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Different vital rates of Engelmann spruce and subalpine fir explain discordance in understory/overstory dominance

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1 **Title:** Different vital rates of Engelmann spruce and subalpine fir explain discordance in
2 understory/overstory dominance

3 **Authors:** Robert A. Andrus^{1a}, Brian J. Harvey², Rachel K. Chai¹, Thomas T. Veblen¹

4 **Affiliations:** ¹Dept. of Geography, University of Colorado Boulder, Boulder, CO

5 ² School of Environmental and Forest Sciences, University of Washington, Seattle, WA

6 ^a Corresponding author; Robert Andrus, Address GUGG 110, 260 UCB, Boulder, CO 80309-
7 0260 USA; Mobile 1-360-774-0449, e-mail: robert.andrus@colorado.edu

8 [non-corresponding author emails: bjharvey@uw.edu, rachel.chai@colorado.edu,](mailto:bjharvey@uw.edu)

9 Thomas.veblen@colorado.edu

Draft

10 ABSTRACT

11 Studies of forest dynamics commonly assume that species composition of the seedling
12 bank reflects the composition of the future forest canopy. However, many forest types exhibit
13 persistent differences in relative dominance of species in the seedling bank versus the forest
14 canopy. Species-specific differences in tree vital rates (e.g. in-growth, mortality, height growth,
15 canopy residence time) across canopy positions may explain this discord in dominance between
16 seedling banks and forest canopies. We tested for differences in tree vital rates for two widely
17 distributed, coexisting species in subalpine forests of the Rocky Mountains, North America. We
18 quantified seedling bank dynamics (> 950 aged seedlings) and vital rates in permanent plots
19 (>2,500 trees) from 1982-2017 to determine if differences in vital rates explained the shift from
20 seedling bank dominance by subalpine fir (*Abies lasiocarpa*) to codominance of the main canopy
21 by subalpine fir and Engelmann spruce (*Picea engelmannii*). Higher rates of fir recruitment into
22 the main canopy were balanced by equally high rates of mortality, whereas spruce exhibited
23 higher rates of net population increase and longer residence time in the main canopy. Projections
24 of future forest trajectories from seedling bank composition can be improved by considering
25 species-specific differences in vital rates.

26 **Key words:** Permanent forest plots, long-term study, forest demography, seedling bank, forest
27 dynamics, Colorado Front Range

28 INTRODUCTION

29 Tree seedlings are the source of the future forest canopy. Studies of forest dynamics
30 commonly assume that species composition of the seedling bank reflects the composition of the
31 future forest canopy (i.e. correspondence, Veblen 1992; or ‘accordance’ criterion of Braun
32 1950). However, in some forest types the relative abundance of tree species in the seedling
33 community commonly differs from the forest canopy and this discrepancy can persist for
34 centuries (Whipple and Dix 1979; Nagel et al. 2010). Initially this discrepancy was interpreted
35 as instability in forests (Braun 1950), but many studies have demonstrated that population
36 processes, disturbance regimes, and non-stationarity in climate may explain a lack of
37 correspondence between the understory and overstory communities (White et al. 1985;
38 Harcombe 1987).

39 Whereas differences in recruitment, in-growth, mortality, and height growth (collectively,
40 vital rates) play an instrumental role in the dynamics of canopy tree replacement and species
41 coexistence (Peet and Christensen 1980), few studies have observed and quantified vital rates
42 (e.g. Harmon and Pabst 2015; Levine et al. 2016). Inference of tree vital rates from static stand
43 structure (age or size distribution at one point in time) and/or multiple stand structures of
44 different ages (i.e. chronosequences or space-for-time substitution) depend on assumptions of
45 constant and equal rates of recruitment and mortality (Veblen 1992; Johnson et al. 1994).
46 However, tree vital rates commonly differ by species, life stage, and environmental conditions
47 (Franklin and DeBell 1988; Levine et al. 2016). A more robust approach to measuring vital rates
48 is to regularly census individually tagged trees in permanent forest plots over decades (Bakker et
49 al. 1996; Harmon and Pabst 2015). The resulting vital rates can be used to test long-standing

50 hypotheses about mechanisms of species coexistence and patterns of vegetation change or stasis
51 through time (Peet and Christensen 1980; Franklin and DeBell 1988; Harmon and Pabst 2015).

