have been generalized for privacy, and because ecoregion boundary polygons are not exact.

Table 1. Ecoregion provinces [30] included in the study, with the number of plots for 12 common tree species on slopes ≥ 5 percent.

Ecoregion Province	Name	# of Plots
313	Colorado Plateau Semi-desert	2385
M313	Arizona-New Mexico Mountains Semi-desert	1659
321	Chihuahuan Semi-desert	342
322	American Semi-desert and Desert	260
M331	Southern Rocky Mountain Steppe	4770
341	Intermountain Semi-desert and Desert	1623
M341	Nevada-Utah Mountains Semi-desert	2049
342	Intermountain Semi-desert	349

2.2. Study Data

Our primary source of data was the Forest Inventory and Analysis (FIA) program of the USDA Forest Service [31]. The FIA sampling system was designed to make population-level estimates of forested conditions [32]. FIA plots are randomly located, occur on a semi-systematic grid, are unbiased geographically, provide unparalleled density in data, and are measured in a nationally consistent way [33]. FIA data are collected on all forested lands of the United States at a density of approximately one plot per 2428 ha⁻¹ [34]. In the western United States, FIA plots are re-measured on a 10-year cycle. Each FIA fixed-area plot is approximately 0.067 ha. On a standard plot, over 120 attributes are recorded to characterize the plot (e.g., elevation, aspect, slope, latitude, longitude) and the vegetation (e.g., species, size, status) [34].

We used forest species occurrence and topographic features measured on Interior West FIA plots from a full cycle (2005–2014) of the annual design (Table 1, ref. [35]). This 10-year sample includes a near-complete measurement for all Interior West states except Wyoming (2011–2014). To limit the effect of continental-scale latitude-elevation relationships, we filtered the full data set first by ecoregion (Figure 1; Table 1), and by the 12 overstory tree species <2.5 cm in diameter that were most common on a plot based on the tree per acre, excluding species that occurred on fewer than ~500 plots (Table 2). These 12 species represent a range of shade tolerance, associated forest cover, and drought tolerance (Table 3). Restricting the extent over which we examined patterns in this way diminished the broad-scale influence that latitude and longitude have on vegetation occurrence [36] and allowed us to more clearly detect the effect of topography on species occurrence. We focused on the 12 most common species for three reasons: (1) they make up the majority of forests in the Interior West and thus are of greatest interest for many ecological and management questions; (2) many of the uncommon species are found in valleys where topography is less likely to have an influence on their occurrence; and (3) sufficient sample size was necessary to conduct subsequent analyses on binned topographical variables (see Section 2.3). For each plot, aspect (degrees), slope (percent), and elevation (determined from hand-held GPS) were recorded per standard FIA protocols [37]. Although substrate (rockiness, soil texture, parent material) has been shown to exert control on patterns of tree distribution locally (e.g., refs. [38,39]), these detailed edaphic data are not explicitly part of the FIA data collection and are not part of the analysis. For each plot, any tree >2.5 cm in diameter at breast height was tallied, under the assumption that any tree that has achieved this size class is more likely to survive and accede to the overstory. In a conservative approach, we did not include seedlings (<2.5 cm diameter) in the analysis, and we only included plots with live trees present.

Table 2. The twelve most common tree species (SPCD) tallied on the Interior West Forest Inventory and Analysis (FIA) plots (2004–2015), and their respective forest types (FORTYPCD). For a forest type to be assigned to a plot, the plurality of stocking must be occupied by the species [40]. SPCD is the FIA label for species codes, and FORTYPCD is the FIA label for forest type codes found in the FIA database [41].

Species	FIA (SPCD)	Forest Type	FIA (FORTYPCD)
Utah juniper (UJ)	65	Juniper woodland	184
Common pinyon (CP)	106	Pinyon/juniper woodland ¹	185
Singleleaf pinyon (SP)	133	Pinyon/juniper woodland ¹	185
Rocky Mountain juniper (RMJ)	66	Rocky Mountain juniper	182
Ponderosa pine (PP)	122	Ponderosa pine	221
Quaking aspen (QA)	746	Quaking aspen	901
Douglas fir (DF)	202	Douglas fir	201
White fir (WF)	15	White fir	261
Lodgepole pine (LP)	108	Lodgepole pine	281
Limber pine (LM)	113	Limber pine ²	366
Subalpine fir (SF)	19	Subalpine fir	268
Engelmann spruce (ES)	93	Engelmann spruce	265

¹ While common pinyon and singleleaf pinyon occur in the same forest type; their geographic distributions barely overlap ($n = 22$ plots with both species), so issues of non-independence are negligible. ² There were only $n = 66$ limber pine forest type plots in the Interior West, insufficient for chi-square tests.

Table 3. Autecological description of the twelve most common tree species. Readers are referred to Burns and Honkala [42] for specifics ¹.

Species	Shade Tolerance	Associated Forest Cover ²	Relative Drought Tolerance
Utah juniper	Intolerant	Woodland	Highly tolerant
Common pinyon	Intolerant	Woodland, montane	Highly tolerant
Singleleaf pinyon	Intolerant	Woodland	Highly tolerant
Rocky Mountain juniper	Intolerant	Woodland, montane	Moderately tolerant
Ponderosa pine	Intolerant	Woodland, montane	Moderate
Quaking aspen	Intolerant	Woodland, montane, subalpine	Low
Douglas fir	Intermediate	Montane, subalpine	Moderate
White fir	Tolerant	Montane, subalpine	Low
Lodgepole pine	Intolerant	Montane, subalpine	Low
Limber pine	Intolerant	Woodland, montane, subalpine	High
Subalpine fir	Tolerant	Montane, subalpine	Low
Engelmann spruce	Tolerant	Subalpine	Low

¹ Details vary by site and region. ² As defined by Bailey [30].

2.3. Analytical Approach

To test the comparisons between observations and expectations with regard to aspect, we created aspect categories shifted 15° from the cardinal directions [43,44]: north = 341° to 60°, east = 61° to 150°, south = 151° to 240°, and west = 241° to 340°. We defined slope categories as 10 percent bins starting with 5–14 percent. Plots with <5 percent slope, and therefore no slope aspect measurement in the FIA database, were not considered in our analysis ($n = 2033$ plots; 13% of total forested plots). Because there were few plots on very steep slopes, we combined all slopes greater than 95% as one category. Categorizing the variables in this simple way allowed examination of broad patterns across the region, ensured sufficient sample size for statistical testing, and allowed direct comparisons between expectations and observation of the role of topography on species distributions.

Previous work has transformed the aspect into a linear, continuous variable representing a gradient of radiation [43,45]. While of obvious value for modeling studies and investigation of variable interactions [12], this transformation obscures information associated with west versus east aspects by merging them as some combination of intermediate radiation between moist northeasterly aspects and the driest southwesterly aspects, and thus is inappropriate for addressing the questions we posed regarding species occurrence in relation to topography. To enable discussion of species-specific patterns, we also categorized the 12 species as woodland, montane, or subalpine, as defined by Bailey [30], based on similarities in the median elevation of the plots where they occurred in the study area to facilitate interpretation of the results (Figure 2).

