Long-term understory vegetation dynamics of mixed aspen forests in Rocky Mountain National Park, USA

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21 **Abstract (300 words)**

22 *Aims*: Forests worldwide are subjected to increasing pressures from altered disturbance regimes,

23 climate change, and their interactions. We resampled previously established vegetation plots to

24 directly assess long-term vegetation dynamics in the forest understory of mixed aspen forests,

25 including species diversity, distribution, and composition.

26 *Location*: Rocky Mountain National Park, Colorado, USA.

27 *Methods*: We resampled 89 vegetation plots that contained aspen (*Populus tremuloides*) in the

28 original sampling in 1972/73 in Rocky Mountain National Park to assess changes in understory

29 diversity, non-native species abundance, community composition, and elevation ranges.

30 Analyses were performed at three spatial scales: landscape (all plots), ecotone (montane vs.

31 subalpine), and seven forest "series" according to the classification presented in the original

32 publication.

33 *Results*: Understory vegetation diversity did not significantly change at the landscape scale but

34 increased in forests of the mesic montane series. Changes in diversity varied with elevation, with

35 predominantly increases at lower elevations and decreases at higher elevations. Furthermore,

36 species turnover and upward shifts were more pronounced at lower elevations. The proportion of

37 plots containing non-native species was similar between data sets, with 48% in 2012/13 and 46%

38 in 1972/73. However, the number of non-native species per plot increased considerably,

39 especially in *Pinus contorta* forests. Significant shifts in understory community composition

40 occurred in mesic montane forests and *Pinus flexilis* forests. Generally, higher floristic overlap

41 was evident between forest types indicating homogenization between 1972/73 and 2012/13

42 understory plant communities.

43 *Conclusions*: Although our results indicate overall little change in understory communities

44 between 1972/73 and 2012/13 in Rocky Mountain National Park, they also suggest that observed

45 changes differ by elevation, possibly due to the interactions between elevation and changes in

46 local climate. Our study underscores the importance of analyzing long-term vegetation dynamics

47 at different spatial scales and provides data from direct observations to improve the predictive

48 power of vegetation models.

49

52 **Introduction**

53   Ecosystems worldwide are experiencing climate-change mediated shifts in plant species

54 distributions, with significant impacts on local biodiversity, species composition, and ecosystem

55 services (Pecl et al. 2017). Knowledge of species elevation range shifts (e.g. Lenoir et al. 2008;

56 Kopp & Cleland 2014; Bretfeld et al. 2016; Rumpf et al. 2018), species dominance shifts (Harte

57 & Shaw 1995; Jagerbrand et al. 2009), and assembly of novel-communities (Williams & Jackson

58 2007) is crucial to inform biodiversity models and develop efficient conservation and

59 environmental protection strategies (Urban et al. 2016). High-elevation environments are at

60 higher risk of species redistribution as they are more insular and experience more rapid changes

61 in temperature than environments at lower elevations (Pepin et al. 2015). From 1953 to 2008, the

62 upper montane and subalpine ecotone of the Colorado Front Range exhibited significant

63 increases in annual mean temperatures of 0.17°C and 0.20°C per decade, respectively (McGuire

64 et al. 2012). In addition to direct effects of altered temperature and moisture regimes on plants

65 (e.g. drought stress), indirect effects associated with climate change can considerably affect a

66 species' distribution. For example, eruptive insect outbreaks are aggravated due to additional

67 annual breeding generations (Mitton & Ferrenberg 2012) and reduced defenses of drought-

68 stressed plants (Bentz et al. 2010), thereby benefiting non-host species (Bretfeld et al. 2015).

69 Furthermore, simulations hint at feedback effects between insect-induced overstory mortality and

70 local climate (Wiedinmyer et al. 2012). Assuming compatible sampling protocols, resulting

71 vegetation dynamics can be assessed directly through long-term monitoring and resampling of

72 previously established plots (Damschen et al. 2010; Kopp & Cleland 2014). We resampled a

73 subset of 89 plots from among 305 0.1 ha vegetation plots first sampled by (Peet 1975; Peet

74 1981) in Rocky Mountain National Park, Colorado in 1972-73, to assess changes in composition

75 and diversity of vascular plants in the forest understory.

76   For this study we focused on forests that contained aspen (*Populus tremuloides*) in the

77 initial sampling (Peet 1978), as aspen is the major deciduous tree species within the upper

78 montane and subalpine ecotones of the Colorado Front Range and is considered a prime indicator

79 of the impacts of climate change on forest growth (Rehfeldt et al. 2009). Throughout most of the

80 western range of aspen, aspen-dominated forests exhibit higher decomposition rates, nutrient

81 availability, and soil moisture (Légaré et al. 2005; Buck & St. Clair 2012), and harbor higher

82 herbaceous biomass in the understory as compared to co-occurring coniferous forests (Stam et al.

83   2008). In southeastern California, plant species richness and diversity in aspen-dominated

84   habitats are significantly higher than in conifer-dominated habitats and are decreasing with

85   succession towards coniferous forests (Kuhn et al. 2011; McCullough et al. 2013). Within Rocky

86   Mountain National Park, aspen habitats exhibit the highest vascular plant species richness and

87   diversity among all upland habitat types (Peet 1975; Peet 1978, 1981; Stohlgren et al. 1997).

88   Thus, landscape-wide changes in aspen abundance are likely reflected in overall plant species

89   diversity changes at the landscape scale. A recent decline of aspen throughout its southern

90   distribution, dubbed "Sudden Aspen Decline", has been linked to drought and resulting xylem

91   cavitation (Michaelian et al. 2011; Anderegg et al. 2012; Anderegg et al. 2013; Worrall et al.

92   2013; Anderegg et al. 2015). Although overstory data from the same dataset as presented in this

93   study show that there has been significant conifer encroachment over the 40-years span from

94   1972/73 to 2012/13 in plots previously dominated by aspen, density of aspen stems larger than

95   2.5 cm diameter at breast height (DBH; measured at 1.37 m) and aspen basal area have not

96   changed significantly at the landscape scale (Bretfeld et al. 2016). Moreover,

97   dendrochronological data suggest that mature aspen are potential beneficiaries of reduced

98   competition from widespread, insect-induced conifer mortality (Bretfeld et al. 2015).

99   There are several other reasons to suspect as responsible for changing understory

100   composition in aspen forests. Compared to other forest types, aspen habitats are among the most

101   heavily invaded forests by non-native plant species (Chong et al. 2001). Non-native species

102   spread at the landscape scale has been potentially further aggravated by selective mortality of

103   coniferous overstory trees due to bark beetles and the resulting opening of the canopy. Moreover,

104   increased nitrogen deposition due to human activities is altering species composition in forests of

105   the Colorado Front Range (Baron et al. 2000), potentially leading to a decline in plants adapted

106   to lower nitrogen levels and soil acidity (Vitousek et al. 1997). Further, a general upward shift of

107   most overstory tree species hints at climate change as a potential driver of changes of species

108   distributions in and around Rocky Mountain National Park (Bretfeld et al. 2016). Lastly, locally

109   intense ungulate herbivory has likely suppressed aspen regeneration and understory growth,

110   especially in the winter ranges of elk within Rocky Mountain National Park (Suzuki et al. 1999;

111   Kaye et al. 2005).

112   The aim of this study was to assess long-term changes in understory diversity and

113   composition at three different spatial scales: landscape-wide, ecotone, and forest community

114   type. We hypothesize that (a) landscape-wide understory species diversity in forests containing

115   aspen has not decreased, in line with relatively persistent aspen abundance in the landscape, and

116   that (b) non-native and invasive species abundance has increased primarily in beetle-affected

117   forests due to these species' ability to disperse effectively following disturbances. In addition, we

118   assess significant shifts in understory community composition and hypothesize that (c) forests

119   heavily affected by bark beetles exhibited significant changes in species composition. Lastly, we

120   quantified altitudinal changes in species distributions, hypothesizing that (d) species moved

121   upslope similar to observations in other long-term studies (Kelly & Goulden 2008; Brusca et al.

