

Topographic control of forest species distributions in the Interior West USA

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3 Running Title: Forest species distributions

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15

16 Abstract

17 **Background**

18 The geographic distribution of forest and woodland ecosystems in the Interior West United
19 States is strongly influenced by topographic gradients that, in part, control moisture availability
20 through their effect on insolation, and precipitation capture and retention. Through an empirical
21 approach, we use unique, plot-level data from the Forest Inventory and Analysis Program ($n =$
22 13,437) over eight ecoregions within eight Interior West states to characterize the distribution of
23 the 12 most abundant tree species with respect to the effects of elevation, slope aspect, and slope
24 steepness.

25
26 **Results**

27 Across species, elevation, and aspect, most plots occurred on gentle slopes and the number
28 decreased with increasing slope. Species-specific differences to microenvironmental conditions
29 were evident in the variation between observed (plots containing a subject tree) and expected (all
30 forest plots from the systematic sample) numbers of plots across the gradient combinations.
31 Species groups, broadly defined as woodland, montane, and subalpine, generally exhibited
32 similar responses and revealed more generality than hypothesized. Only Douglas-fir, white fir,
33 subalpine fir, and Engelmann spruce exhibited significant patterns of affinity for particular
34 aspects—most often on north and least often on south—with the relative importance of south
35 aspects decreasing with increasing elevation. Limber pine showed unique, unimodal patterns of
36 affinity for moderately steep slopes, with no consistent patterns by aspect or elevation. Although
37 not significant, at high elevations woodland species exhibited a tendency to occur more often on
38 south aspects on gentle to intermediate slopes, and less often on north aspects.

39 **Conclusions**

40 Unique microenvironments created by interactions between aspect, slope, and elevation create
41 some predictability in patterns of geographic distribution. However, the general lack of species-
42 specific response suggests that patterns of occurrence in relation to physiographic gradients is
43 much broader than in common generalizations.

44

45 **Key words:** topography, slope aspect, insolation, elevation, microclimate, forest distributions,
46 Forest Inventory and Analysis, Great Basin, Central and Southern Rocky Mountains

47 **Background**

48 The distribution of vegetation in the semi-arid, Interior West United States (i.e., Great Basin and
49 central and southern Rocky Mountains) is strongly influenced by topographical factors, such as
50 elevation, slope aspect (hereafter “aspect”), and slope steepness (hereafter “slope”), which
51 directly and indirectly control solar radiation, moisture available to plants, and edaphic
52 characteristics (Peet 2000). Mountains—clearly associated with forests in arid and semi-arid
53 environments (Marston 2008)—are critically important in modifying macroclimate, as the
54 presence, juxtaposition, height, and orientation of mountains directly influence the amount and
55 type of precipitation that is delivered. Indeed, previous work has documented the role of
56 elevation on the occurrence of forests, with the view that mountains are “islands” of suitable
57 habitat among a “sea” of hotter and drier valleys (Wells 1983; Charlet 2007). However, just as
58 non-forested valleys may not be uniformly unsuitable for trees (Kupfer et al. 2006), mountain
59 environments themselves are heterogeneous, providing a range of potentially suitable habitat
60 across interacting microclimatic gradients of aspect and steepness. Assuming relatively
61 consistent propagule pressure, the establishment and survival of tree species in these
62 heterogeneous environments will be influenced by their autoecological traits. In a break with
63 traditional gradient analysis, we make use of a large, systematic random sampling design to
64 document and investigate empirical relationships between elevation, slope, and aspect, and their
65 possible effect on the occurrence of the 12 most abundant tree species in the Interior West. This
66 basic characterization, heretofore impossible due to required sampling effort, provides a
67 fundamental underpinning to previous work on vegetation distributions.

68

69 Gradient analysis (Whittaker 1967), whereby groups of sampled species are typically displayed
70 along gradients of elevation, as a proxy for temperature, and topographic characteristics,
71 representing soil moisture, has yielded insight into broad-scale patterns of species composition
72 (Allen et al. 1991), potential competitive interaction (Peet 1978), variation in disturbance
73 characteristics (Bekker and Taylor 2001), and ecological change (Gosz 1992). However, these
74 non-random sampling approaches across large areas (e.g., elevation, latitude, longitude) are
75 likely to nuance our understanding of natural patterns, as they often seek to maximize variation
76 in gradients. More recent efforts have emphasized that topographic variables are proxies for
77 multiple environmental factors that directly control the establishment and survival of forest tree
78 species (Lookingbill and Urban 2005), and that they interact to amplify or dampen
79 microenvironmental conditions, making their collective influence important, but they are rarely
80 explored directly (Stage and Salas 2007).

81

82 Temperature control on vegetation occurrence that is associated with elevation is evident from
83 broad-scale analyses of upper treeline (Körner and Paulsen 2004), and the relationship between
84 temperature and insolation is reflected in the decreasing elevation of typical vegetation zones
85 with increasing latitude (Peet 1978). Elevation also enhances precipitation from storm tracks due
86 to orographic lifting; windward slopes predictably receive much higher moisture than leeward,
87 and this holds regardless of the orientation of the landform. For example, north-south trending
88 Basin and Range mountains clearly exhibit this pattern, but the east-west trending Uinta
89 Mountains in Utah do as well (Munroe et al. 2006). The apparent affinity of some species to
90 particular elevation bands may be masked, or accentuated, by aspect and slope controls on

91 vegetation occurrence (Shaw and Long 2007), and by temporal variability in low-frequency
92 climatic conditions (Millar et al. 2015).

93

94 Aspect, like elevation, is also a proxy for environmental variables that directly influence forest
95 characteristics (Måren et al. 2015) and could control the occurrence of particular species. In mid-
96 latitudes of the Northern Hemisphere, aspect controls the influence of insolation on how
97 moisture is retained (primarily in the soil) making NNE aspects the coolest and wettest, while
98 SSW aspects are the most exposed and driest (Whittaker 1956; McCune and Dylan 2002).

99 Important for the Interior West United States, most of which receives a majority of its
100 precipitation as wintertime snow from Pacific-origin westerlies (Mock 1996), is the rainshadow
101 effect exhibited by large mountains, generally producing wetter west aspects and drier east
102 aspects. However, this difference is at least partially mediated by a reduction in insolation on
103 either west or east slopes in comparison to south slopes. Similarly, at treeline, dynamics of
104 species distribution can vary between north and south slopes (Elliott and Cowell 2015).

105

106 Slope can also directly and indirectly influence the retention of moisture available to plants.

107 Directly, slope affects runoff and infiltration rates (Parker 1982), and indirectly, it can influence
108 soil development rates (Carter and Ciolkosz 1991), loss of soil through mass movement (Butler
109 et al. 2007), and can amplify or dampen the effect of aspect on insolation intensity (Mayland
110 1972). Depending on latitude and time of year, steep slopes can produce perpendicular solar rays
111 on south aspects, resulting in the highest possible concentration of insolation. In contrast, steep,
112 northerly slopes may rarely, if ever, receive direct insolation, resulting in cooler, moister
113 microclimates. The combined effects of slope and elevation result in north aspects at low

114 elevations having very similar moisture conditions to south aspects at high elevations (Roise and
115 Betters 1981; Stage and Salas 2007).