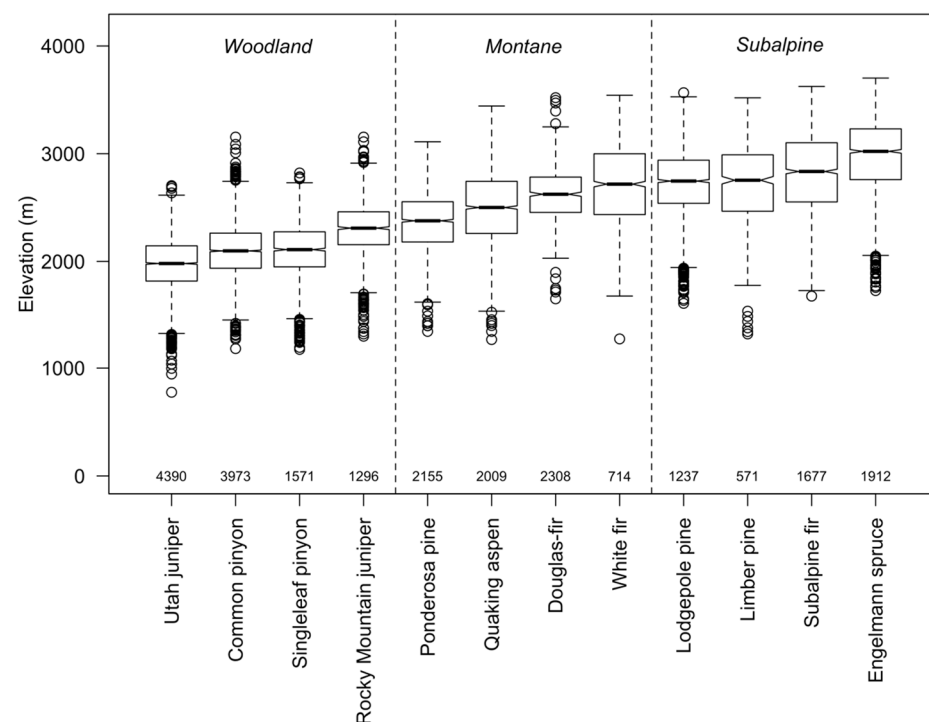


Figure 2. Elevation boxplots are arranged by species-specific median and categorized as woodland, montane, or subalpine. The number of plots on which each species was present is listed above the x-axis. The number of observations by species will not add to the total number of plots because many species co-occur on any given plot. Boxes represent the 1st and 3rd quartiles, whiskers denote 1.5 times the interquartile range, the horizontal line inside the box indicates the median, notches indicate an area around the mean roughly proportional to a 95% confidence interval, and unfilled circles indicate outliers.

The random design of the FIA inventory lent itself to answering our simple but fundamental research questions because the existence of any forest trees represented an expectation of where forests can occur, and the actual occurrence of a particular species represented an observation, making analysis of the data conducive to a chi-square test statistic. To determine whether any individual aspect-by-slope category was different from or similar to expectations, we conducted one-sample chi-square tests for each possible combination, with bootstrapped, post hoc tests of significance. In the contingency table, the observed variable was the number of plots where the species of interest occurred, and the expected value was the total number of forest plots from FIA restricted to the elevation range, latitude range, and longitude range of the particular species of interest (which was therefore different for each of the 12 species, given their varying traits, as can be seen in Table 3). This expectation assumes that any FIA plot where forested conditions were

found represents the possible, or expected, distribution of forest in the Interior West ($n = 13,437$ total plots, Figures 1 and 3). Significant differences were determined at the $p < 0.05$ level. As an arbitrary cutoff, the 0.05 level of statistical significance does not necessarily reflect ecological significance, but the plotted bars help visualize the range of variability that occurs between the expected distribution (Figure 3) and those that were observed by slope and aspect classes. Cramér's V was calculated as an estimate of effect size using a bias correction for tables larger than 2×2 [46] and can range from 0 to 1.0, where values near 0 indicate no effect, values >0.1 to 0.3 indicate a weak effect, values 0.3 to 0.5 indicate a moderate effect, and values >0.5 indicate strong differences. Significant differences are denoted on associated graphics above the slope-aspect categories as positive (+) for observations with more than expected and negative (−) for observations with less than expected. All analyses were conducted using R [47].

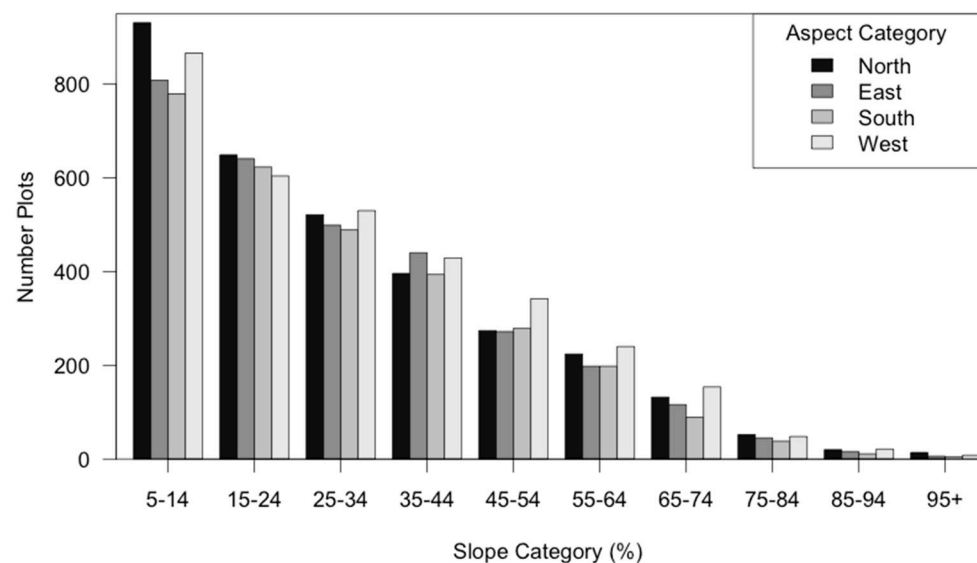


Figure 3. Distribution of slope groups by aspect category (≥ 5 percent slope) for all FIA plots ($n = 13,437$ out of $n = 15,470$) in the study area, which represents the expected distribution of slope-by-aspect categories for all forested plots with slopes $\geq 5\%$ in the Interior West, based on a systematic random sample. This distribution of plots represents the ‘population’ of forests (anywhere a tree occurs), appropriate given the sample design, and serves as the basis against which species-specific observations were tested.

We repeated the chi-square tests across subsets of low, moderate, and high elevation groups for each species by dividing the species-specific range of plot elevations into three equal bins and restricting the latitude and longitude range for the given elevation group. In addition to occurrence (presence or absence on a plot), we also examined whether there were any differences in the patterns of topographic control for each species where they were most abundant (Table 2) by repeating the chi-square test after filtering the species-specific observations to those where the species occurs only within its own forest type (Table 2), as determined in standard FIA protocol for stand stocking [37,40], which can be interpreted as being the dominant species on the plot.