52 Persistent pools of suppressed tree seedlings in the forest understory (i.e. seedling banks)
53 are often the source of replacement for canopy tree mortality and therefore play a pivotal role in
54 structuring the future forest canopy (Grime 1979; Canham 1989). Whereas new seedling
55 establishment (germination and survival) may be the primary mode of canopy tree replacement
56 following some disturbances such as fire which kill the previous understory (White 1979),
57 existing trees in the seedling bank have a considerable advantage over new establishment for
58 filling canopy gaps (Grime 1979; Antos et al. 2005) and for growing a new canopy following
59 disturbances such as bark beetle outbreaks or blowdown (Kulakowski and Veblen 2003; DeRose
60 and Long 2010). Live trees in the seedling bank respond to overstory tree mortality with
61 accelerated growth (i.e. growth releases) or suppression-release cycles as they compete for a
62 position in the canopy (Wright et al. 2000). Greater relative abundance for one species in the
63 seedling bank may appear advantageous, but faster height growth by another species may
64 counterbalance this perceived advantage (Antos et al. 2000). Such trade-offs in life history traits
65 of tree species may partially explain species coexistence in some forest types in temperate (Antos
66 et al. 2005) and tropical regions (Denslow 1980). While seedling bank composition is expected
67 to influence the species composition of the future forest canopy, using static tree age or size
68 structure data to predict trajectories in relative abundances of different species in the forest
69 canopy depends on several assumptions that cannot be tested without long-term demographic
70 measurements (White et al. 1985; Veblen 1992; Lertzman 1995).

71 Engelmann spruce (*Picea engelmannii* Parry ex Engelmann) and subalpine fir (*Abies*
72 *lasiocarpa* (Hook) Nutt.) coexist in old-growth stands (dominated by trees > 200 yr old) in the

73 Rocky Mountains of western North America and are the source of a long-standing paradox of
74 stand dynamics. For more than a century, researchers have documented that the seedling bank (<
75 4 cm dbh) of old-growth stands is dominated by fir, often times outnumbering spruce several
76 fold, but the species composition of the forest canopy is roughly co-dominated by spruce and fir
77 (Hodson and Foster 1910; Oosting and Reed 1952; Whipple and Dix 1979; Kneeshaw and
78 Burton 1997). These conditions regularly persist for time periods greater than that required for
79 species turnover (centuries) at the stand-scale (i.e. *compositional equilibrium*, Veblen 1992; or
80 *near steady-state*, Antos and Parish 2002). Three non-mutually exclusive hypotheses may
81 explain the coexistence of spruce and fir (summarized in Veblen 1986a). First, according to a
82 non-equilibrium hypothesis, coarse-scale disturbance by fire, blowdown, or bark beetles create
83 conditions that are favorable to new establishment or release of spruce juveniles, and the interval
84 between successive disturbances is insufficient for competitive exclusion of spruce by fir
85 (Whipple and Dix 1979; Peet 1981; Aplet et al. 1988). Second, according to a hypothesis based
86 on regeneration niche differentiation, the two conifers require different levels of resource
87 availability (solar radiation, seed bed conditions) for establishment so that heterogeneity of
88 understory conditions prevent fir from excluding spruce (Knapp and Smith 1982). Third,
89 according to a hypothesis based on species differences in life history traits (i.e. vital rates), the
90 greater abundance of fir in the understory is balanced by a substantially lower death rate among
91 spruce adults (Oosting and Reed 1952; Veblen 1986a; Antos and Parish 2002). The latter
92 viewpoint is supported by the greater longevity of spruce versus fir (> 600 y versus c. 350 y;
93 Oosting and Reed 1952, Bigler and Veblen 2009) and higher treefall rates of fir (Veblen 1986a).
94 In the current study, we further examine differences in adult tree recruitment (i.e. in-growth into
95 larger size classes), mortality, and persistence (i.e. residence time in a size class) as likely

119 *Picea-Abies* (E-6)] in the CFR as described by Peet (1981). The *permanent plots* are distributed
120 across the Niwot Ridge Long Term Ecological Research (LTER) site (40° 3' N, 105° 33' W)
121 from 2980 to 3260 m (Supplement A³). Plots are located in stands composed of spruce and fir in
122 compositional equilibrium (n = 4) and in old seral stands composed of spruce and fir mixed with
123 lodgepole (*Pinus contorta* var. *latifolia*) and/or limber pine (*Pinus flexilis*) (n=2). The maximum
124 tree ages in the compositional equilibrium spruce-fir stands are >460 yr, whereas maximum tree
125 ages in the old seral correspond to their origin after stand-replacing fires, c. 355 to 375 yr ago
126 (Smith et al. 2015). *Seedling plots* were clustered in four sampling areas that span 25-km north-
127 south and c. 400 m in elevation across the core distribution of subalpine forests (c. 2,900 – 3,400
128 m). *Seedling plots* were predominately located in stands dominated by spruce and fir, but we also
129 included an open stand dominated by limber pine with spruce and fir in the understory. Stand
130 structures where seedlings were destructively sampled range from c. 120 yr-old post-fire stands
131 to stands with tree ages > 500 yr. Both sample plot types are distributed across moisture
132 gradients (hydic, mesic, xeric) representative of CFR subalpine forests and located in areas
133 without evidence of recent (last 100 yr) major disturbance (e.g. fire, blowdown, avalanche).