116

117 There is, perhaps, no better region than the U.S. Interior West where the influence of mountains
118 on vegetation via topographical controls are so striking at multiple scales. For example, steep,
119 north-facing slopes dominated by Douglas-fir (DF, *Pseudotsuga menziesii* Franco. Mirb.)
120 directly adjacent to broad, south-facing slopes dominated by Utah juniper (UJ, *Juniperus*
121 *osteosperma* Torr. Little) are obvious from many mountain valleys. While this observation is
122 partially explained by invoking the autecological traits of each species, e.g., DF's affinity for a
123 moist microclimate (Hermann and Lavender 2014), versus the ability of UJ to tolerate very dry
124 sites (Lanner 1984; Grayson 2011), a more empirical, broad-scale examination is warranted.
125 Using the U.S. Forest Service, National Forest Inventory and Analysis data, an extensive, semi-
126 systematic, random sampling grid, we explore the effect of slope, aspect, and elevation on the
127 occurrence of tree species in the semi-arid Interior West. We build upon previous work by
128 explicitly examining the influence of topographical gradients on individual species, using direct
129 observations of site conditions and species presence across the study area. In particular, we
130 address the following research questions: 1) where are individual species most likely to occur
131 based on aspect and slope in comparison to population-level expectations? 2) Does observed
132 occurrence by aspect and slope change with increased elevation due to lower temperature and
133 increased moisture availability? 3) Do these relationships with topographic variables differ when
134 species are analyzed only where they are dominant (i.e., abundance rather than presence)? and 4)
135 are there important similarities or differences among groups of species? We hypothesized that 1)
136 regardless of species, most forested plots would be found on gentle slopes and north aspects,

137 representing more mesic conditions with better soil development; 2) shade-tolerant species
138 would be more likely to occur on northerly aspects compared to shade-intolerant species; 3)
139 woodland species would be less aspect-specific than montane or subalpine species; and 4)
140 patterns in distribution of species where they are abundant would be markedly different than
141 when considering occurrence only.

142

143 **Methods**

144 *Study Area*

145 Our study area included the intersection of the eight Interior West states (Idaho, Montana,
146 Wyoming, Nevada, Utah, Colorado, Arizona and New Mexico) that fall in eight ecoregion
147 provinces (Cleland et al. 2007) where topographical relief has been shown to provide a
148 particularly strong contrast with dry, surrounding valleys (Wells 1983; Charlet 2007). The
149 provinces included all seven “semi-desert” provinces, as well as one “steppe” (southern Rocky
150 Mountains) that contains vegetation similar to interior mountains (Figure 1, Table 1). Climate in
151 this region is characterized as seasonally dry with extremely variable precipitation dominated by
152 winter precipitation that originates in the Pacific. In the southerly portion of the study area the
153 North American Monsoon typically brings mid- to late-growing season rain (Mock 1996).

154

155 *Study data*

156 Our primary source of data was the Forest Inventory and Analysis (FIA) program of the USDA
157 Forest Service (Gillespie 1999). The FIA sampling system was designed to make population-
158 level estimates of forested conditions (McRoberts et al. 2005). FIA plots are randomly located,
159 occur on a semi-systematic grid, are unbiased geographically, provide unparalleled density in

160 data, and are measured in a nationally consistent way (Smith 2002). FIA data are collected on all
161 forested lands of the United States at a density of approximately one plot per 2428 ha⁻¹ (Bechtold
162 and Patterson 2005). In the western United States, FIA plots are re-measured on a 10-year cycle.
163 Each FIA fixed-area plot is approximately 0.067 ha. On a standard plot, over 120 attributes are
164 recorded to characterize the plot (e.g., elevation, aspect, slope, latitude, longitude) and the
165 vegetation (e.g., species, size, status).

166

167 We used forest species occurrence and topographic features measured on Interior West FIA plots
168 from a full cycle (2005-2014) of the annual design. This 10-year sample includes a near-
169 complete measurement for all Interior West states except Wyoming (2011–2014). To limit the
170 effect of continental-scale latitude-elevation relationships, we filtered the full data set first by
171 ecoregion (Figure 1; Table 1), and by the 12 overstory species that were most commonly tallied
172 on a plot, excluding species that occurred on fewer than ~500 plots (Table 2). Restricting the
173 extent over which we examined patterns in this way diminished the broad-scale influence that
174 latitude, longitude, and elevation have on vegetation occurrence (Grafius et al. 2012) and
175 allowed us to more clearly detect the effect of topography on species occurrence. We focused on
176 the 12 most common species for three reasons: 1) they make up the majority of forests in the
177 Interior West and thus are of greatest interest for many ecological and management questions; 2)
178 many of the uncommon species are found in valleys where topography is less likely to have an
179 influence on their occurrence; and 3) sufficient sample size was necessary to conduct subsequent
180 analyses on binned topographical variables (see *Analytical approach*). For each plot, aspect
181 (degrees), slope (percent), and elevation (determined from hand-held GPS) were recorded per
182 standard FIA protocols (U.S. Department of Agriculture, Forest Service. 2013). Although

183 substrate (rockiness, soil texture, parent material) has been shown to exert control on patterns of
184 tree distribution locally (e.g., Wright and Mooney 1965; Whitesides and Bekker 2011), these
185 detailed edaphic data are not explicitly part of the FIA data collection. For each plot any tree >
186 2.5 cm in diameter at breast height was tallied, under the assumption that any tree that has
187 achieved this size class is more likely to survive and accede to the overstory. In a conservative
188 approach we did not include seedlings (< 2.5 cm diameter) in the analysis, and we only included
189 plots with live trees present.

190

191 *Analytical approach*

192 To test comparisons between observations and expectations with regards to aspect, we created
193 aspect categories shifted 15° from the cardinal directions (Beers et al. 1966; Roberts and Cooper
194 1989): north = 331° to 60°, east = 61° to 150°, south = 151° to 240°, and west = 241° to 340°.
195 We defined slope categories as 10 percent bins starting with 5–14 percent. Plots with <5 percent
196 slope, and therefore no slope aspect measurement in the FIA database (n=2,033 plots; 13% of
197 total forested plots), were not considered in our analysis. Because there were few plots on very
198 steep slopes, we combined all slopes greater than 95% as one category. Categorizing the
199 variables in this simple way allowed examination of broad patterns across the region, ensured
200 sufficient sample size for statistical testing, and allowed direct comparisons between
201 expectations and observation of the role of topography on species distributions. Previous work
202 has transformed aspect into a linear, continuous variable representing a gradient of radiation
203 (Beers et al. 1966). While of obvious value for modeling studies and investigation of variable
204 interactions (Stage and Salas 2007), this transformation obscures information associated with
205 west versus east by merging them as some combination of intermediate radiation between moist

206 northeasterly aspects and the driest southwesterly aspects, and thus is inappropriate for
207 addressing the questions we posed regarding species occurrence in relation to topography. To
208 enable discussion of species-specific patterns, we also categorized the 12 species as woodland,
209 montane, or subalpine based on similarities in the median elevation of the plots where they
210 occurred in the study area (Figure 2).

211

212 The design of the FIA inventory lent itself to answering our simple but fundamental research
213 questions because the existence of any forest trees represented an expectation of where forests
214 can occur, and the actual occurrence of particular species represented an observation, making
215 analysis of the data conducive to a straightforward chi-square test statistic. To determine whether
216 any particular aspect-by-slope group was different from or similar to expectations, we conducted
217 one-sample chi-square tests for each possible combination, with bootstrapped, post-hoc tests of
218 significance. In the contingency table, the observed variable was the number of plots where the
219 species of interest occurred, and the expected was the total number of forest plots from FIA
220 restricted to the elevation range, latitude range, and longitude range of the particular species of
221 interest (which was therefore different for each of the 12 species). This expectation assumes that
222 any FIA plot where forested conditions were found represents the possible, or expected,
223 distribution of forest in the Interior West (n=13,437 total plots, Figures 1 & 3). Significant
224 differences were determined at the $p < 0.05$ level. As an arbitrary cutoff, this level of statistical
225 significance does not necessarily reflect ecological significance, but the plotted bars help
226 visualize the range of variability that occurs between the expected distribution (Figure 3) and
227 those that were observed by slope and aspect classes.

228

229 We repeated the chi-square tests across subsets of low, moderate and high elevation groups for
230 each species by dividing the range of elevations into three equal bins, and restricted to latitude
231 and longitude range for the given elevation group. In addition to occurrence (presence or absence
232 on a plot), we also examined whether there were any differences in patterns of topographic
233 control for each species where they were most abundant (Table 2) by repeating the chi-square
234 test after filtering the species-specific observations to those that occur in their own forest type as
235 determined in standard FIA protocol (Arner et al. 2001; U.S. Department of Agriculture, Forest
236 Service. 2013).

237

238 This simple analytical approach takes advantage of an extensive dataset to accomplish what was
239 heretofore impossible: empirically and parsimoniously identify where each species occurs with
240 respect to where it could be, and thus identify species-level differences with regards to
241 topography, using the observed distribution of all forest trees as a basis. To display important
242 differences in geographical patterns of species distribution we mapped the location of all plots
243 (expectation), and overlaid plots of a subset of key species differentiated by aspect.