This simple analytical approach takes advantage of an extensive dataset to accomplish what was heretofore impossible: empirically and parsimoniously identify where each species occurs with respect to where it could be, and thus identify species-level differences with regard to topography, using the observed distribution of all forest trees as a basis. To display important differences in geographical patterns of species distribution,

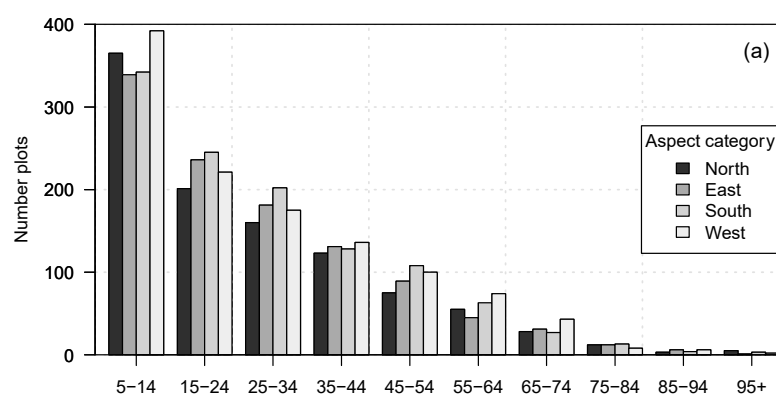
we mapped the location of all plots (expectation), and overlaid plots of a subset of key species differentiated by aspect.

3. Results

The distribution of plots by aspect and slope categories across the entire data set established the baseline expectation for forest tree species occurrence (Figure 3). As hypothesized, more than 60% of forested plots occurred on shallow slopes (13.1% in the <5% class, (not included in analysis due to the absence of aspect), 28.1% in the 5–14% class, and 20.1% in the 15–24% class). The range of Cramer’s V across all species, elevation groups, and abundance (0.05 to 0.22) indicated that differences from the expected population distribution were negligible to moderate. Within slope categories, the variability of plots by aspect category was quite small, which indicated that overall, trees occur relatively evenly across aspects. However, it is noteworthy that for the lowest slope category, and to a lesser extent across most other categories, north and west aspects had more plots than south and east. This pattern did not change when aspect categories were centered on the cardinal directions rather than offset by 15°. Contrary to expectations (hypothesis 4), filtering the species-specific data by their occurrence within their associated forest type to indicate that they dominate the plot resulted in no marked difference in patterns of occurrence by slope, slope aspect, or elevation.

3.1. Woodland Species

When compared against their expected distributions, all woodland species occurred as hypothesized (hypothesis 3), with most plots on the gentlest slopes (5–14 percent), and diminished numbers with increasing slope (Figures 4a–d and S1a–d). All four woodland species exhibited small effect sizes (V ranged from 0.05 to 0.09), which indicated no difference between slope aspect distributions when compared to the larger population. There was a large drop from the 5–14% category to the 15–24% category for UJ (Figure 4a) that was driven primarily by observations at low and moderate elevations (Figure S2a,b). At the highest elevations, UJ showed a trend of fewer plots on north aspects when compared to east and south aspects (Figure S1c). The pattern in distribution was mirrored when the analysis was repeated using only plots where UJ was most abundant (Figure S1a).



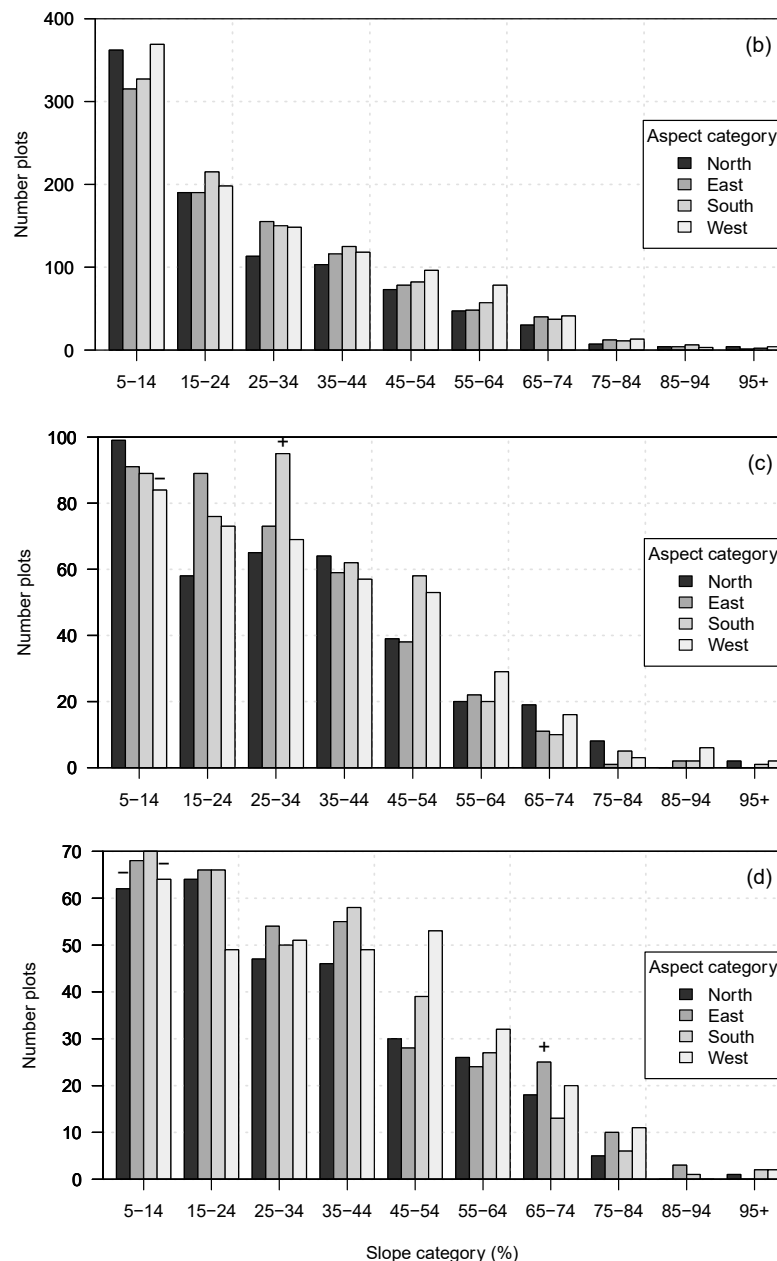


Figure 4. Woodland species (a) Utah juniper ($V = 0.05$), (b) common pinyon ($V = 0.06$), (c) singleleaf pinyon ($V = 0.09$), and (d) Rocky Mountain juniper ($V = 0.08$). Note, the y-axes may differ between panels. Significant differences are denoted above the slope-aspect categories as positive (+) for observations with more than expected and negative (−) for observations with less than expected at the 0.05 level.