122   2013). Specific understanding of these types of changes in forest community dynamics will aid

123   in improving management strategies and vegetation models of future vegetation trajectories,

124   including spread of non-native species.

125   **Methods**

126   *Data Collection*

127   During 1972/73, Peet (1975; 1981) sampled 305 0.1 ha forest plots, spanning the eastern

128   slope of the northern Colorado Front Range from the foothills to the alpine in and adjacent to

129   Rocky Mountain National Park. The sampling method was a modified version of that used by

130   Whittaker (1960). Plots typically were 20 x 50 m with 25 contiguous 0.5 x 2 m sub-plots located

131   along the center line. Smaller plots were used in areas of high local heterogeneity or in extremely

132   dense aspen stands. Frequency and percent cover for species < 1 m height were recorded within

133   each of the 25 sub-plots; cover for species > 1 m was estimated along the 50 m center line.

134   Additional species that occurred elsewhere in the 20 x 50 m plot were recorded as present

135   without an estimate of overall cover.

136   Plant communities were delimited by (Peet 1975); Peet (1981) using a hybrid of indirect

137   and direct gradient analysis (Whittaker 1967). The final presentation used elevation (from

138   topographic maps and altimeter readings) and topographic-moisture (derived from records of

139   aspect and slope, and subjective estimates of site conditions) as the two primary axes for

140   representing community variation. Based on these gradients, eight vegetation "series" and 29

141   community types were identified (Peet 1981; Appendix S1).

142   During 2012/13, a subset of 95 plots that originally contained aspen of the original 305

143   plots of Peet (1981) were selected to be resampled. In 1972/3 locations were recorded as

144   accurately as possible on USGS topographic maps, and data were recorded as to slope and

145   aspect. Locations of these 95 plots (11 aspen-dominated, 84 containing aspen) were transferred

146   from the original topographic maps into a GPS unit (Garmin Montana 600). After reaching the

147   marked location, abiotic factors (slope, aspect, rock cover) and woody species composition as

148   previously recorded were compared with local characteristics to reassure accurate plot location.

149   If abiotic factors at the site did not match with previous data, the surrounding area was searched

150   in a 150 m radius (based on original asserted plot location accuracy) for matching topography

151   and site characteristics. In two justifiable cases, the search radius from the original location was

152   deliberately increased. A total of 89 plots were sampled while six plots were not sampled as a

153   result of changes in land ownership, land use, or uncertainty of exact plot location. Except for

154   two plots (plot 31 was burned in 1999 and plot 292 was subject to a thinning treatment in 2006),

155   no plots were subject to disturbances known to the authors other than bark beetles.

156   Resampling followed the Carolina Vegetation Survey protocol (CVS, Peet et al. 1998;

157   Peet et al. 2018) at the highest sampling depth (level 5). The CVS protocol was developed to

158   maintain maximum comparability to other widely-used methods (Peet et al. 1998), including the

159   Whittaker method that was utilized for the original sampling, and ensures comparability to future

160   sampling efforts. The CVS protocol is a modular approach, with ten 10×10 m sampling units

161   (modules) following a 50 m center line (five on each side) resulting in a 20 by 50 m rectangle.

162   The center line was laid out perpendicular to the slope as in Peet (1981). In four modules (i.e.

163   intensive modules), the presence of species smaller than breast height (1.37 m) was recorded in

164   nested sub-quadrats (0.01, 0.1, 1.0, 10 m^2) in two corners each, and for the entire module (100

165   m^2). All other modules (i.e. residual modules) were searched for additional species that were not

166   present in the intensives (presence/absence in full 0.1 ha plot). In 19 plots, fewer than ten

167   modules were used due to newly-established trails in the plot, standing water, deviations of

168   aspect/slope from the original data set, or to match the plot size of the original sampling. In four

169   plots, fewer than four intensive modules were established. Site characteristics recorded include

170   aspect, slope, substrate depth, and percent cover for organic debris, rock, and water. Each plot

171   was GPS-documented, and photographs were taken at the plot origin (at 0 m on center line).

Data Compatibility

173   All non-woody vascular plants and all woody plants smaller than breast height were

174   classified as part of the understory. Whenever possible, plants were identified to the species level

175   following Ackerfield (2015) and verified using specimens in the University of Northern

176   Colorado herbarium. For each species identified in the 2012/13 sampling, a voucher specimen

177   was placed in the University of Northern Colorado herbarium. When positive identification was

178   not possible, samples were grouped according the lowest possible identifiable taxonomic unit,

179   from family to genus. Remaining samples were labeled as "unknown" but treated as unique taxa

180   in the data set. Taxa that were identified to species level were classified as to whether they were

181   exotic in Rocky Mountain National Park and noxious at the state-level (Colorado) according the

182   "Invasive Exotic Plant Management Plan and Environmental Assessment, Rocky Mountain

183   National Park" (U.S. Department of the Interior 2003) and the "USDA PLANTS Database"

184   (U.S. Department of Agriculture 2018), respectively. Species names from the 1972/73 data

185   largely conformed to Weber (1972) and were changed to synonyms following Ackerfield (2015)

186   where applicable (Appendix S2). Voucher specimens were deposited at the Rocky Mountain

187   National Park herbarium.

188   Due to different sampling protocols, a subset of the data from both data sets was used for

189   comparative analyses to ensure an unbiased comparison of understory community composition

190   and diversity indices. For both data sets, a frequency value was calculated for each species based

191   on the proportion of presence/absence in eight 1 m^2 sub-plots in each data set: From the 1972/73

192   data set, species frequencies were calculated from presence/absence in eight of the 25 1 m^2 sub-

193   plots from along the center line. To reduce autocorrelation from adjacent sub-plots, only data

194   from sub-plots 1, 5, 8, 11, 15, 18, 21, and 25 were included. From the 2012/13 data set, species

195   frequencies were calculated from presence/absence in all of the eight nested 1 m^2 sub-quadrants

196   from within the intensive modules. In the 2012/13 sampling, three plots contained six 1 m^2 sub-

197   quadrants and one plot contained four 1 m^2 sub-quadrants instead of the typical eight. To account

198   for different sampling areas between data sets, sub-sample sizes of the 1972/73 data were

199   adjusted to match the 2012/13 sub-sample sizes in these four plots. Resulting frequency values

200   were used to calculate Shannon and Simpson diversity indices (Peet 1974) and evenness (Pielou

201   1966), whereas assessments of changes in species distributions and exotic species spread were

202   based on presence/absence in the entire plot.