134 The climate of the study area is continental – characterized by long, snowy winters and a
135 short, dry growing season. The majority (c. 70%) of the 670 ±130 mm of precipitation falls as
136 snow during the winter and spring months (Oct. – May), but convective storms during the
137 summer can produce sporadic, intense rainfall (Kittel et al. 2015). The average annual
138 temperature is 1.8°C with temperatures reaching an average monthly maximum of 19.8°C in July
139 and a minimum of -1.9°C in January (C-1 climate station: 40.0362 N, -105.5434 W, 3048 m,
140 1953 – 2016, NWT LTER 2016). Although annual precipitation has not significantly changed

³ Supplement A

141 from 1978 to 2010 (Kittel et al. 2015), mean (0.2°C per decade) and maximum (0.44°C per
142 decade) annual average temperatures increased in the subalpine zone in the CFR from 1953-2008
143 (McGuire et al. 2012).

144 **Field Methods**

145 *Permanent forest plot installation and remeasurement protocol:* Permanent plots were installed
146 in summer 1982 or 1983, and subjectively located in areas not disturbed by logging (i.e. lacking
147 cut stumps, Veblen 1986b). Two sizes of permanent plots were included in this study. The four
148 large permanent forest plots (hereafter ‘large plots’) range in size from 0.19 to 0.29 ha. Size was
149 determined by the area necessary to include > 400 trees. Twenty-four smaller permanent forest
150 plots (size range: 60 to 336 m²) were located beneath canopy openings adjacent to two of the
151 large permanent plots (c. 50 m separation between plot types). Each smaller plot includes c. 40
152 trees per plot. Canopy openings did not originate from timber cutting, rather they were created
153 by small natural openings in the forest or treefalls. In the current study, data from each cluster of
154 smaller permanent plots (hereafter “gap plots”) was aggregated to produce one sampling unit,
155 which was approximately the same size as the larger permanent plots. To justify including gap
156 plots and large permanent plots in our analyses, we demonstrate similarity in patterns of stand
157 dynamics and vital rates for both plot types (‘gap’ and ‘large’) in Supplement B⁴.

158 In 1982, all trees were permanently tagged, and the following was measured for all live
159 and dead trees > 4 cm dbh: diameter at breast height (1.4 m), status (live or dead), height class
160 (main canopy, intermediate, subcanopy). Additionally, all seedlings (c. 5 cm to 1.4 m in height)
161 and saplings (1.4m in height to < 4 cm dbh) were counted by species in 1982 within both the
162 large and gap permanent plots. Species composition and structure is described in an initial study

⁴ Supplement B

163 of stand dynamics (Veblen 1986b) and a more recent study of tree mortality (Smith et al. 2015).
164 Censuses of tree mortality, including cause of death, were conducted every three years, except
165 during the period 1997 – 2003, and censuses of recruitment into the > 4 cm dbh size class were
166 only conducted in 2007 and 2016. Given differences in frequency of censuses and our goal of
167 examining long-term trends in vital rates (rather than interannual effects of climate) and to avoid
168 census period bias, vital rates were calculated over the total period of the study. Following Sheil
169 and May (1996), trees that recruited into the > 4 cm dbh size class and then died were not
170 included in the study.

171 Following the original installation protocol (described above, Veblen 1986b), we
172 conducted a complete re-census of trees (> 4 cm dbh) in summer 2016 and counted all seedlings
173 and saplings (< 4 cm dbh) by species in summer 2017 in all four large permanent plots and
174 associated gap plots. For all trees, we remeasured dbh, status, and canopy position. Trees
175 recruiting (i.e. in-growth) into the > 4 cm dbh class were tagged and measured.

176 *Seedling plots and lab procedures*

177 For the purpose of developing age versus height relationships and calculating growth
178 rate, we destructively sampled c. 50 spruce and c. 50 fir seedlings (> 5 cm and < 100 cm in
179 height) originating from seed in ten randomly located plots (Fig. 1). Plot size varied based on
180 seedling density³. The height of each seedling was measured as the length of the stem (including
181 curvature) from the root collar to the tip of the terminal bud. Seedling germination year was
182 assessed for each seedling as the maximum annual ring count from multiple cross-sections cut at
183 the root-shoot boundary. Each cross-section was sanded with progressively finer sandpaper and
184 dated with multiple ring counts from the outer ring to the pith with a microscope (40x

³ Supplement A

185 magnification). Field and laboratory procedures are described in more detail in Andrus et al.
186 (2018).