There was a drop in the 15–24% category from the 5–14% class for common pinyon (CP, *Pinus edulis* Engelm.) (Figure 4b), driven again by observations at low and moderate elevations (Figure S3a,b). CP plots on north slopes were less common than south (Figure S3c). The distribution of CP on plots where it was the most abundant species appeared identical to the entire population, except for the west aspect category in the lowest slope category (Figure S3b). Both singleleaf pinyon (SP, *Pinus monophylla* Torr. & Frem) and Rocky Mountain juniper (RMJ, *Juniperus scopulorum* Sarg.; Figure 4c,d), decreased more linearly with increasing slope. At high elevations, observations of both SP and RMJ peaked in the intermediate slope categories (Figures S4 and S5), and like UJ and CP, both exhibited a trend of more plots on south aspects at the highest elevations (Figures S4c and

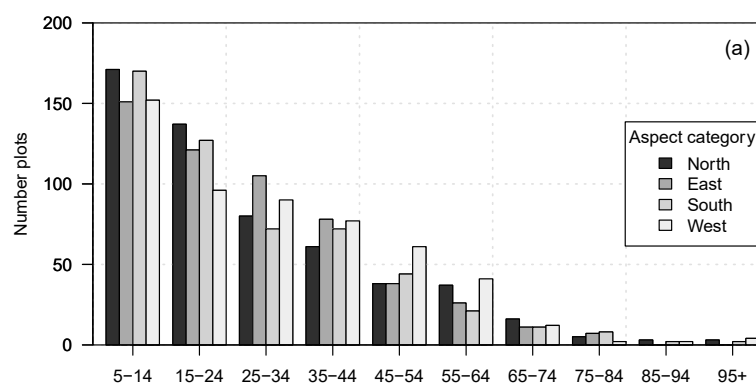
S5c). The distribution of SP where it was most abundant was virtually identical to its occurrence, including the large number of south-facing plots in the 25–34 slope category (Figure S1c). RMJ had fewer plots than expected in the lowest slope categories on west and north aspects (Figure 4d), driven by differences at moderate and high elevations (Figure S5a–d). Where RMJ was dominant, the distribution appeared different than its overall occurrence (Figure S1d), which is likely because it rarely occurs in pure stands, and therefore the number of RMJ forest types was small.

3.2. Montane Species

When compared against the larger population, results for the montane species were mixed. The montane species exhibited a range of effect sizes from 0.06 for Ponderosa pine (PP, *Pinus ponderosa* Lawson and C. Lawson) to 0.20 for DF, which indicated no difference to moderate differences from the larger population (Figure 5). PP exhibited a linearly decreasing pattern in occurrence as the slope increased (Figure 5a). PP had no significant differences from the larger population, and this mostly held true across the elevation categories, with only two significant differences, one each at moderate and high elevations (Figure S7b,c). When the PP distribution was considered only where it is abundant, two significant patterns emerged: south-facing slopes in the 5–14% category, and north-facing slopes in the 15–24% category were both more common than expected (Figure S6a).

Like PP, quaking aspen (QA, *Populus tremuloides* Michx.) also exhibited a linear pattern in occurrence as the slope increased (Figure 5b). QA occurred much less than expected on the south, east, and west aspects on the shallowest slopes (Figure 5b), driven by observations at low and middle elevation categories (Figure S8a,b). Where QA was dominant, the significant differences in occurrence in the 5–14% slope category disappeared. (Figure S6b).

Both DF and white fir (WF, *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.) exhibited unimodal distributions across slope categories, which resulted in the strongest deviations from expected occurrences of any of the species examined. At the shallow slope categories, there were significantly fewer DF and WF plots, regardless of aspect (Figure 5c,d), whereas at steeper slope categories, there were significantly more plots with the two species, but primarily on north aspects for WF, and north and west aspects for DF. The significant differences from expected for DF and WF were driven entirely by observations at low and moderate elevations (Figures S9 and S10). When filtered for abundance, DF still occurred significantly less often in the lowest slope categories, whereas WF did not (Figure S6c,d), and DF maintained this negative relationship at both low and moderate elevations, while the pattern for WF was strongest only at low elevations (Figures S9 and S10).



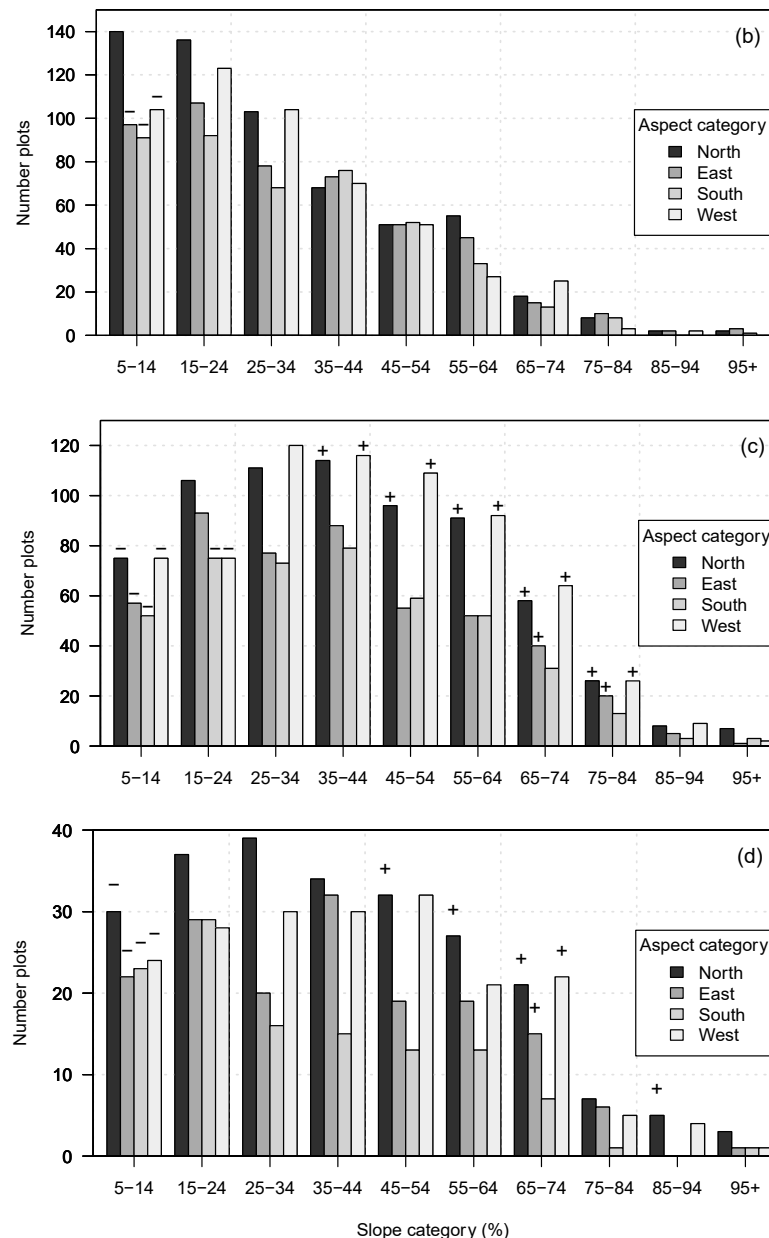


Figure 5. Montane species (a) ponderosa pine ($V = 0.06$), (b) quaking aspen ($V = 0.08$), (c) Douglas fir ($V = 0.20$), and (d) white fir ($V = 0.14$). Note, the y-axes may differ between panels. Significant differences are denoted above the slope-aspect categories as positive (+) for observations with more than expected and negative (−) for observations with less than expected.