203   *Data Analysis*

204   For this study, vegetation dynamics were assessed at three different spatial scales to

205   account for topographic influences and site-specific responses nested within regional patterns

206   (Malanson et al. 2011): all plots combined (landscape scale), per ecotone [montane and

207   subalpine; 2100-2700 m and 2700-3500 m, respectively, based on Hess and Alexander (1986)],

208   and per series (forest type) – the latter based on the original classification by Peet (1981). Of the

209   89 plots, 37 fell into the montane (< 2700 m) and 52 into the subalpine (> 2700 m) elevation

210   range (Hess and Alexander 1986). Of the seven forest series sampled in this study (Table 1),

211   analysis for two series was limited to descriptive statistics due to low sample sizes (series A with

212   two plots and series E with one plot). In contrast, analyses at the ecotone and landscape scale

213   provide ample sample size for robust statistical testing. All statistical comparisons were limited

214   to vegetation data from 1 m^2 sub-plots to ensure highest comparability resulting from identical

215   sampling areas.

216   Changes in taxonomic richness, evenness, and diversity indices (Shannon and Simpson)

217   were statistically assessed using Wilcoxon-Signed-Rank tests, and linear regression was used to

218   test for a relationship between changes in diversity indices and elevation. Taxonomic turnover

219   was assessed by calculating the proportion of lost and new taxa from among the total taxa per

220   plot. Relative taxonomic turnover per plot was calculated from the proportion of gained (i.e. taxa

221   that were previously not present in a plot) and lost taxa (i.e. taxa that are no longer present in a

222   plot) compared to the total number of taxa present in that plot. A total turnover value per plot

223   was calculated from the sum of these proportions. To assess elevation range shifts, the median

224   elevation for each species that was present in at least 10% of the 1972/73 plots (i.e. 9 plots) was

225   compared to the median elevation in the 2012/13 sampling. Median elevation was calculated

226   from the elevations of plots in which its presence was recorded. A linear regression model was

227   used to test for a relationship between initial median elevation and changes in median elevation

228   and elevation range.

229   Changes in understory community composition were explored using non-metric

230   multidimensional scaling (NMS; Bray-Curtis dissimilarity, 2 axes) using the R-package vegan

231   (Oksanen et al. 2017) and frequency data as input. To account for repeated sampling, statistical

232   comparisons between data sets were based on a blocked multi-response permutation procedure

233   (MRBP) using Euclidean distance measure (median alignment, no average distance function

234   commensuration) at the series scale, grouped by dataset and blocked by plot.

235   All statistical tests were performed in R (Version 3.3.2) or PC-ORD (Version 6.08) with

236   alpha = 0.05. Where multiple tests were performed, test results were adjusted based on the false

237   discovery rate (FDR) controlling procedure (Benjamini & Hochberg 1995; Pike 2011).

238   **Results**

239   *Diversity and Distribution*

240   Of 327 previously found vascular plant taxa, 254 (78%) were still present, whereas 73

241   were not found. An additional 67 taxa not previously found were identified, resulting in 321 taxa

242   found in the 2012/13 sampling and 394 taxa found when both data sets are considered (Appendix

243   S2). Number of taxa per series and proportion of series-specific taxa were similar between data

244   sets (Table 1). The taxonomic richness was found in mesic montane forests, with a total of 233

245   unique taxa in 1972/73 (44 ± 4 taxa per plot) and 228 (41 ± 2 taxa per plot) in 2012/13. Of these,

246   29% (68 taxa) in 1972/73 and 24% (54) in 2012/13 were only found in this series – the highest

247   proportion among all forest types. In 1972/73, *Populus tremuloides* dominated forests contained

248   148 taxa (34 ± 3 taxa per plot) of which 8% (11) were unique to this series compared to 142 taxa

249   (33 ± 3 taxa per plot) in 2012/13 of which 4% (6) were unique to this series.

250   Taxa that were gained or lost were present on average in 1.9 plots in 1972/72 and 1.6

251   plots in 2012/13. The majority of species found in either sampling was classified as perennials

252   and forbs, with a net decrease in most groups except shrubs and trees (Table 2). Relative species

253   turnover was somewhat higher at lower elevations; however, this trend was not significant (Fig.

254   1). There was a significant (before FDR adjustment) increase in evenness that drives increases in

255   Shannon and Simpson diversity indices in the montane ecotone (Fig. 2). Changes of richness,

256   evenness, or diversity metrics at landscape scale, in the subalpine ecotone, or in any series were

257   non-significant.

258   Elevation had a weak but significant effect on changes in Shannon (R^2: 0.036; P: 0.042)

259   and Simpson (R^2: 0.033; P: 0.049) diversity indices, with predominantly increases at lower

260   elevations and decreases at higher elevations (Fig. 3). There was a weak (R^2: 0.092) but

261   significant (P: 0.002) relationship between species median elevations in 1972/73 and 2012/13

262   (Fig. 4 a). No trend with elevation was detected in changes of species elevation ranges (Fig. 4 b).

263   *Exotic Species*

264   We identified a total of 18 exotic plant species across both data sets, including seven

265   classified as noxious in Colorado (Table 3). Of the 89 resampled plots, 43 (48%) contained one

266   or more exotic species in 2012/13, compared to 41 (46%) plots in 1972/73. The total number of

267   exotic species occurrences (i.e. a given species is present in a plot), has increased by 26% from

268   73 to 92 at the landscape scale. The highest relative increase was observed in *Pinus contorta*

269   forests, where the occurrences of exotic species increased by 80% from 15 to 27. The only

270   decreases were observed in *Pinus ponderosa* woodlands and *Pinus ponderosa-Pseudotsuga*

271   forests. *Populus tremuloides* forests show a slight increase in occurrences of exotic species, from

272   17 to 19. It should be noted that the observed decrease in abundance of *Poa pratense* at the

273   landscape scale is potentially due to difficulty of identification without presence of an

274   inflorescence, and some occurrences may have been counted under the umbrella taxa *Poa* sp. or

275   Poaceae sp.

276   *Community Assessment*

277   Shifts in understory community structure are evident for mesic montane and *Pinus flexilis*

278   forests, as indicated by large offsets in centroid positions among sampling periods (Fig. 5 a). In

279   2012/13, the convex hull of plots in the *Populus tremuloides* series is notably larger than in

280   1972/73. The visible shift in understory community structure is reflected in the MRBP test

281   results, with significant differences (before FDR adjustment) in mesic montane (*P*: 0.013) and

282   *Pinus flexilis* forests (*P*: 0.012; Table 4). Generally, increased proximity between centroids of

283   different forest series and higher overlap of 95% confidence ellipses can be observed in the

284   2012/13 analysis (Fig. 5 b).

285   **Discussion**

286   *Diversity and Distribution*

287   To assess long-term changes in understory vegetation in montane and subalpine forests

288   containing aspen, we resampled 89 plots originally established in 1972/73 by Peet (1981). While

289   we acknowledge that it is unlikely that exact locations were resampled as permanent markers

290   were not permitted in the park, we feel confident that our sampled plots are within 150 m of

291   Peet's original plots based on comparison of local site characteristics (aspect, slope, slope

292   position, ground cover). The validity of our comparison is further supported by Kopecký and

293 Macek (2015), who have shown that resurveys of historical plots are robust to plot location

294 uncertainty.