244

245 **Results and Discussion**

246 The distribution of plots by aspect and slope groups across the entire data set established the
247 baseline expectation for forest tree species occurrence (Figure 3). As hypothesized, more than
248 60% of forested plots occurred on shallow slopes (13.1% in the < 5% class, 28.1% in the 5-14%
249 class, 20.1% in the 15-24% class). Within slope classes, the variability of plots by aspect class
250 was quite small, which indicated that overall, trees occur relatively evenly across aspects.
251 However, it is noteworthy that for the lowest slope class, and to a lesser extent across most other

252 classes, north and west aspects had more plots than south and east. This pattern did not change
253 when aspect classes were centered on the cardinal directions rather than offset by 15° (data not
254 shown).

255

256 *Woodland species*

257 When compared against their expected distributions, all woodland species occurred as
258 hypothesized, with the most plots on the gentlest slopes (5–14 percent), and diminished numbers
259 with increasing slope (Figure 4a–d). There was a large drop from the 5–14% class to the 15–24%
260 class for UJ (Figure 4a) that was driven primarily by observations at low and moderate
261 elevations (Figure S1a, b). At the highest elevations UJ showed a trend of fewer plots on north
262 aspects when compared to east and south aspects (Figure S1c). The pattern in distribution was
263 mirrored when the analysis was repeated using only plots where UJ was most abundant (Figure
264 S2a).

265

266 There was also a drop in the 15–24% class from the 5–14% class for common pinyon (CP, *Pinus*
267 *edulis* Engelm.) (Figure 4b) driven again by observations at low and moderate elevations (Figure
268 S3a, b). Like UJ, plots on north slopes were less common than south (Figure S3c). The
269 distribution of CP on plots where it was the most abundant species appeared identical to the
270 entire population, except for the west aspect class in the lowest slope class (Figure S2b). Both
271 singleleaf pinyon (SP, *Pinus monophylla* Torr. & Frem) and Rocky Mountain juniper (RMJ,
272 *Juniperus scopulorum* Sarg.; Figure 4c & d), decreased more linearly with increasing slope. At
273 high elevations, observations of both SP and RMJ peaked in the intermediate slope classes
274 (Figures S4 & S5), and like UJ and CP, both exhibited a trend of more plots on south aspects at

275 the highest elevations (Figures S4c & S5c). The distribution of SP where it was most abundant
276 was virtually identical to its occurrence, including the large number of south-facing plots in the
277 25–34 slope class (Figure S2c). RMJ had fewer plots than expected in the lowest slope classes on
278 west and north aspects (Figure 4d), driven by differences at moderate and high elevations (Figure
279 S5a–d). Where RMJ was dominant, the distribution appeared different than its
280 overall occurrence (Figure S2d), which is due to the fact that it rarely occurs in pure stands, and
281 therefore the number of RMJ forest types was small.

282

283 For UJ and CP, which commonly coexist on the Colorado Plateau (Romme et al. 2009), and SP
284 and UJ, which are common associates in the Great Basin (Lanner 1984), very gentle slopes
285 might simply reflect their dominant environment—the transition from basins to ranges. At the
286 highest elevations, SP may be outcompeted by montane species on north aspects, but it was more
287 dominant than UJ, which was relegated to lower elevations. In contrast, RMJ had the widest
288 spatial distribution of the woodland species (DeRose et al. 2016), occupied the greatest range of
289 slopes and showed the greatest (but inconsistent) differentiation by aspect across all elevations.
290 In general, at high elevations woodland trees typically dominate south (high insolation) and east
291 (rainshadow) aspects, likely because they are best adapted to the hottest, driest environments. All
292 the woodland species occurred in slope by aspect classes in proportion to the distribution of
293 overall forest, and this was mirrored across elevation groups, suggesting the patterns for these
294 species are very hard to generalize with respect to slope and aspect.

295

296 *Montane species*

297 Ponderosa pine (PP, *Pinus ponderosa* Lawson and C. Lawson) exhibited a linearly decreasing
298 pattern in occurrence as slope increased (Figure 5a). PP had no significant differences from the
299 larger population, and this mostly held true across the elevation classes with only two significant
300 differences, one each at moderate and high elevations (Figure S6b, c). When the PP distribution
301 was considered only where it is abundant two significant patterns emerged: south-facing slopes
302 in the 5–14% class, and north-facing slopes in the 15–24% class were both more common than
303 expected (Figure S7a).

304

305 Like PP, quaking aspen (QA, *Populus tremuloides* Michx.) also exhibited a linear pattern in
306 occurrence as slope increased (Figure 5b). QA occurred much less than expected on south, east,
307 and west aspects on the shallowest slopes (Figure 5b), driven by observations at low and middle
308 elevation classes (Figure S8a, b). Where QA was dominant, the significant differences in
309 occurrence in the 5–14% slope class disappeared. (Figure S7b).

310

311 Both DF and white fir (WF, *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.) exhibited
312 unimodal distributions across slope classes, which resulted in the strongest deviations from
313 expected occurrences of any of the species examined. At the shallow slope classes there were
314 significantly fewer DF and WF plots, regardless of aspect (Figure 5c & d), whereas at steeper
315 slope classes there were significantly more plots with the two species, but primarily on north
316 aspects for WF, and north and west aspects for DF. The significant differences from expected for
317 DF and WF were driven entirely by observations and low and moderate elevations (Figures S9 &
318 S10). Plots where DF was most abundant exhibited virtually the same pattern as all plots
319 containing the species (Figure S7c). Similarly, plots where WF was most abundant exhibited a

320 similar pattern, but there were fewer significant differences, likely due to the low number of
321 observations (Figure S7d). The distributions of DF (Figure 6) and WF (Figure 7) highlight the
322 importance of north and west aspects in the eastern Great Basin (eastern Nevada and western
323 Utah) for both species, although west aspects are arguably more important for DF than for WF.
324 As Nevada and Utah are the driest states in the U.S., north aspects appear to represent important
325 mesic microsites for DF and WF, while the strong west-east differential for DF and its complete
326 absence in Nevada suggest a particularly strong rainshadow effect for this species. Although WF
327 and DF co-occur over much of their ranges, it is notable that DF occupies a much larger
328 proportion of the Interior West than WF.

329

330 While DF and WF are common associates in many western forests, the explanations of their
331 patterns by slope and aspect may differ. DF is known to grow best on well-drained soils, while
332 WF is more tolerant of a wide range of soil conditions (Burns and Honkala 1990). When filtered
333 for abundance, DF still occurred significantly less often in the lowest slope class, whereas WF
334 did not (Figures S7c & d), and DF maintained this negative relationship at both low and
335 moderate elevations while the pattern for WF was strongest only at low elevations (Figures S9 &
336 S10). Together, these patterns suggest that DF may be responding more to site (soil) conditions,
337 while WF may be primarily responding to competition with PP, DF, or woodland species at the
338 lower elevations of its distribution and most gentle slopes.

339

340 *Subalpine species*

341 Lodgepole pine (LP, *Pinus contorta* (Engelm.) Critchfield) exhibited a linear decreasing pattern
342 of occurrence across slope classes, with very few significant differences from expected (Figure

343 8a). Significantly more north-facing plots in the 15–24% slope class overall, was driven by a
344 similar pattern at moderate elevations (Figure S11b & d). Where LP was most abundant,
345 insignificant differences in occurrence by slope or aspect were indicated, but the linear
346 decreasing pattern was maintained (Figure S12a).

347

348 Limber pine (LM, *Pinus flexilis* James) exhibited a unimodal distribution across slopes and had
349 significantly fewer plots than expected for all aspects in the 5–14% slope class, and significantly
350 more plots than expected on most aspect classes on moderate to steep slopes (Figure 8b), driven
351 primarily by observations at high elevations (Figure S13). As with slope, LM exhibited the
352 widest variation in distribution by aspect, but had no consistent pattern of affinity for a particular
353 aspect, which is consistent with its characterization as a bird-dispersed species with a tolerance
354 for a wide range of environmental conditions (Lanner and Vander Wall 1980; Schoettle and
355 Rochelle 2000; Tomback and Achuff 2010; Windmuller-Campione and Long 2016). The
356 geographical distribution of LM with regards to aspect was also virtually random in the Interior
357 West (Figure 9). These results are in contrast to site-specific studies (Millar et al. 2019), which
358 found a preference for north aspects in 20th-century recruitment of the species across its
359 elevational range. There was an insufficient number of LM-dominated plots to conduct a
360 statistical test for abundance.