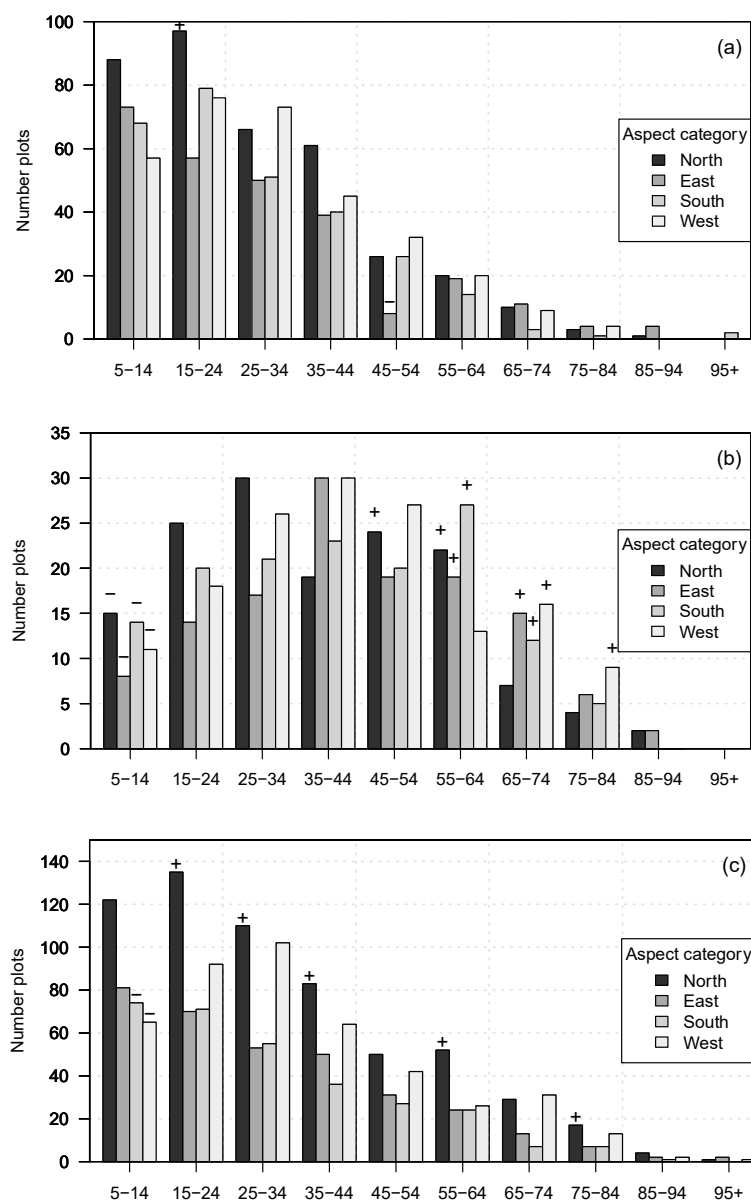
3.3. Subalpine Species

The subalpine species exhibited a range of weak effect sizes from 0.10 to 0.15 (Figure 6a–d). Lodgepole pine (LP, *Pinus contorta* (Engelm.) Critchfield) exhibited a linear decreasing pattern of occurrence across slope categories, with very few significant differences from expected (Figure 6a). Significantly more north-facing plots in the 15–24% slope category overall were driven by a similar pattern at moderate elevations (Figure S12b,d). Where LP was most abundant, insignificant differences in occurrence by slope or aspect were indicated, but the linear decreasing pattern was maintained (Figure S11a).

Limber pine (LM, *Pinus flexilis* James) exhibited a unimodal distribution across slopes and had significantly fewer plots than expected for all aspects in the 5–14% slope category, and significantly more plots than expected on most aspect categories on moderate to steep

slopes (Figure 6b), driven primarily by observations at high elevations (Figure S13). There were insufficient plots to examine patterns of occurrence for LM, where it was most abundant.

Both subalpine fir (SF, *Abies lasiocarpa* (Hook) Nutt.) and Engelmann spruce (ES, *Picea engelmannii* Parry ex. Engelm.) exhibited similar trends of decreasing plots with slope, but at the lowest slope categories they both had significantly fewer plots than expected in the south and west aspect categories (Figure 6c,d), driven entirely by observations at low and moderate elevations (Figures S14 and S15). At the moderate range of slope categories, SF and ES showed significantly more plots than expected on north aspects, also driven by observations at low and moderate elevations. The pattern of occurrence for both SF and ES when filtered for abundance was virtually identical to that for all plots, and there were no significant differences (Figure S11b,c).



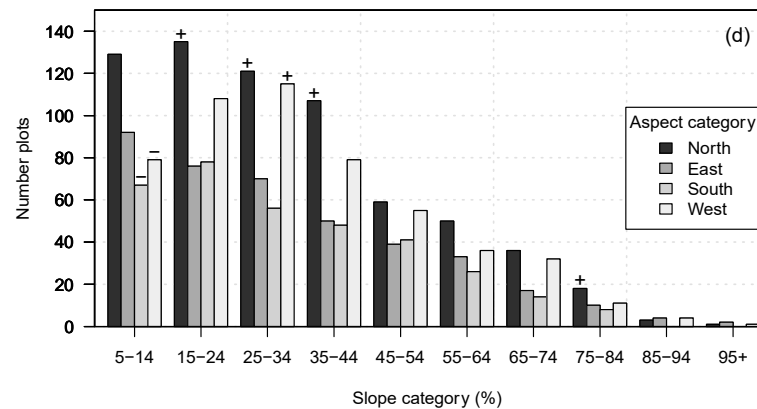


Figure 6. Subalpine species. (a) Lodgepole pine ($V = 0.10$), (b) limber pine ($V = 0.15$), (c) subalpine fir ($V = 0.11$), and (d) Engelmann spruce ($V = 0.11$). Note, the y-axes may differ between panels. Significant differences are denoted above the slope-aspect categories as positive (+) for observations with more than expected and negative (−) for observations with less than expected.

4. Discussion

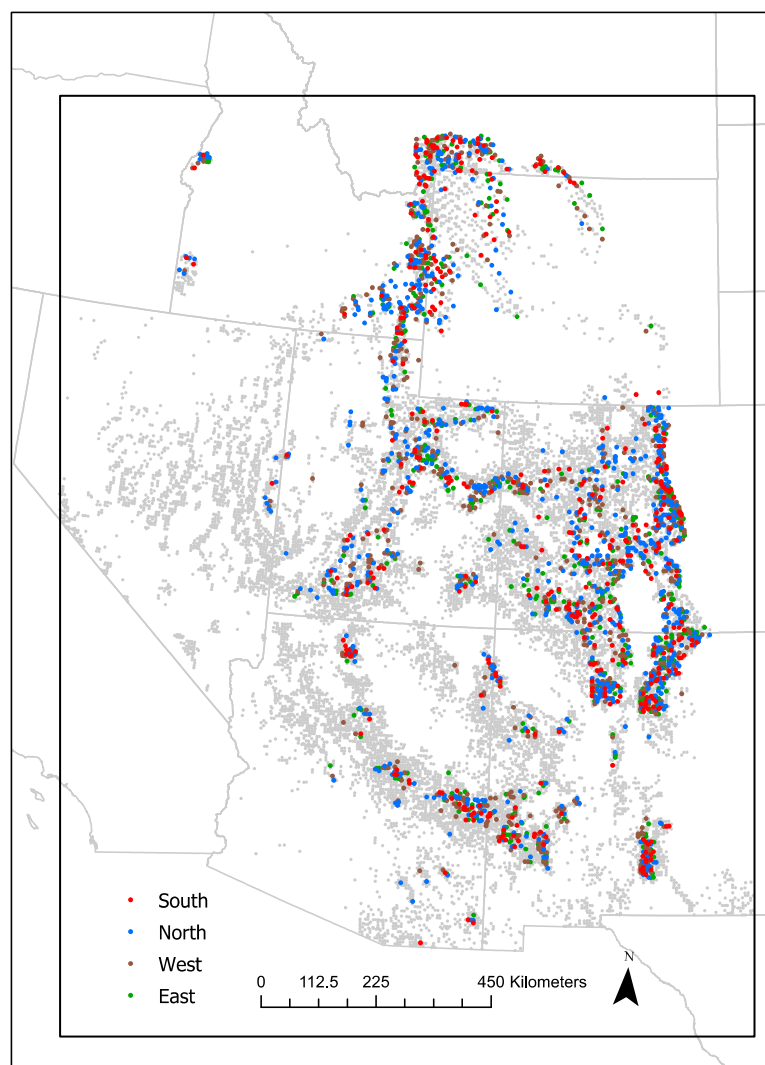
Topographical control of moisture likely influences many life stages necessary for an individual tree to persist, including germination, establishment, and subsequent competition. Important tree species in the mountain regions of the Interior West exhibit unique adaptations (e.g., seed dispersal, drought tolerance, shade tolerance) that allow them to take advantage of edaphic microsites that may exist with combinations of slope and aspect [28]. In this study, we examined established, extant trees (having passed through the germination and establishment phases to become part of the forest community) to test whether individual species are more likely to occur at different slopes, aspects, and elevations. Although there were a few big differences, there were some subtle generalities. Understanding and quantifying the environmental barriers to species-specific establishment, and how physiographic features influence them, will help us further understand current and future topographic controls on species distributions.