295   The hypothesis of no change in understory species diversity at the landscape scale was

296 supported by our data. All plots had aspen present in the initial sampling in 1972/73 and one

297 initial motivation of this study was to test whether changes in aspen basal area or stem density

298 relate to changes in understory species diversity. Although studies in Utah and Quebec link

299 higher species diversity observed under aspen to underlying surface deposits and soil conditions

300 that inherently favor both aspen and higher species diversity (Warner & Harper 1972; Legare et

301 al. 2001), other studies have shown that aspen increase soil moisture, nutrients, and

302 decomposition rates (Buck & St. Clair 2012), generating more fertile soils and thus promoting

303 higher biodiversity. Since neither landscape-wide understory diversity (this study) nor landscape-

304 wide aspen basal area or density of stems larger than 2.5 cm DBH have exhibited significant

305 change in the Colorado Front Range over the past 40 years (Bretfeld et al. 2016), we could not

306 test for a relationship between changes in aspen abundance and understory diversity. Although

307 plant diversity has been shown to decrease with progressing succession towards coniferous

308 forests (Kuhn et al. 2011; McCullough et al. 2013), no changes in diversity metrics were detected

309 in our data (Fig. 2 c/d). Based on basal area data, relative abundance of conifers in plots of the

310 aspen-dominated forests (series H) increased on average from 10% to approximately 45%, but

311 basal area across all species decreased by 30% from 1972/73 to 2012/13 (Bretfeld et al. 2016). In

312 their study of 29 aspen stands in the southern Cascade/northern Sierra Nevada mountains,

313 McCullough et al. (2013) found that for a 10% increase in relative conifer abundance, species

314 richness decreased by 1 species. No such relationship was found in our data. In addition to

315 different climates between studies, the overall decrease in basal area in our plots potentially

316 counteracts this trend.

317   Significant changes in diversity were detected at smaller spatial scales, most notably in

318 lower-elevation plots and plots of the mesic montane forest series. This is reflected in our linear

319 model results that detected a significant elevation effect on changes in diversity indices (Fig. 3)

320 and shifts in species median elevations (Fig. 4 a). However, using elevation as the sole predictor

321 expectedly yields a large proportion of unexplained variance in all models because elevation is

322 used merely as a proxy for local temperature and moisture dynamics and does not accurately

323 reflect actual local biotic interactions and abiotic conditions.

324   Observed elevational trends in species turnover and diversity changes agree with Rumpf
325 et al. (2018) who report greater species dynamics at lower elevations in the European Alps and
326 attribute this trend to differences in species-specific thermal and nutritional demands. Although
327 we did not group species based on their respective nutrient demands and thermal optima and thus
328 cannot test this hypothesis, Colorado Front Range forests have been subjected to elevated
329 nitrogen deposition (Baron et al. 2000) and increasing temperatures (McGuire et al. 2012) over
330 the past decades, providing a potential explanation for observed trends. McGuire et al. (2012)
331 report significantly higher mean and maximum temperatures over 56 years from 1953 to 2008,
332 and significantly higher minimum temperatures over 20 years from 1989 to 2008 at subalpine
333 elevations in the Colorado Front Range. These relatively rapid changes have the potential to
334 decrease survival and reproductive ability of high-elevation species already at the fringe of their
335 physiological niche.

336   Owing to recent bark beetle outbreaks, both *Pinus contorta* and *Pinus flexilis* dominated
337 forests have undergone substantial decreases in basal area of the dominant overstory species
338 (Bretfeld et al. 2016). Observed trends of increasing species richness in these forests, despite
339 being statistically non-significant, agree with Stone and Wolfe (1996) who report increased
340 species richness and diversity in lodgepole pine forests affected by moderately-severe beetle-
341 induced mortality in the Wasatch National Forest, northern Utah. This pattern is also consistent
342 with decreasing species richness observed with increasing successional development and
343 associated tree density of these forests in Rocky Mountain Park by Peet (1978).

344   Another major disturbance in the montane and subalpine forests of this study is fire.
345 Precise fire history data based on dendrochronological analysis was available for 43 of the 89
346 plots (Buechling & Baker 2004; Sibold et al. 2006). The average stand age of these plots was
347 ~208 years since last fire at the time of resampling, with the oldest stand being 477 and the most
348 recently burned stand 57 years old. Excluding plot 86 that burned in the 2012 Fern Lake Fire, no
349 plots showed evidence of recent fire. Owing to different stand ages, varying typical fire intervals
350 depending on their respective plant community, and the apparent lack of fires between
351 samplings, it is likely that observed vegetation changes can in part be attributed to long-term
352 plant community changes associated with natural succession (Peet 1978).

353 *Exotic Species*

354   Similar to our results, Stohlgren et al. (2000) report one or more exotic species in 42% of

355 their plots in Rocky Mountain National Park. While the number of plots containing exotics has

356 not increased considerably between the two data sets examined in this study, the total number of

357 exotic species occurrences within plots has increased by 26% at the landscape scale (Table 3).

358 This increase is most evident in the *Pinus contorta* forests with an increase of 80%, supporting

359 the hypothesis that areas affected by bark beetle outbreaks show highest rates of invasion by

360 exotic species. Exotic species abundance and richness increased considerably following thinning

361 and burning treatments in northern Arizona ponderosa pine forests (Griffis et al. 2001) and

362 salvage logging of beetle-killed lodgepole pine forest in north-central Colorado (Fornwalt et al.

363 2018). Stone and Wolfe (1996) report that grasses benefited most from beetle-induced overstory

364 mortality in northern Utah. Likewise, we found the strongest increases at the landscape scale in

365 the exotic grasses *Bromus tectorum* and *Poa pratense*. Anemochorous species are likely

366 beneficiaries of increased wind in forests thinned by bark beetles, allowing for more effective

367 dispersal.

368   Varying levels of herbivory and elevated nitrogen deposition may have further

369 aggravated shifts in composition in favor of non-native species (Baron et al. 2000). While signs

370 of heavy ungulate browsing were observed in some plots, we did not specifically quantify

371 browsing pressure. Although very few elk were observed during the original sampling, the elk

372 population in the winter range of the park was estimated to be between 500 and 700 individuals

373 in 1972/73 compared to 200 to 300 individuals in 2012/13, with several spikes of more than

374 1000 individuals between the 1980s and early 2000s (Lubow et al. 2002; Hobbs 2014). Between

375 2002 and 2012, a shift in the winter range was observed with fewer elk wintering inside the park

376 (Johnson et al. 2016), and successful management programs have been put in place to protect

377 key vegetation communities (Zeigenfuss & Johnson 2015). The impact of these dynamics on

378 species distribution remains subject to research and future resampling of long-term plots will be

379 required.

380 *Community Assessment*

381   The hypothesis that forest community shifts are most evident in areas that were affected

382 by extensive conifer mortality due to bark beetles, was not supported by our data. Significant

383 shifts (after FDR adjustment) in community composition were detected only in mesic montane

384   and *Pinus flexilis* forests, whereas heavily beetle-affected forests of the *Pinus contorta* series

385   exhibited no significant difference. In our study, plots of the mesic montane and *Pinus flexilis*

386   forests were predominantly located at the lower and upper boundary of the elevational gradient,

387   suggesting an interaction between elevation and climate change as an important driver of plant

388   community dynamics.