361

362 Both subalpine fir (SF, *Abies lasiocarpa* (Hook) Nutt.) and Engelmann spruce (ES, *Picea*
363 *engelmannii* Parry ex. Engelm.) exhibited similar trends of decreasing plots with slope, but at the
364 lowest slope class they both had significantly fewer plots than expected in the south and west
365 aspect classes (Figure 8c & d), driven entirely by observations at low and moderate elevations

366 (Figures S14 & S15). At the moderate range of slope classes, SF and ES showed significantly
367 more plots than expected on north aspects, also driven by observations at low and moderate
368 elevations. SF and ES exhibited strikingly similar distributions by slope and aspect, which is not
369 surprising given that the spruce-fir forest type is one of the most common and well-known
370 associations in Interior West mountains (Daubenmire 1943). Both species occurred more on
371 north than south aspects, but this differential decreased at high elevations. With increasing slope,
372 the positive effects of lower insolation intensity on soil moisture may be counteracted by
373 negative effects via decreased photosynthetic capacity on north aspects. The pattern of
374 occurrence for both SF and ES when filtered for abundance was virtually identical to that for all
375 plots and there were no significant differences (Figure S12b & c). The geographical distribution
376 of ES highlights few plots on south aspects and a prominence of north aspects in the eastern
377 Great Basin, where both ES and SF (not shown) barely extend (Figure 10).

378

379 *Generalities in species distributions*

380 Topographical control of moisture likely influences many life stages necessary for an individual
381 tree to persist, including germination, establishment, and subsequent competition. Important tree
382 species in the mountain regions of the Interior West exhibit unique adaptations (e.g., seed
383 dispersal, drought tolerance, shade tolerance) that allow them to take advantage of edaphic
384 microsites (Lanner 1984). In this study we examined established, extant trees (having passed
385 through the germination and establishment phases to become part of the forest community) to
386 test whether individual species are more likely to occur at different slopes, aspects, and
387 elevation. Although there were few strong differences there were some subtle generalities.
388 Understanding and quantifying the environmental barriers to species-specific establishment, and

389 how physiographic features influence them, will help us further understand current and future
390 controls on species distributions.

391

392 The observation that nine of the 12 species showed a pattern of decreasing abundance with
393 increasing slope regardless of aspect, and to a lesser extent, elevation, and occurred on gentle
394 slopes, was consistent with our expectations and suggests a dominant influence of runoff on
395 steeper slopes, and perhaps a lack of soil development. Mass movement may also play an
396 important role (Butler et al. 2007), and this supposition is strengthened by the observation that
397 across species there was very little difference in the number of plots across aspects on the
398 steepest slopes, particularly at high elevations. The three species with exceptions to the pattern of
399 decreasing abundance with increasing slope (LM, DF, and WF) were all most abundant on
400 moderate slopes.

401

402 Contrary to our hypothesis, only five of the 12 species showed more than a few statistically
403 significant differences from expected by slope, aspect, and elevation. These represent five of the
404 six highest-elevation species examined (Figure 2), and logically, occurrence is more likely to be
405 driven by topographical factors with increasing elevation. WF, SF, and ES all had significantly
406 more plots on north aspects across a range of slope classes, and DF had significantly more plots
407 on both north and west aspects. The significant differences for these four species were found
408 entirely at low and moderate elevations, again suggesting the potential importance of mesic
409 aspects as low-elevation refugia. The increase in plots on south aspects with increasing elevation
410 across virtually all species was also expected and can likely be explained by the higher intensity

411 of insolation on south aspects producing similar microclimatic conditions as north aspects at
412 lower elevations (Beers et al. 1966; Roise and Betters 1981; Stage and Salas 2007).

413

414 Our expectation that there would be more plots, regardless of species, on north aspects, held only
415 for montane and subalpine species, and was more pronounced for those that might be
416 characterized as shade-tolerant (DF, WF, ES, SF) at low and moderate elevations. In fact, at high
417 elevations, all of the woodland species exhibited the opposite pattern: on gentle to intermediate
418 slopes most plots occurred on south aspects, with the fewest on north. For many of the montane
419 and subalpine species at low and moderate elevations, west aspects were second in importance
420 behind north and east was third, demonstrating the strong secondary role of orographic
421 precipitation and rainshadow effects for most forests in the Interior West. Interestingly, at high
422 elevations this pattern was exactly reversed for the three woodland species adapted to the driest
423 environments (UJ, CP, SP).

424

425 The apparent lack of significant differences for aspect, slope, and elevation for PP, QA, and LP
426 is intriguing. These three species are well known for their adaptations to stand-replacing fires,
427 which helps to explain their lack of response to topographical variables (Shinneman et al. 2013).
428 Indeed, QA and LP often each make up a component of spruce-fir forest types in regions of the
429 Interior West, where they typically occur as shade-intolerant seral species. Over time, shade-
430 tolerant SF and ES slowly make their way into aging LP and QA stands. We speculate that a
431 combination of fire and competitive interactions likely help explain the lack of strong patterns
432 for these three widespread, important Interior West species. The lack of strong relationships for

433 the woodland species may also be due to fire effects in combination with occurrence on typically
434 gentler slopes.

435

436 **Conclusions**

437 Using an empirical data set collected with a systematic random sampling design allowed us to
438 test observations versus expectations of species distribution patterns. While more sophisticated
439 statistical methods exist, the power of our analysis is based on the random sampling design that
440 makes inference to forest populations appropriate. Moreover, any statistical approach conducted
441 on a non-random sample, such as elevation transects commonly used in traditional gradient
442 analysis, could be limited in inference, and certainly in representation. The general lack of
443 species-specific response that we found, regardless of consideration of occurrence or abundance,
444 runs counter to our hypothesis that this distinction would be crucial in identifying species fidelity
445 to topographic conditions. Therefore, our unbiased (systematic sample), quantitative analysis has
446 indicated that species site preferences are more general than typically characterized. Our analysis
447 adds to the literature a very basic, but nontrivial, characterization of species occurrence that is
448 likely the closest approximation of true species distributions.

449

450 Among the 12 common trees in the Interior West, only five demonstrated strong, statistically
451 significant patterns in relation to topographic variables, again suggesting that species affinity is
452 much more general than commonly thought. Those species with significant patterns highlighted
453 the autecological characteristics and adaptations of Interior West forests and helped to indicate
454 species groupings that were largely consistent with decades-old characterizations of vegetation
455 zones (Daubenmire 1943). For example, the classic montane species DF exhibited consistent

456 preference for moist aspects and intermediate slopes, whereas LM exhibited random occurrence
457 across a wide range of aspect, slopes, and elevations, consistent with its characterization as a
458 generalist able to occupy poor sites across a range of environmental conditions (Schoettle and
459 Rochelle 2000; Schoettle 2004; Tomback and Achuff 2010). In fact, we identified other species
460 that are likely generalists (RMJ in woodland and QA in montane) in part due to their ability to
461 tolerate wide-ranging environmental conditions, but could also be explained by the interaction of
462 disturbance dynamics and competitive ability. In particular, species adapted to fire (i.e., QA and
463 PP) or post-fire conditions (i.e., LP, Rebertus et al. 1991), had largely unpredictable
464 distributions, whereas montane species (i.e., DF and WF) appear to have a competitive
465 advantage on north and west aspects at low and moderate elevations over PP, QA, and woodland
466 species. Similarly, SF and ES appear to out-compete LM on north and west aspects at high
467 elevations, consistent with previous studies (Veblen 1986; Donnegan and Rebertus 1999).