4.1. Woodland Species

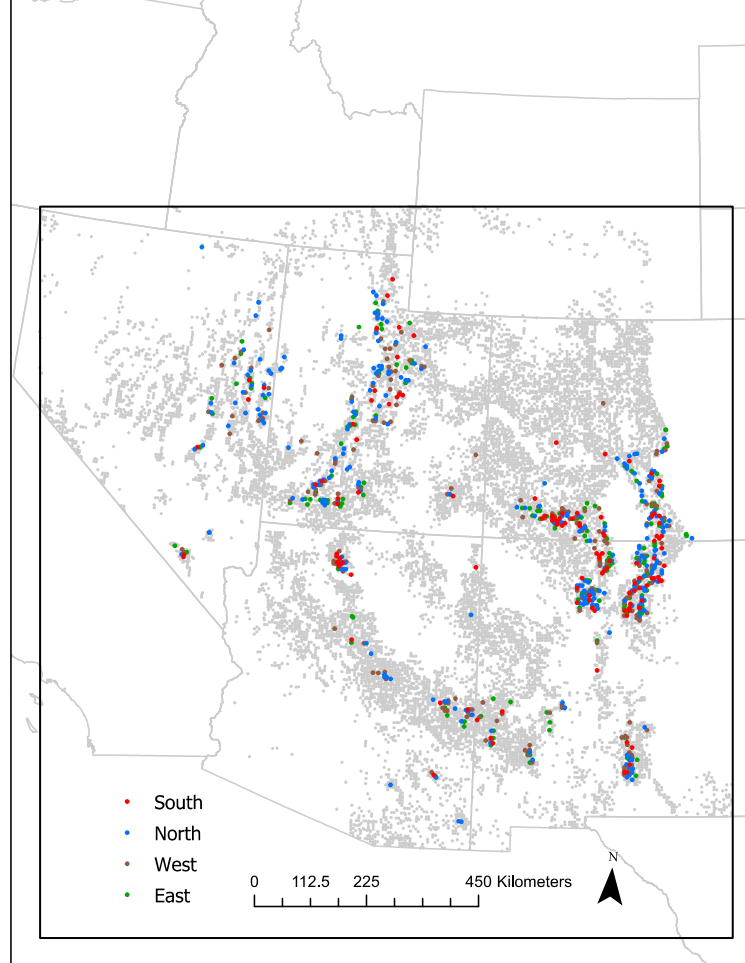
For UJ and CP, which commonly coexist on the Colorado Plateau [48], and SP and UJ, which are common associates in the Great Basin [28], very gentle slopes might simply reflect their dominant environment—the transition from basins to ranges. At the highest elevations, SP may be outcompeted by montane species on north aspects, but it was more dominant than UJ, which was relegated to lower elevations. In contrast, RMJ had the widest spatial distribution of the woodland species [49], occupied the greatest range of slopes, and showed the greatest (but inconsistent) differentiation by aspect across all elevations. In general, at high elevations, woodland trees typically dominate south (high insolation) and east (rain shadow) aspects, likely because they are best adapted to the hottest, driest environments. All the woodland species occurred in the slope by aspect categories in proportion to the distribution of the overall forest, and this was mirrored across elevation groups, suggesting the patterns for these species are very hard to indicate with respect to slope and aspect.

4.2. Montane Species

The distributions of DF (Figure 7) and WF (Figure 8) highlight the importance of north and west aspects in the eastern Great Basin (eastern Nevada and western Utah) for both species, although west aspects are arguably more important for DF than for WF. As Nevada and Utah are the driest states in the U.S., north aspects appear to represent important mesic microsites for DF and WF, while the strong west–east differential for DF and its complete absence in Nevada suggest a particularly strong rain shadow effect for this species. Although WF and DF co-occur over much of their ranges, it is notable that DF occupies a much larger proportion of the Interior West than WF. While DF and WF are common associates in many western forests, the explanations of their patterns by slope and aspect may differ. DF is known to grow best on well-drained soils, while WF is more s suggest that DF narily responding of its distribution



by aspect category.