389   The increased convex hulls observed for *Populus tremuloides* forests suggest more

390   dissimilarity within and more overlap between forest types and are an indicator of succession

391   driving change (Fig. 5). Increased proximity of centroids further suggests a general

392   homogenization among forests series over the 40-year timespan between sampling periods. Plots

393   in the *Populus tremuloides* series were subjected to considerable conifer encroachment as part of

394   natural succession (Bretfeld et al. 2016) but did not exhibit significant changes in understory

395   plant composition. Although their plots were not subjected to significant conifer encroachment,

396   Coop et al. (2014) report relatively stable understory plant community composition over a 46-

397   year timespan (1964-2010) near Crested Butte, Colorado, despite considerable loss of overstory

398   aspen. Our results further support that understory plant community composition in aspen-

399   dominated forests is relatively resilient to aspen overstory changes, at least within the temporal

400   scale and degree of overstory change observed in our study.

401   *Conclusion*

402   Resampling studies of long-term vegetation plots provide unique opportunities to directly

403   assess change over time as ecosystems worldwide are responding to a changing climate and other

404   anthropogenic pressures. Species and communities in mountainous regions are believed to be

405   especially sensitive to climate change. Our results show that forests containing aspen in Rocky

406   Mountain National Park (Colorado) have exhibited no landscape-wide change in understory

407   plant species diversity over the past 40 years. However, some forest series exhibited significant

408   changes in diversity and composition and observed vegetation dynamics varied by elevation.

409   Thus, our results underscore the need to analyze vegetation data at different spatial scales across

410   long time periods.

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Author contributions

417   M.B., S.B.F. (2012/13), and R.K.P. (1972/73) collected data; M.B., with contribution

418   from S.B.F., performed statistical analyses; M.B. wrote the manuscript; all authors discussed the

419   results and revised the manuscript.

Data accessibility

421   Original data collected by Peet at the plot level are available at VegBank, Project

422   "Vegetation of the east slope of the Colorado Front Range (http://vegbank.org). Species

423   occurrence and cover in subplots collected by Peet plus resampled data are available at

424   Scholarship & Creative Works @ Digital UNC PhoPlots Database

425   (https://digscholarship.unco.edu/phoplots/).

426

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634

635   **Appendices**

636   Appendix S1. Vegetation series of the northern Colorado Front Range as described in Peet 1981.

637

638   Appendix S2. Complete list of taxa, their family, and synonyms found in either 1972/73,

639   2012/13, or both sampling efforts.

640 **Tables**

641 Table 1: Average number of taxa (plus standard error) and total number of unique taxa found at
642 landscape, ecotone, and series scales based on presence/absence in plots. Series are sorted from
643 containing highest to lowest number of total unique taxa. Ecotone and series scales also include
644 number and proportion of taxa that were specific to that ecotone or series (i.e. not found
645 anywhere else). Note that series A and E were only represented by two and one samples,
646 respectively. Accordingly, series E does not have standard error estimate associated with the
647 average number of taxa per plot.

648

Scale	Plots	1972/73			2012/13		
		Taxa per plot	Total unique taxa	specific	Taxa per plot	Total unique taxa	specific
Landscape	89	33 ±1	327	n/a	31±1	321	n/a
Montane ecotone	37	40 ±3	274	97 *(35%)*	39±2	273	93 *(34%)*
Subalpine ecotone	52	27 ±1	230	53 *(23%)*	25±1	228	48 *(21%)*
Mesic montane forest (C)	22	44 ±3	233	68 *(29%)*	41±2	228	54 *(24%)*
P. contorta forest (D)	35	26 ±1	176	14 *(8%)*	26±2	205	19 *(9%)*
Populus tremuloides forest (H)	11	34 ±3	148	12 *(8%)*	33±3	142	6 *(4%)*
P. ponderosa-Pseudotsuga forest (B)	9	34 ±5	113	11 *(10%)*	33±5	131	11 *(8%)*
P. flexilis forest (F)	9	23 ±2	75	9 *(12%)*	18±4	79	10 *(13%)*
P. ponderosa woodland (A)	2	51 ±1	68	4 *(6%)*	46±6	71	5 *(7%)*
Picea, Abies forest (E)	1	49	49	0 *(0%)*	19	19	0 *(0%)*

649
650

651

652 Table 2: Lost and gained species by functional group and growth behavior (excluding lost/new
653 taxa that were not identified to species level). The total number of species per group/growth is
654 based on combined data from both data sets. Grouping and growth behavior data are based on
655 "USDA PLANTS Database" classification (U.S. Department of Agriculture 2018).

656

	New species found	Species lost	Total number of species
Functional group			
fern[1]	0	5	9
forb	36	47	234
graminoid	14	15	70
grass	10	12	50
rush	0	2	4
sedge	4	1	16
shrub	4	2	38
tree	2	1	19
Growth duration			
annual	4	7	16
annual/biennial	3	2	7
annual/biennial/perennial	1	1	3
annual/perennial	0	2	3
biennial	3	1	5
biennial/perennial	4	3	12
perennial	41	54	324

[1] includes fern-allies

657

658 Table 3: Number of plots with exotic and noxious species present at series, ecotone, and
659 landscape scale. The first number of each entry denotes data from the 1972/73 sampling, the
660 second number data from the 2012/13 sampling. Exotic and noxious classifications were
661 according National Park Service and USDA Forest Service, respectively.
662

Species	Pinus ponderosa woodland (series A; 2 plots)	Pinus ponderosa-Pseudotsuga forest (series B; 9 plots)	Mesic montane forest (series C; 22 plots)	Pinus contorta forest (series D; 35 plots)	Picea, Abies forest (series E; 1 plot)	Pinus flexilis forest (series F; 9 plots)	Populus tremuloides forest (series H; 11 plots)	Montane	Subalpine	Landscape
Exotic										
Agrostis gigantea			1/2	0/2				1/3	0/1	1/4
*Bromus inermis**			0/1	0/2				0/1	0/2	0/3
*Camelina microcarpa**							0/1		0/1	0/1
Conyza canadensis†			2/0	1/0				2/0	1/0	3/0
*Descurainia sophia**		0/1							0/1	0/1
Phleum pratense			5/3	0/1			3/3	6/4	2/3	8/7
Poa annua†				1/0					1/0	1/0
Poa compessa†			1/0					1/0		1/0
Poa pratensis	1/0	5/1	6/7	6/7		1/0	6/4	12/12	13/7	25/19
Taraxacum officinale	1/0	2/2	12/13	5/9	0/1	0/1	7/6	17/17	10/15	27/32
Tragopogon dubius	1/0	1/0	0/3	1/3			0/2	2/4	1/4	3/8
Noxious (List B)										
*Carduus nutans**			0/3					0/3		0/3
Cirsium arvense			1/1					1/1		1/1
Cirsium vulgare†							1/0		1/0	1/0
*Cynoglossum officinale**			0/1					0/1		0/1
*Elymus repens**			0/1	0/1				0/1	0/1	0/2
Noxious (List C)										
Bromus tectorum		0/1	1/2	1/2			0/2	1/4	1/3	2/7
*Verbascum thapsus**			0/2				0/1	0/2	0/1	0/3
Total	3/0	8/5	29/39	15/27	0/1	1/1	17/19	43/53	30/39	73/92