468

469 The paleobiogeography of Interior West forest species is inherently tied to topography (Wells
470 1983; Lanner 1984; Charlet 2007), and while the role of elevation in past and future (Bartlein et
471 al. 1997) dynamics is noted, its interactive effects with slope and aspect demonstrated
472 empirically by this study downplays the role of topographic variation in species occurrence or
473 abundance, when compared to disturbance, coexistence, and competition. A species at the
474 extremes of its latitudinal and longitudinal range can continue to thrive, and coexist in close
475 proximity with other species, on suitable microsites produced by particular combinations of
476 elevation, slope, and aspect. For example, along the eastern border of the Great Basin, north
477 aspects may provide the last western outpost at low elevations for montane species such as DF,
478 while south aspects provide the last eastern outpost at high elevations for woodland species such

479 as SP. Such mountain refugia may strongly influence future changes in Interior West biota.
480 Future work that accounts for species occurrence in combination with the putative role of
481 climate, biotic interactions, disturbance regimes, and other variables like life history—perhaps
482 using this same systematically collected data set—will lend further clues to possible mechanisms
483 that drive the patterns observed in this study.

484

485 **Abbreviations**

486 **FIA:** Forest Inventory and Analysis

487 **DF:** Douglas-fir

488 **UJ:** Utah juniper

489 **CP:** common pinyon

490 **SP:** singleleaf pinyon

491 **RMJ:** Rocky Mountain juniper

492 **PP:** ponderosa pine

493 **QA:** quaking aspen

494 **WF:** white fir

495 **LP:** lodgepole pine

496 **LM:** limber pine

497 **SF:** subalpine fir

498 **ES:** Engelmann spruce

499

500 **Declarations**

501 **Ethics approval and consent to participate**

502 Not applicable

503 **Consent for publication**

504 Not applicable

505 **Availability of data and materials**

506 The datasets used and/or analyzed during the current study are available from the corresponding
507 author upon reasonable request. Forest Inventory and Analysis Data are publicly available.

508 **Competing interests**

509 The authors declare that they have no competing interests.

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514 **Authors' contributions**

515 M.F.B. and R.J.D. developed the research idea and wrote and edited the manuscript. R.J.D.
516 provided the FIA data and performed statistical analyses.

517 **Authors' Information**

518 Prior to his current position, R.J.D. was a USDA Forest Service Research Ecologist for the
519 Interior West Forest Inventory and Analysis Program.

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524

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668 **Figure captions**

669 **Figure 1.** Study area, showing the intersection of eight Interior West states and eight ecoregions
670 with locations of plots on which the twelve tree species occur. Some plots appear outside of the
671 study area because plot locations have been generalized for privacy, and because ecoregion
672 boundary polygons are not exact.

673
674 **Figure 2.** Elevation boxplots arranged by species-specific median and categorized as woodland,
675 montane, or subalpine. Number of plots on which species was present are listed above the x-axis.
676 Number of observations by species will not add to total number of plots because many species
677 co-occur on any given plot. Boxes represent the 1st and 3rd quartiles, whiskers denote 1.5 times
678 the interquartile range, the horizontal line inside the box indicates the median, notches indicate
679 an area around the mean roughly proportional to a 95% confidence interval, and unfilled circles
680 indicate outliers.

681
682 **Figure 3.** Distribution of slope groups by aspect category (≥ 5 percent slope) for all FIA plots
683 ($n=13,347$ out of $n=15,470$) in the study area, which represents the expected distribution of
684 slope-by-aspect categories for all forests with slope $\geq 5\%$ in the Interior West, based on a
685 systematic random sample. This distribution of plots represents the ‘population’ of forests
686 (anywhere a tree occurs), appropriate given the sample design, and serves as the basis against
687 which species-specific observations are tested.

688
689 **Figure 4.** Woodland species (a) Utah juniper, (b) common pinyon, (c) singleleaf pinyon, and (d)
690 Rocky Mountain juniper. Note, the y-axes differ between panels.

691 **Figure 5.** Montane species (a) ponderosa pine, (b) quaking aspen, (c) Douglas-fir, and (d) white
692 fir. Note, the y-axes differ between panels.

693

694 **Figure 6.** Geographic distribution of plots on which Douglas-fir (DF) occurs by aspect class.

695

696 **Figure 7.** Geographic distribution of plots on which white fir (WF) occurs by aspect class.

697

698 **Figure 8.** Subalpine species (a) lodgepole pine, (b) limber pine, (c) subalpine fir, and (d)

699 Engelmann spruce. Note, the y-axes differ between panels.

700

701 **Figure 9.** Geographic distribution of plots on which limber pine (LM) occurs by aspect class.

702

703 **Figure 10.** Geographic distribution of plots on which Engelmann spruce (ES) occurs by aspect

704 class.

705

706

707 **Table 1.** Ecoregion provinces included in the study, with number of plots for 12

708 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

709

Table 2. The twelve most common tree species on the Interior West Forest Inventory and Analysis (FIA) plots (2004-2015), and their respective forest types. For a forest type to be assigned to a plot, the plurality of stocking must be occupied by the species (Arner et al. 2001).

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

710

711 ¹ While common pinyon and singleleaf pinyon occur in the same forest type, their geographic
712 distributions barely overlap (n=22 plots with both species) so issues of non-independence are
713 negligible.

714 ² There were only n=66 limber pine forest type plots in the Interior West, insufficient for chi-
715 square tests.

Figures

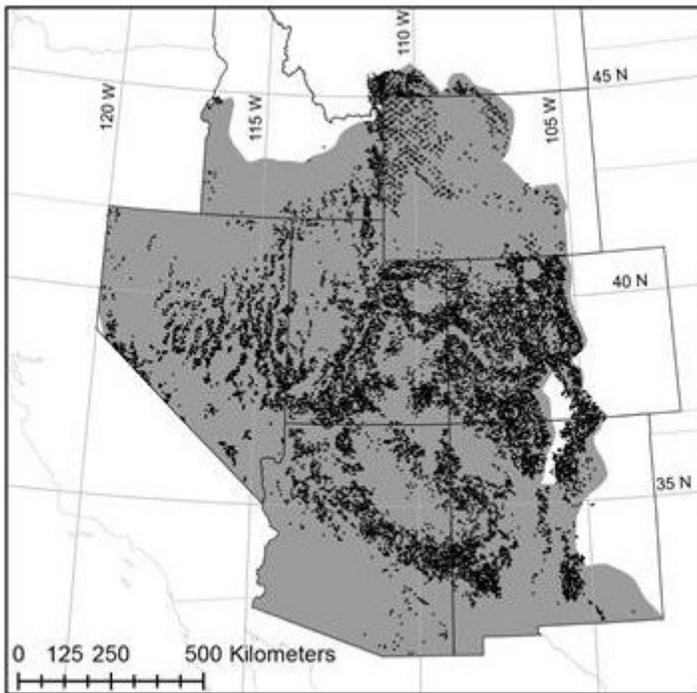


Figure 1

Study area, showing the intersection of eight Interior West states and eight ecoregions 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.

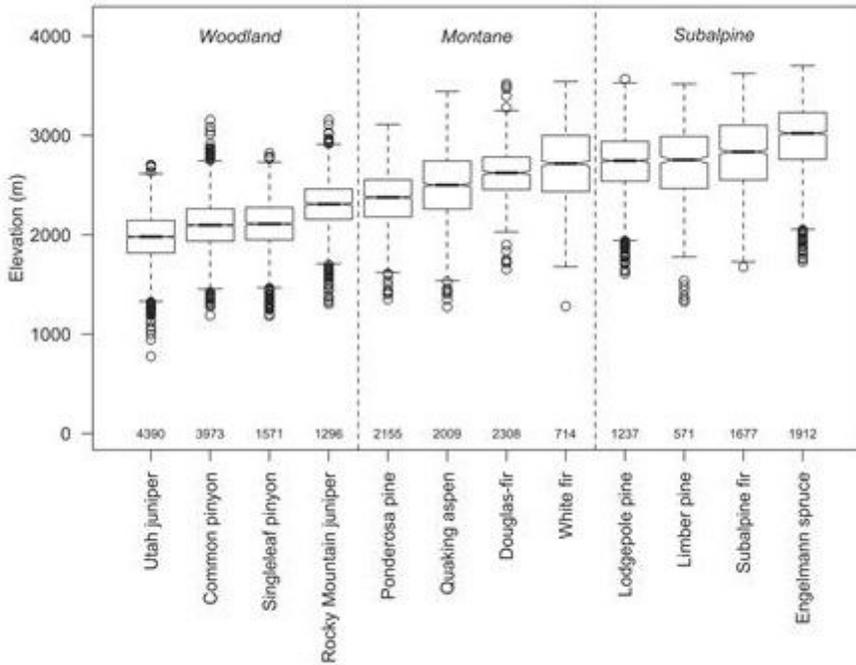


Figure 2

Elevation boxplots arranged by species-specific median and categorized as woodland, montane, or subalpine. Number of plots on which species was present are listed above the x-axis. Number of observations by species will not add to 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.