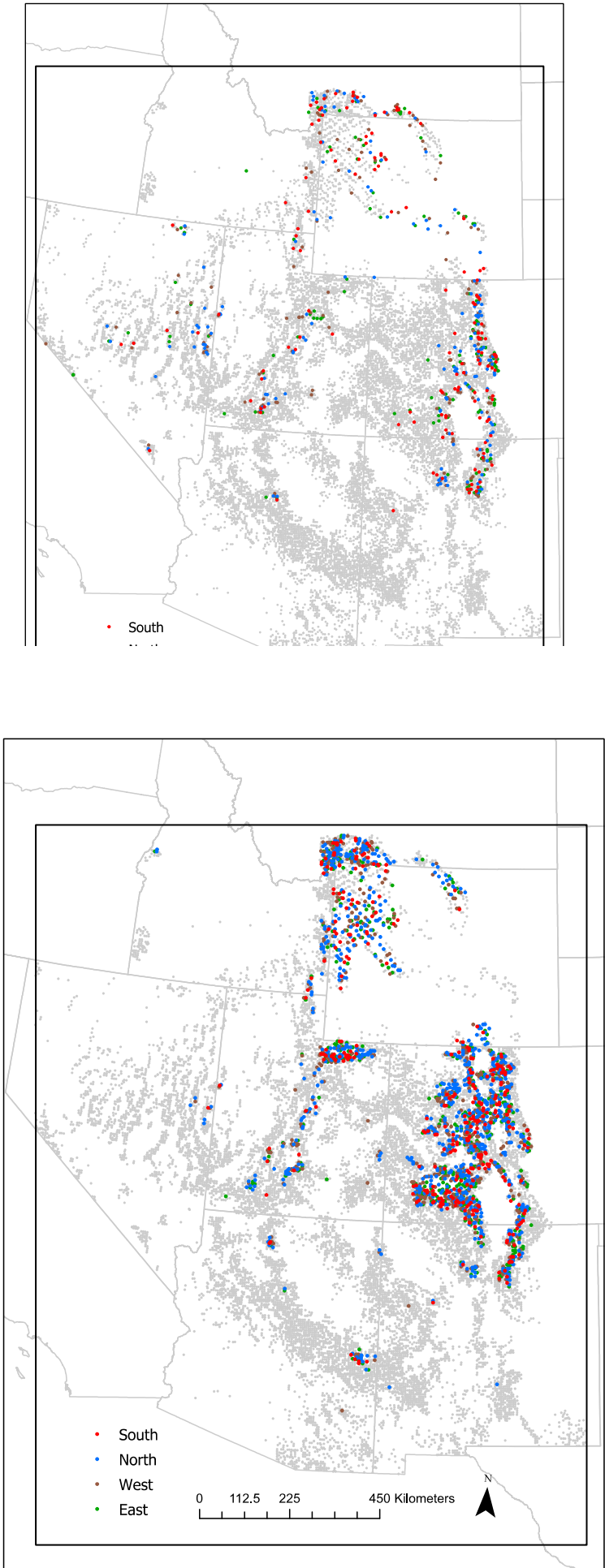


Aspect category. Gray

4.3. Subalpine Species

As with slope, LM exhibited the widest variation in distribution by aspect, but had no consistent pattern of affinity for a particular aspect, which is consistent with its characterization as a bird-dispersed species with a tolerance for a wide range of environmental conditions [50–53]. The geographical distribution of LM across aspects was also virtually random in the Interior West (Figure 9). These results are in contrast to site-specific studies [54] that found a preference for north aspects in 20th-century recruitment of the species across its elevational range. However, LM has been in decline in the West over the last decade [55], due to a combination of white pine blister rust (*Cronartium ribicola*) and mountain pine beetle (*Dendroctonus ponderosae*)-caused mortality, which may be playing a role in where it occurs.

SF and ES exhibited strikingly similar distributions by slope and aspect, which is not surprising given that the spruce-fir forest type is one of the most common and well-known forest associations in the Interior West mountains [56]. Both species occurred more on north than south aspects, but this differential decreased at high elevations. With increasing slope, the positive effects of lower insolation intensity on soil moisture may be counteracted by negative effects via decreased photosynthetic capacity on north aspects. The geographical distribution of ES highlights a few plots on south aspects and a prominence of north aspects in the eastern Great Basin, where both ES and SF barely extend (Figure 10).



occurs by aspect category.

occurs by aspect cate-

4.4. Generalities in Species Distributions

The observation that nine of the 12 species showed a pattern of decreasing abundance with increasing slope, regardless of aspect—and to a lesser extent, elevation—and occurred on gentle slopes, was consistent with our first hypothesis and suggests a dominant influence of runoff on steeper slopes, and perhaps a lack of soil development. Mass movement may also play an important role [24], and this supposition is strengthened by the observation that across species, there was very little difference in the number of plots across aspects on the steepest slopes, particularly at high elevations. The three species with exceptions to the pattern of decreasing abundance with increasing slope (DF, WF, and LM, Figures 7–9) were all more abundant on moderate slopes.

Contrary to our first three hypotheses, only five of the 12 species showed more than a few statistically significant differences from expected by slope, aspect, and elevation. These represent five of the six highest-elevation species examined (Figure 2), and logically, occurrence is more likely to be driven by topographical factors with increasing elevation, something we did not hypothesize. WF, SF, and ES all had significantly more plots on north aspects across a range of slope categories, and DF had significantly more plots on both north and west aspects (Figure 7). The significant differences for these four species were found entirely at low and moderate elevations of their respective ranges, again suggesting the potential importance of mesic aspects as low-elevation refugia [57]. The increase in plots on south aspects with increasing elevation across virtually all species can likely be explained by the higher intensity of insolation on south aspects producing similar microclimatic conditions as north aspects at lower elevations [12,26,43].

The apparent lack of significant differences for aspect, slope, and elevation for PP, QA, and LP is intriguing, considering hypothesis 2. These three species are intolerant of shade and well known for their adaptations to stand-replacing fires, which helps to explain their lack of response to topographical variables [58]. Indeed, QA and LP can often make up a considerable portion of the composition in spruce-fir forest types in many areas of the Interior West, where they typically occur as shade-intolerant seral species. Over time, shade-tolerant SF and ES slowly establish and persist in aging LP and QA stands. We speculate that a combination of fire and competitive species interactions likely explains the lack of strong topographical patterning for these three widespread and important Interior West species. The lack of strong relationships for the woodland species may also be due to fire effects in combination with their occurrence on typically gentler slopes.

Our second hypothesis, that there would be more plots, regardless of species, on north aspects, held only for montane and subalpine species, and was more pronounced for those that might be characterized as shade-tolerant, depending on site (DF, WF, SF, and ES) at low and moderate elevations. In fact, at high elevations, all the woodland species exhibited a pattern contrary to hypothesis 3: on gentle to intermediate slopes, most plots occurred on south aspects, with fewer on north aspects. For many of the montane and subalpine species at low and moderate elevations, west aspects were second in number after north and east, demonstrating the strong secondary role of orographic precipitation and rain shadow effects for most forests in the Interior West. Interestingly, at high elevations, this pattern was exactly reversed for the three woodland species adapted to the driest environments (UJ, CP, SP).

Contrary to hypothesis 4, virtually none of the species examined showed a difference in relationship to the overall population when compared using species presence or species abundance. Apparently, the occurrence of species is unlikely to vary when we consider where they ‘dominate,’ measured as consisting of the plurality of stocking. This may suggest that the autecological traits play a stronger role than topographic factors. The lack of

big differences between presence and abundance may also be related to the relatively large scale of the analysis and the general plasticity of the tree species examined.

Species with significant patterns highlighted the role of both autecological characteristics and disturbance adaptations, and helped to indicate species groupings that corroborated decades-old characterizations of vegetation zonation [56]. For example, the classic montane species DF exhibited consistent preference for moist aspects and intermediate slopes, whereas LM exhibited random occurrence across a wide range of aspects, slopes, and elevations, consistent with its characterization as a generalist able to occupy poor sites across a range of environmental conditions [51,52,59]. In fact, we identified other species that are likely generalists in part due to their ability to tolerate wide-ranging environmental conditions (RMJ in woodland and QA in montane). Their generality could also be explained by the interaction of disturbance dynamics and competitive ability. In particular, species that are adapted to fire (i.e., QA and PP) or post-fire conditions (i.e., LP, ref. [60]) had largely unpredictable distributions, whereas montane species (i.e., DF and WF) appear to have a competitive advantage on north and west aspects at low and moderate elevations over PP, QA, and woodland species. Similarly, SF and ES appear to out-compete LM on north and west aspects at high elevations, consistent with previous studies [61,62].