† found only in 1972/73 sampling
* found only in 2012/13 sampling

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664 Table 4: Test statistics (*T*) and probability values (*P*) of blocked multi-response permutation
665 procedures (MRBP) per series. Asterisks indicate significant differences in understory
666 community composition between 1972/73 and 2012/13. No analysis was performed for series A
667 and E due to small number of plots (N < 5).
668

Series	*T*	*P*
Pinus ponderosa woodland (series A; 2 plots)	n/a	n/a
Pinus ponderosa-Pseudotsuga forest (series B; 9 plots)	-1.812	0.051
Mesic montane forest (series C; 22 plots)	-2.681	0.013 *
Pinus contorta forest (series D; 35 plots)	-1.552	0.074
Picea, Abies forest (series E; 1 plot)	n/a	n/a
Pinus flexilis forest (series F; 9 plots)	-3.127	0.012 *
Populus tremuloides forest (series H; 11 plots)	-0.228	0.387

* significant ($\alpha=0.05$, unadjusted)

669

670   **Figures**
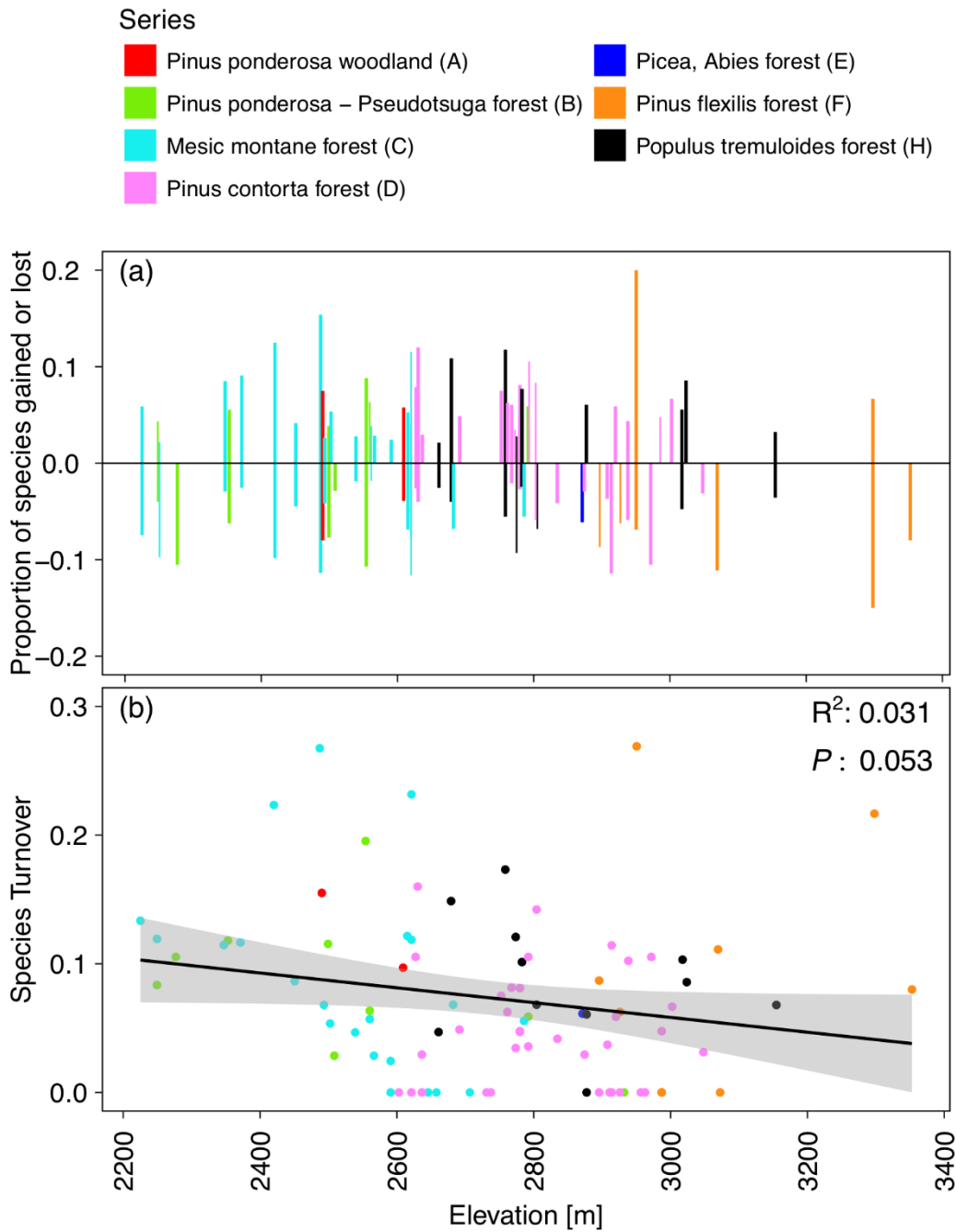
671

672   Fig. 1: Proportions of gained or lost species per total number of species per plot, along an
673   elevation [m] axis. (a) Each vegetation plot is represented by one line, with negative values
674   indicating the proportion of species lost and positive values indicating the proportion of gained
675   species. (b) Total turnover (i.e. the sum of the absolute values of proportions of lost and gained
676   species per plot), where each point represents one plot. The black line is the linear regression line
677   with the shaded area denoting the 95% confidence band. R^2 and p values of regression are
678   printed in the plot.