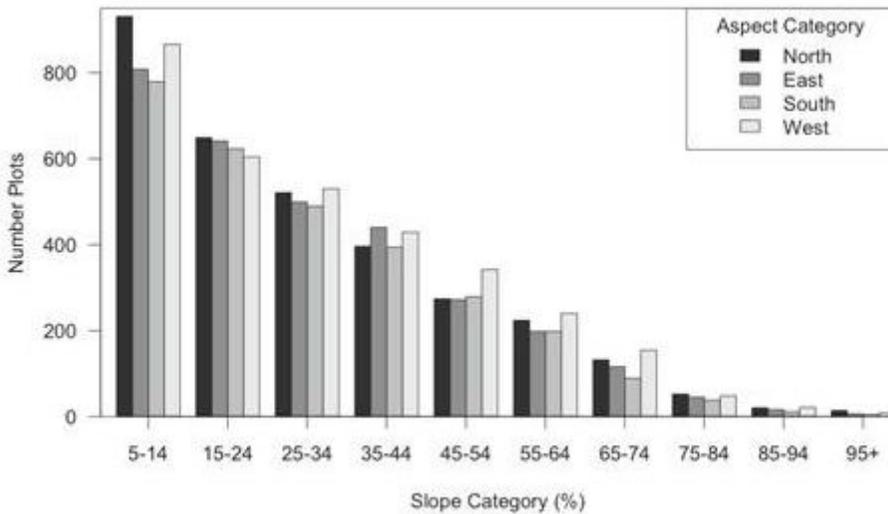


Figure 3

Distribution of slope groups by aspect category (≥ 5 percent slope) for all FIA plots ($n=13,347$ out of $n=15,470$) in the study area, which represents the expected distribution of slope-by-aspect categories for all forests with slope $\geq 5\%$ 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 are tested.

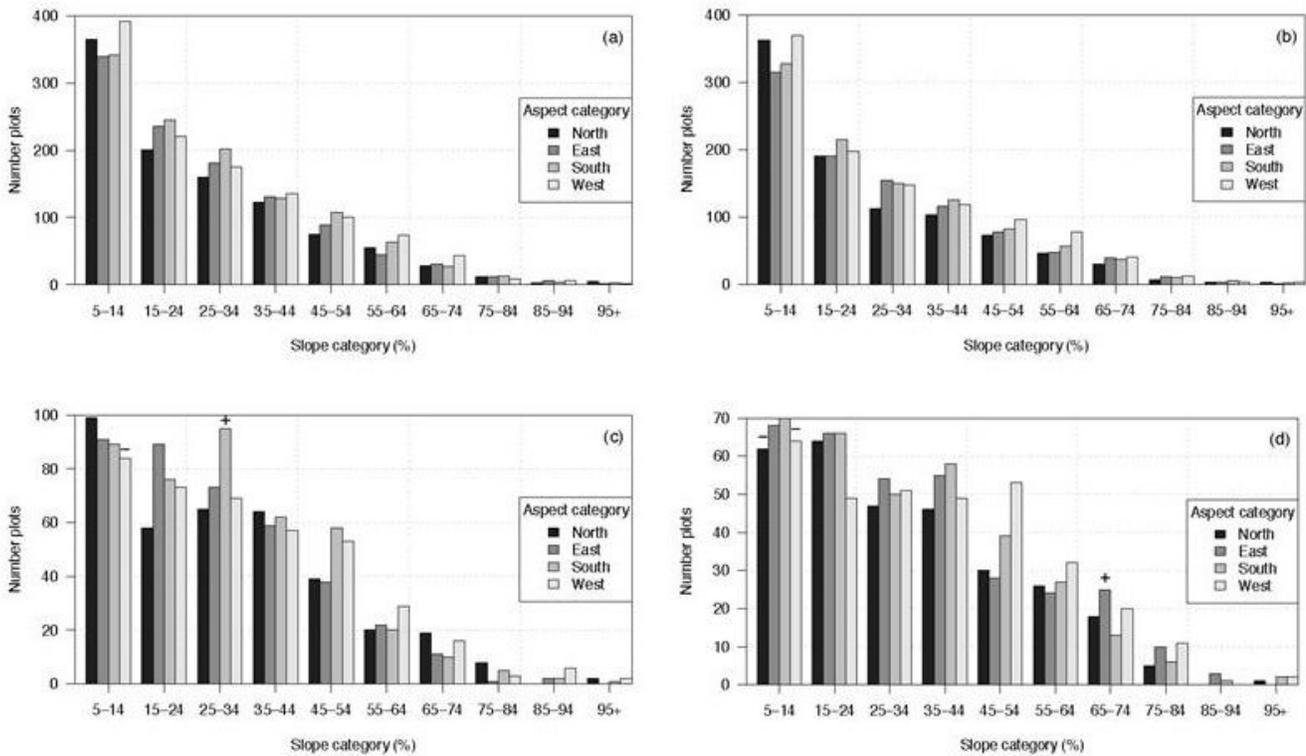


Figure 4

Woodland species (a) Utah juniper, (b) common pinyon, (c) singleleaf pinyon, and (d) Rocky Mountain juniper. Note, the y-axes differ between panels.

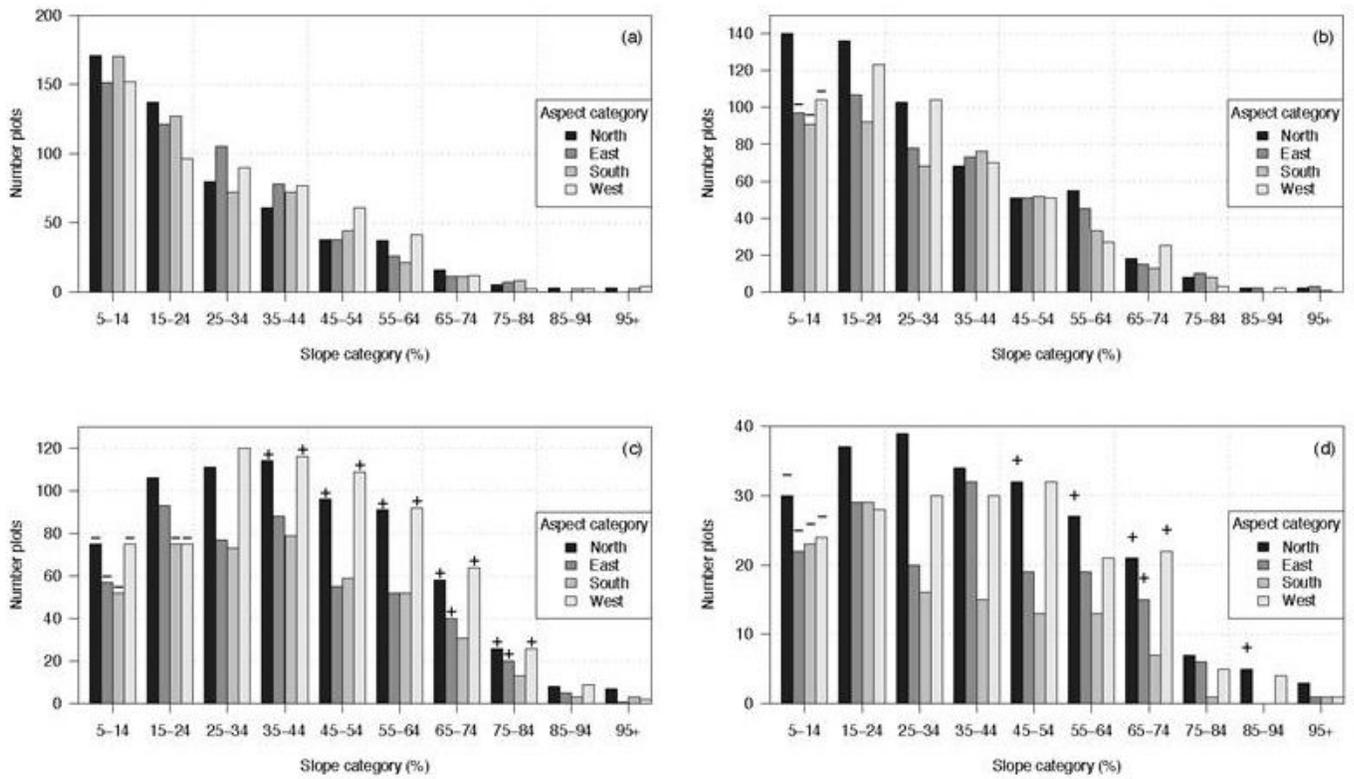


Figure 5

Montane species (a) ponderosa 691 pine, (b) quaking aspen, (c) Douglas-fir, and (d) white fir. Note, the y-axes differ between panels.