4.5. Study Limitations

In this study, we imposed some strict limits on the data set composition, extent, and explanatory factors. This approach was required to strictly test slope, slope aspect, and elevation observations against the larger population. As such, results might differ if considering a differing spatial area (smaller or larger) a different set of ecoregion provinces, or a different group of species. Similarly, alternative analytical approaches might be able to better discern the likelihood of occurrence using, e.g., a binary (logistical) approach with additional predictors. An approach like this would need to deal with the issue of aspect as a continuous as opposed to a categorical variable, which would necessarily require a different interpretation of aspect. Furthermore, the use of more specific physiological variables such as radiation and soil moisture, as opposed to slope and slope aspect, could be considered in future work. Pairing detailed physiological measurements with extensive forest inventory data, such as FIA, would be no small undertaking if the similarity in sample sizes was desired.

5. Conclusions

Using an empirical data set collected with a systematic random sampling design allowed us to test observations versus expectations of topographical control on species distribution patterns. While more sophisticated statistical methods exist, the power of our analysis is based on the random sampling design that makes inference to forest populations appropriate. Moreover, any statistical approach conducted on a non-random sample, such as elevation transects commonly used in traditional gradient analysis, could be limited in inference, and in representation of the species population. Only the montane species Douglas fir and white fir, and the subalpine species limber pine, subalpine fir and Engelmann spruce had significant differences from population expectations. Otherwise, the general lack of species-specific response that we found, regardless of whether we considered occurrence or abundance, runs counter to our hypothesis that this distinction would be crucial in identifying species' fidelity to slope, slope aspect, and elevation. Therefore, our unbiased (systematic sample), quantitative analysis has indicated that species-specific site preferences are more general than typically characterized. Our analysis adds to the literature a very basic, but nontrivial, characterization of species occurrence that is likely the closest approximation of true species distributions for the area analyzed.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f17070758/s1>, **Figure S1.** Woodland species (a) Utah juniper ($V=0.07$), (b) common pinyon ($V=0.07$), (c) singleleaf pinyon ($V=0.13$), and (d) Rocky Mountain juniper ($V=0.06$) where they represent the most abundant proportion of the plot. Note, the y-axes differ between panels. Significant differences are denoted above the slope-aspect categories as positive (+) for observations with more than expected and negative (-) for observations with less than expected at the 0.05 level. **Figure S2.** Utah juniper relationships for (a) low ($V=0.07$), (b) moderate ($V=0.11$), and (c) high elevation ($V=0.08$) groups and (d) all plots ($V=0.05$). Note, the y-axes differ between panels. Significant differences are denoted above the slope-aspect categories as positive (+) for observations with more than expected and negative (-) for observations with less than expected at the 0.05 level. **Figure S3.** Common pinyon relationships for (a) low ($V=0.06$), (b) moderate ($V=0.12$), (c) high elevation ($V=0.10$) groups and (d) all plots ($V=0.06$). Note, the y-axes differ between panels. Significant differences are denoted above the slope-aspect categories as positive (+) for observations with more than expected and negative (-) for observations with less than expected at the 0.05 level. **Figure S4.** Singleleaf pinyon relationships for (a) low ($V=0.10$), (b) moderate ($V=0.15$), (c) high elevation ($V=0.13$) groups and (d) all plots ($V=0.09$). Note, the y-axes differ between panels. Significant differences are denoted above the slope-aspect categories as positive (+) for observations with more than expected and negative (-) for observations with less than expected at the 0.05 level. **Figure S5.** Rocky Mountain juniper relationships for (a) low ($V=0.13$), (b) moderate ($V=0.09$), (c) high elevation ($V=0.11$) and (d) all plots ($V=0.08$). Note, the y-axes differ between panels. Significant differences are denoted above the slope-aspect categories as positive (+) for observations with more than expected and negative (-) for observations with less than expected at the 0.05 level. **Figure S6.** Montane species (a) ponderosa pine ($V=0.07$), (b) quaking aspen ($V=0.07$), (c) Douglas-fir ($V=0.18$), and (d) white fir ($V=0.14$) where they represent the most abundant proportion of the plot. Note, the y-axes differ between panels. Significant differences are denoted above the slope-aspect categories as positive (+) for observations with more than expected and negative (-) for observations with less than expected at the 0.05 level. **Figure S7.** Ponderosa pine relationships for (a) low ($V=0.06$), (b) moderate ($V=0.06$), (c) high elevation ($V=0.12$) groups and (d) all plots ($V=0.06$). Note, the y-axes differ between panels. Significant differences are denoted above the slope-aspect categories as positive (+) for observations with more than expected and negative (-) for observations with less than expected at the 0.05 level. **Figure S8.** Quaking aspen relationships for (a) low ($V=0.09$), (b) moderate ($V=0.08$), (c) high elevation ($V=0.09$) groups and (d) all plots ($V=0.08$). Note, the y-axes differ between panels. Significant differences are denoted above the slope-aspect categories as positive (+) for observations with more than expected and negative (-) for observations with less than expected at the 0.05 level. **Figure S9.** Douglas-fir relationships for (a) low ($V=0.22$), (b) moderate ($V=0.20$) (c) high elevation ($V=0.14$) groups and (d) all plots ($V=0.20$). Note, the y-axes differ between panels. Significant differences are denoted above the slope-aspect categories as positive (+) for observations with more than expected and negative (-) for observations with less than expected at the 0.05 level. **Figure S10.** White fir relationships for (a) low ($V=0.17$), (b) moderate ($V=0.14$), (c) high elevation ($V=0.11$) groups and (d) all plots ($V=0.14$). Note, the y-axes differ between panels. Significant differences are denoted above the slope-aspect categories as positive (+) for observations with more than expected and negative (-) for observations with less than expected at the 0.05 level. **Figure S11.** Subalpine species (a) lodgepole pine ($V=0.09$), (b) subalpine fir ($V=0.07$), and (c) Engelmann spruce ($V=0.08$) where they represent the most abundant proportion of the plot. Note: there were insufficient limber pine-dominated plots to conduct an analysis. Note, the y-axes differ between panels. Significant differences are denoted above the slope-aspect categories as positive (+) for observations with more than expected and negative (-) for observations with less than expected at the 0.05 level. **Figure S12.** Lodgepole pine relationships for (a) low ($V=0.09$), (b) moderate ($V=0.12$), (c) high elevation ($V=0.15$) groups and (d) all plots ($V=0.10$). Note, the y-axes differ between panels. Significant differences are denoted above the slope-aspect categories as positive (+) for observations with more than expected and negative (-) for observations with less than expected at the 0.05 level. **Figure S13.** Limber pine relationships for (a)

low ($V=0.14$), (b) moderate ($V=0.14$), (c) high elevation ($V=0.17$) groups and (d) all plots ($V=0.15$). Note, the y-axes differ between panels. Significant differences are denoted above the slope-aspect categories as positive (+) for observations with more than expected and negative (-) for observations with less than expected at the 0.05 level. **Figure S14.** Subalpine fir relationships for (a) low ($V=0.12$), (b) moderate ($V=0.10$), (c) high elevation ($V=0.11$) groups and (d) all plots ($V=0.11$). Note, the y-axes differ between panels. Significant differences are denoted above the slope-aspect categories as positive (+) for observations with more than expected and negative (-) for observations with less than expected at the 0.05 level. **Figure S15.** Engelmann spruce relationships for (a) low ($V=0.12$), (b) moderate ($V=0.09$), (c) high elevation ($V=0.04$) groups and (d) all plots ($V=0.11$). Note, the y-axes differ between panels. Significant differences are denoted above the slope-aspect categories as positive (+) for observations with more than expected and negative (-) for observations with less than expected at the 0.05 level.

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