679
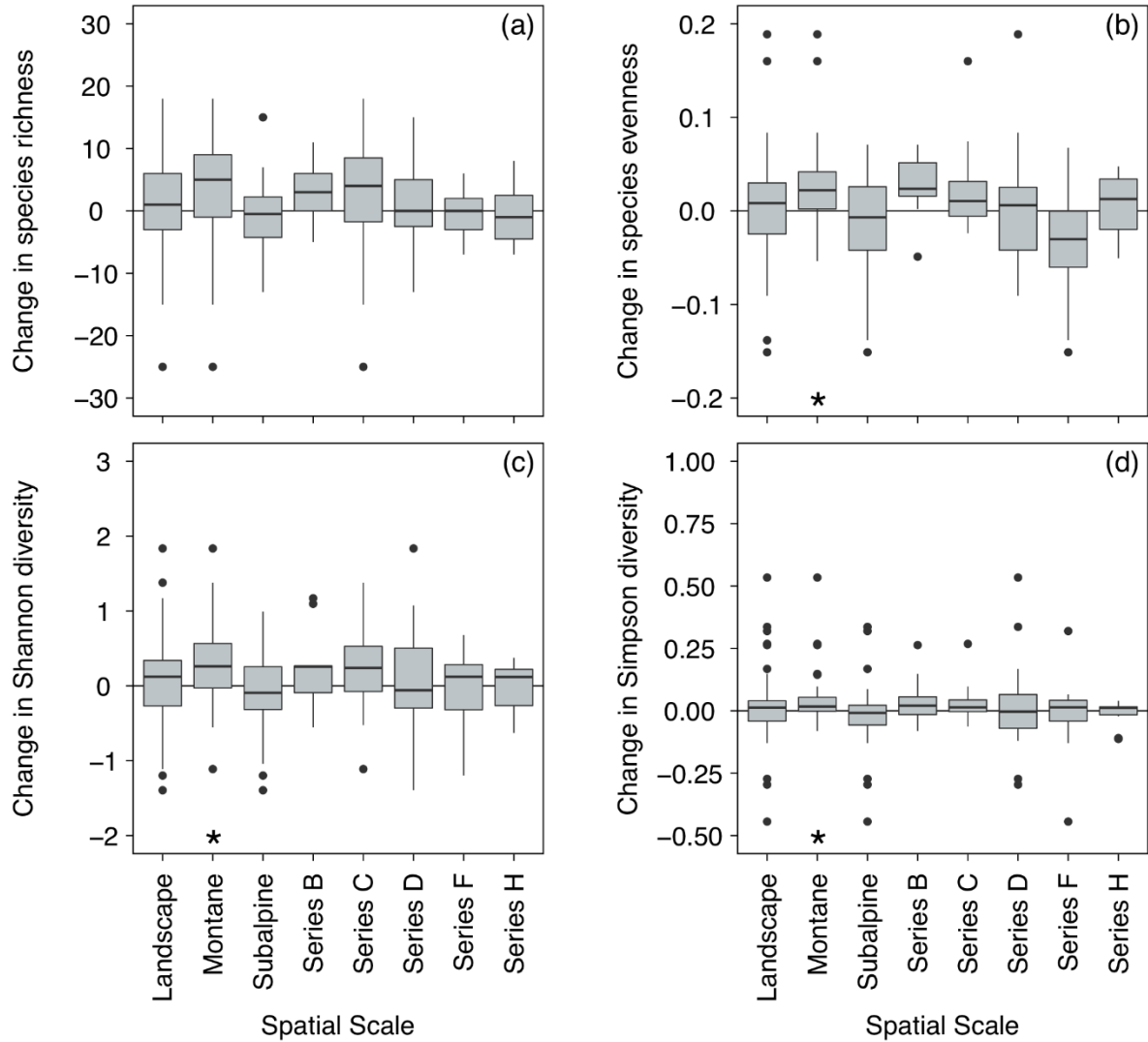
Fig. 2 (a) Changes in species richness, (b) evenness, (c) Shannon's diversity index, and (d)
Simpson's diversity index for landscape, ecotone (montane and subalpine), and series scales
(Series B: *Pinus ponderosa-Pseudotsuga* forest, Series C: mesic montane forest, Series D: *Pinus
contorta* forest, Series F: *Pinus flexilis* forest, Series H: *Populus tremuloides* forest) based on
nested sub-plot data. Asterisks indicate significant changes ($\alpha=0.05$; non-adjusted). Horizontal
lines inside boxes correspond to the median, the lower and upper box boundaries correspond to
first and third quartiles (25th and 75th percentile, respectively), lower and upper whiskers extend
no further than 1.5×IQR (inner quartile range) from the first and third quartiles, and dots
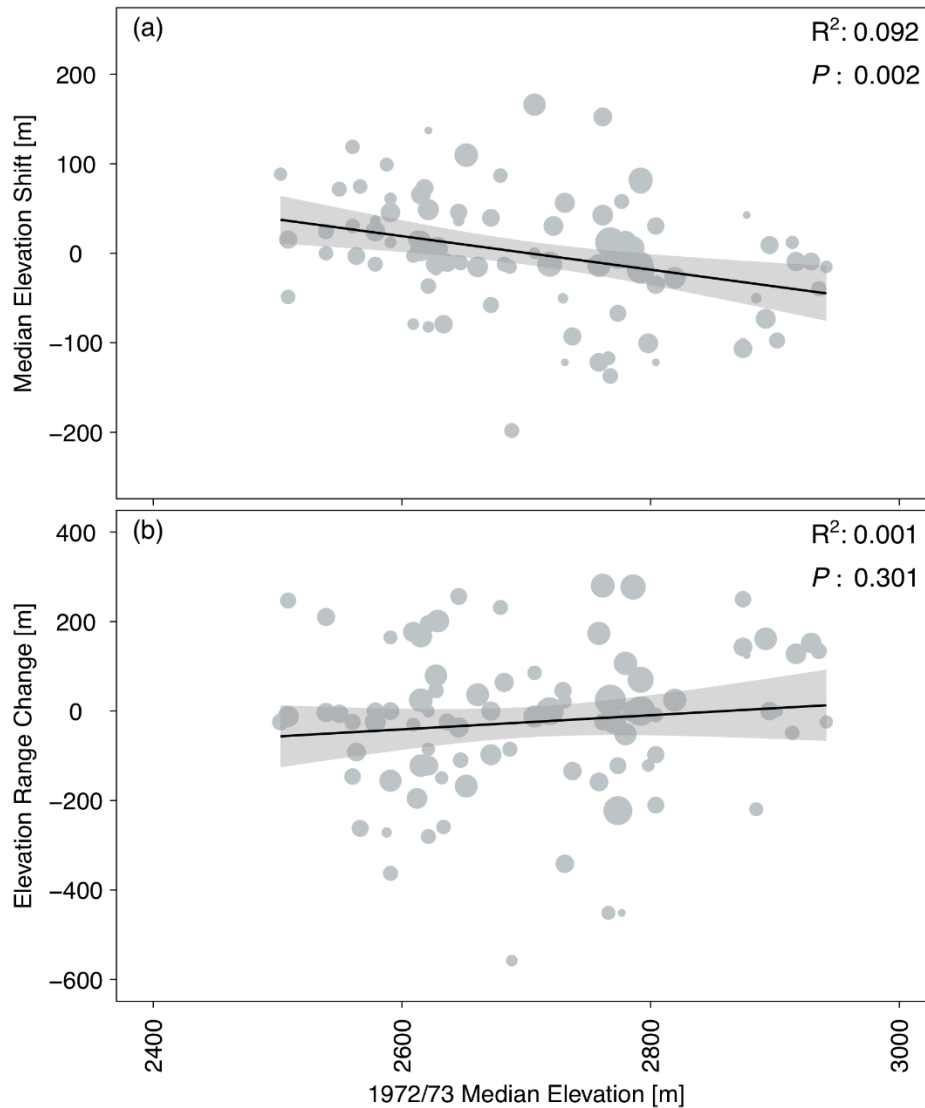represent data points beyond this range.