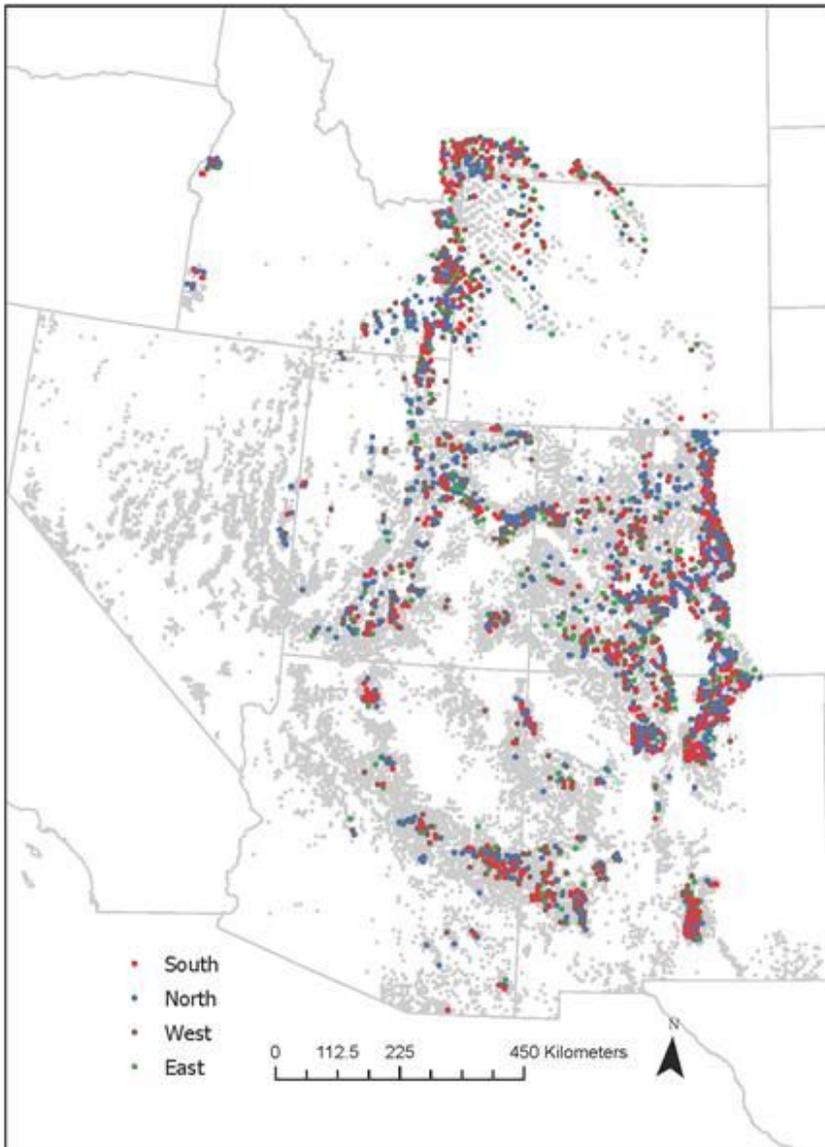


Figure 6

Geographic distribution of plots on which Douglas-fir (DF) occurs by aspect class.

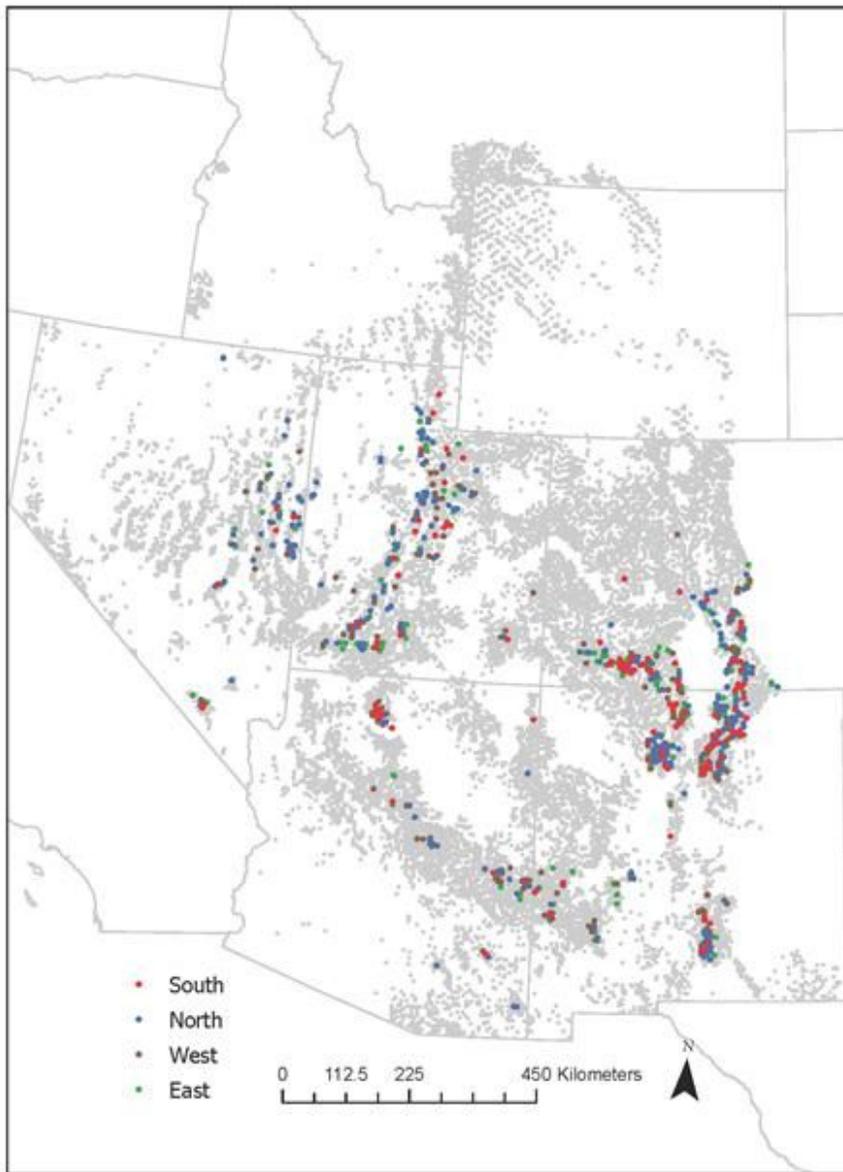


Figure 7

Geographic distribution of plots on which white fir (WF) occurs by aspect class.

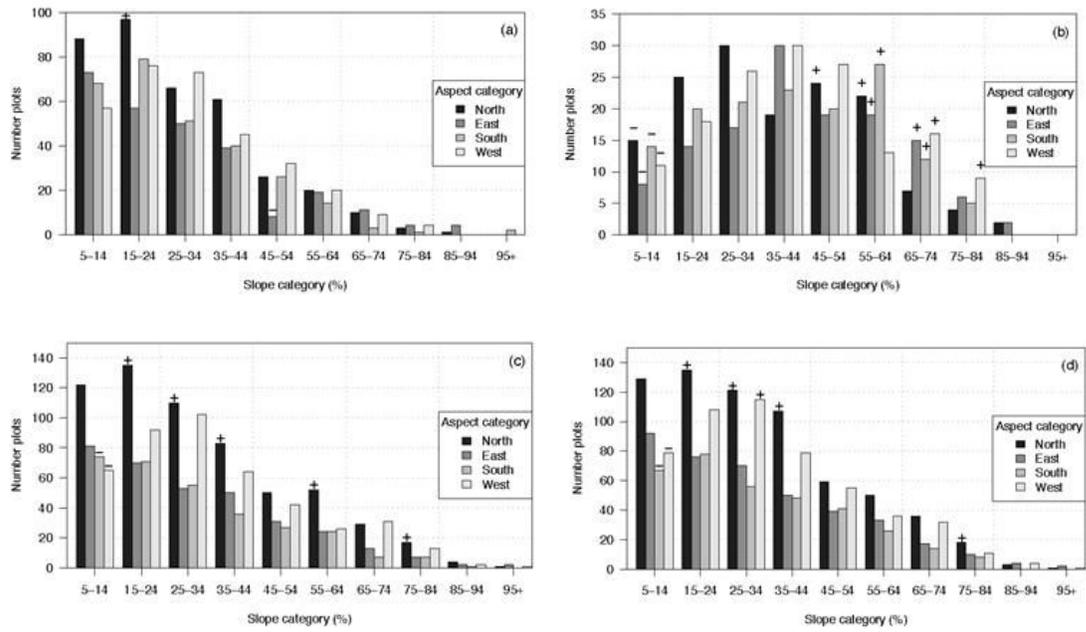


Figure 8

Subalpine species (a) lodgepole pine, (b) limber pine, (c) subalpine fir, and (d) Engelmann spruce. Note, the y-axes differ between panels.

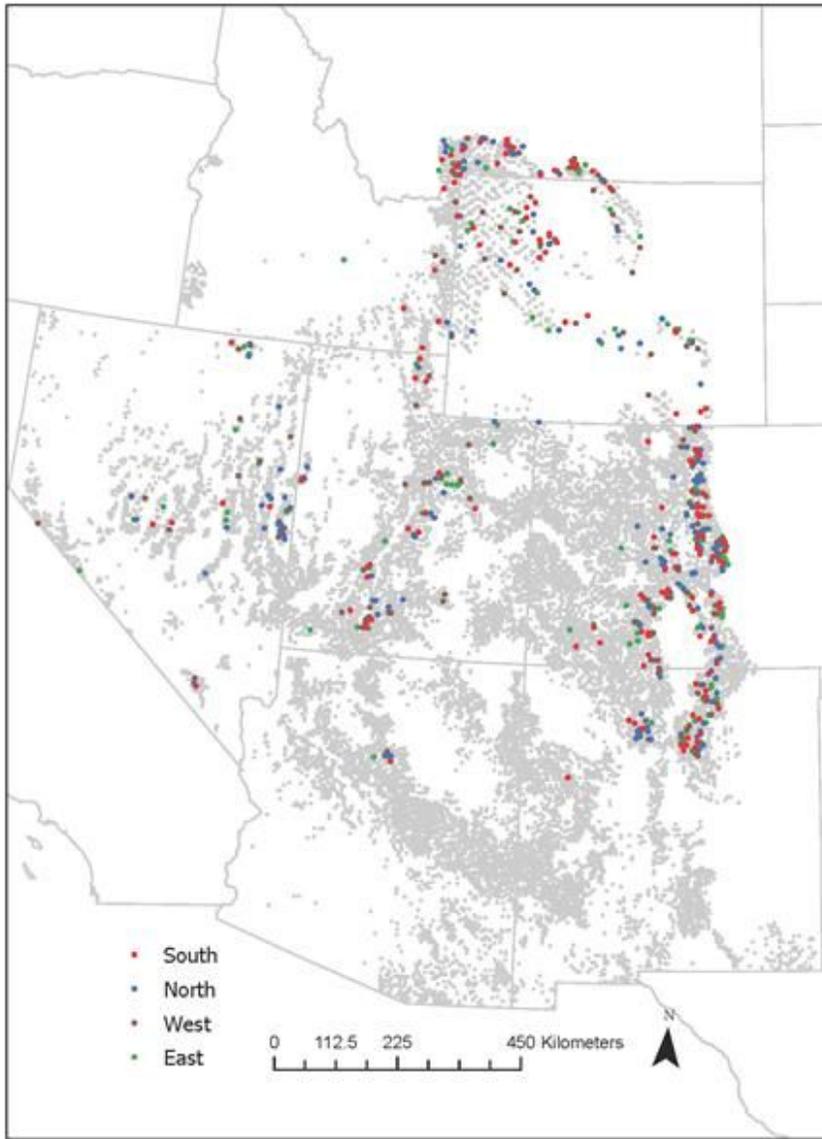
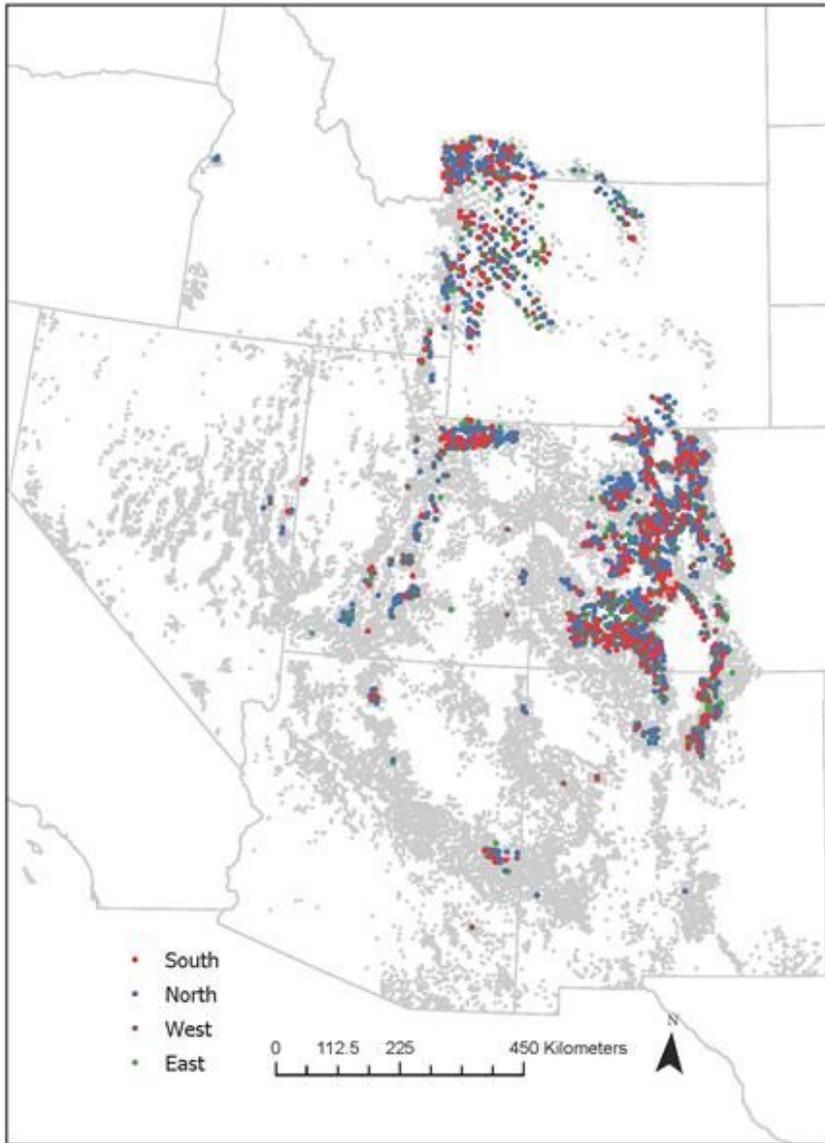


Figure 9

Geographic distribution of plots on which limber pine (LM) occurs by aspect class.



1

Figure 10

Geographic distribution of plots on which Engelmann spruce (ES) occurs by aspect class.

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