689
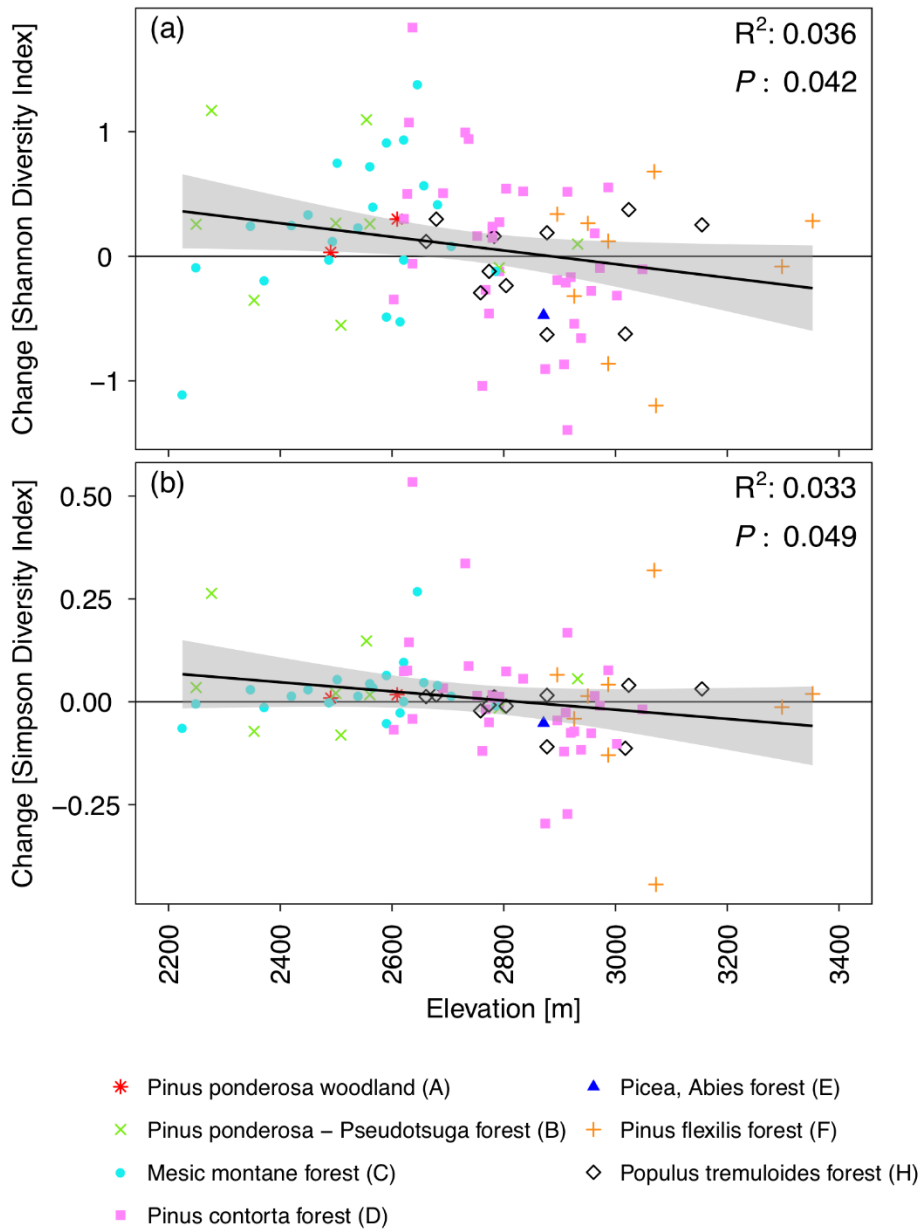
690

691 Fig. 3 Changes in (a) Shannon and (b) Simpson diversity per plot along elevation [m]. The black
692 line is the linear regression line with the shaded area denoting the 95% confidence band. R^2 and p
693 values of regression are printed in the plot.

694

695

Fig. 4 (a) Shifts in median elevation of plots in which a species was present, and (b) changes in
elevation ranges (i.e. highest minus lowest elevation of plots in which a species was found) of
species that were present in at least 10% (9) of sampled plots in the 1972/73 sampling. Data were
plotted against their median elevation in the 1972/73 data set. The black line is the linear
regression line with the shaded area denoting the 95% confidence band. R^2 and p values of
regression are printed in the plot. Size of points represents the number of plots in which a species
was present, with larger points indicating more common species in the landscape.

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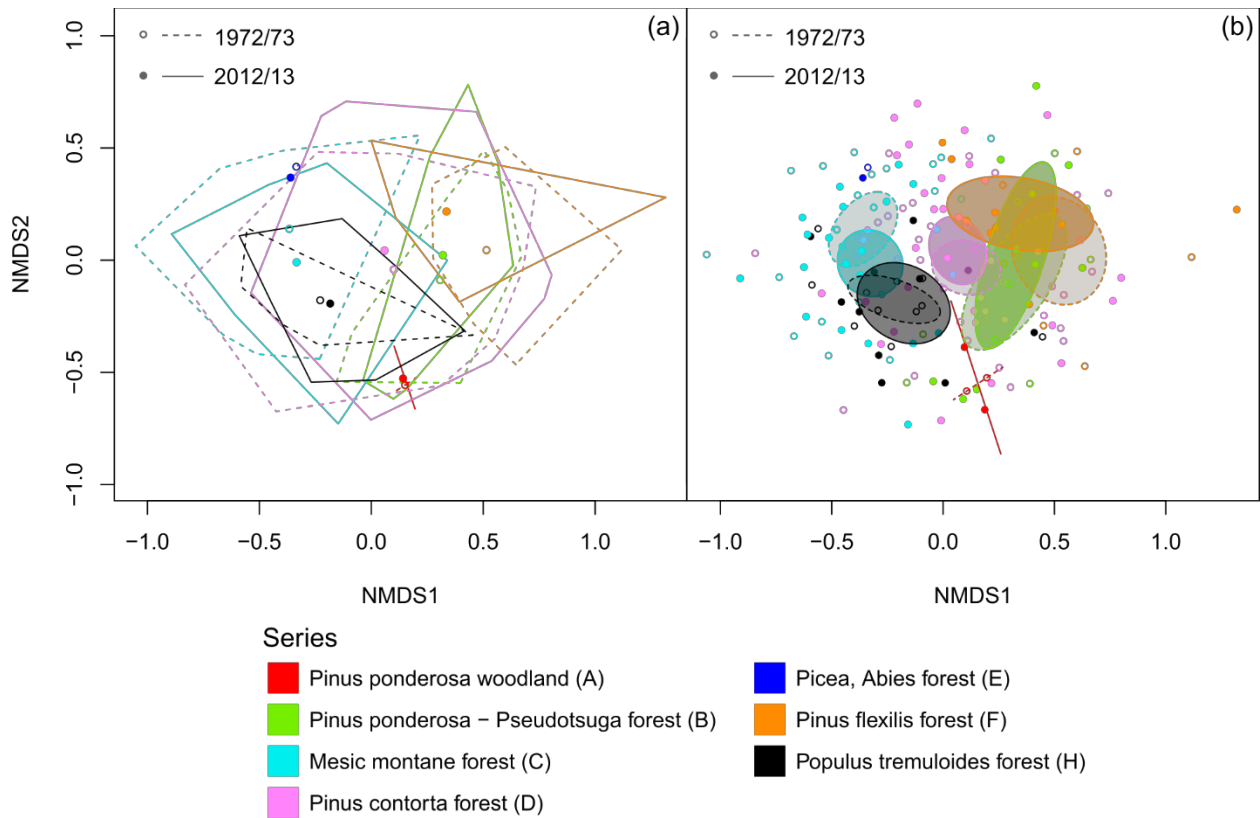
706

707   Fig. 5. NMS-Ordination plots comparing understory vegetation communities grouped by series
708   *sensu* Peet (1981) between data from 1972/73 (dashed lines empty circles) and 2012/13 (solid
709   lines, filled circles). Centroids and covex hulls are shown in (a), individual plots, and 95%
710   confidence ellipses are shown in (b). Note that due to low sample sizes, series A (2 plots) and E
711   (1 plot) are represented by lines or points rather than polygons.

712