187 **Data analysis**

188 *Testing for differences in seedling growth rates and sapling recruitment rates*

189 To test our hypothesis that spruce seedlings have a shorter residence time in the seedling
190 bank by growing faster and are more likely to transition out of the sapling size class, we modeled
191 spruce and fir age against height relationships, compared growth rates from our destructively
192 sampled seedling plots, and computed sapling recruitment rates. To exclusively compare
193 seedlings with the shortest residence time in the seedling bank and those most likely to transition
194 out of the seedling size class, we selected the upper 10th percentile of growth rates for each
195 species from each destructively sampled plot. These criteria were intended to exclude damaged
196 seedlings (Antos et al. 2000) and the slower growing seedlings that are less likely to attain a
197 position in the main canopy in comparison with undamaged, faster growing individuals. Species
198 differences in growth rates based on inclusion of all seedlings were similar to those exhibited by
199 the upper 10th percentile (Supplement C⁵). Seedling average annual growth rate was computed as
200 height (cm) divided by age, and differences in spruce and fir growth rates were statistically tested
201 using a non-parametric Mann-Whitney *U* test ($\alpha = 0.05$). We also modeled the growth rate of
202 spruce and fir from the age vs. height relationship using linear regression models forced through
203 the zero origin (R Core Team 2016) for comparison with similar studies (Antos et al. 2000).

204 Higher rates of recruitment (i.e. in-growth) from the sapling size class into the tree size
205 class (> 4cm dbh) for spruce than fir may illustrate a possible advantage for spruce and
206 difference in life history strategies. Using data from the permanent plots, annualized recruitment

⁵ Supplement C

207 (R) from the sapling to the tree size class was computed for each species as $(T_r / T_i) / P * 100 = R$,
208 where T_r represents the number of trees that recruited from sapling size class to next larger size
209 class during the time period P (entire study period) and T_i represents the initial live sapling count
210 at time of plot installation (Levine et al. 2016). Slow growth rates of seedlings in subalpine
211 forests (Antos et al. 2000) make it unlikely that new recruits into the > 4 cm dbh class would
212 have been < 1.4 m in height in the initial census. Following Levine et al. (2016), we computed
213 recruitment rates over the entire length of the study to not introduce census-period dependence
214 bias.

215 *Testing for differences in vital rates*

216 To quantify changes in the size of tree populations in the permanent plots from 1982-
217 2017, we compared percent change in stems per hectare (> 4 cm dbh) by species in the following
218 size classes: SC1 (< 4 cm dbh), SC2 (> 4 to < 20 cm dbh), and SC3 (> 20cm dbh). These size
219 classes correspond to seedling and saplings (SC1), subcanopy trees (SC2), and main canopy trees
220 (SC3), which were also applied at the time of plot installation (Veblen 1986a).

221 We compared differences in vital rates for spruce and fir by monitoring tree populations
222 in the permanent plots from the early 1980s to 2016-17. In three size classes [SC2, SC3, and total
223 stems (SC2 and SC3 combined)], we quantified the following four vital rates over the entire
224 study period (i.e. results of individual censuses were excluded, see explanation above): 1)
225 annualized recruitment rates (percent) into each size class; 2) annualized tree mortality rates
226 (percent) in each size class; 3) annualized net change (percent) in the size of the population in
227 each size class; and 4) annualized persistence of tree stems (percent) in each size class. Trees in
228 SC1 were not tagged and therefore vital rates could not be quantified accurately for this size
229 class.

230 Annualized recruitment rate (i.e. in-growth) into larger size classes was computed as $(T_r/$
231 $T_i)/P*100 = R$, where T_r represents the number of trees that recruited to the next larger class
232 during the time period P and T_i represents the initial live tree count in the larger size class (see
233 justification above, Levine et al. 2016). Annualized mortality rate was computed as $(T_m/$
234 $T_i)/P*100 = M$, where T_m represents the number of trees that died in a size class during time
235 period P and T_i represents the initial live tree count in the same size class (Smith et al. 2015).
236 Mortality from all causes was aggregated (e.g. bark beetles, blow down, unknown agents) and
237 included. One mortality rate was calculated for each species in each site over the entire study
238 period to not introduce census-period bias (Sheil and May 1996). The annual net change in
239 population was computed as $((T_r - T_m) / T_i) / P * 100 = N_c$. This rate indicates whether a species is
240 increasing or decreasing in abundance within a size class. Annualized persistence of tree stems in
241 each size class was computed as $(T_p / T_i) / P * 100 = P$, where T_p represents the number of trees that
242 remained in a size class during time period P and T_i represents the initial live tree count in the
243 size class. Persistence indicates the capacity to remain in a size class without either dying or
244 recruiting into a larger size class (i.e. residence time). Persistent populations below the main
245 canopy may be necessary for future recruitment into the main canopy; e.g., following future
246 mortality of canopy trees from windthrow, insects or other pulses of mortality. All these
247 demographic measures are based on complete censuses of the monitored populations rather than
248 samples. Thus, probability measures of the accuracy (e.g. standard errors) of parameters, such as
249 means, are not appropriate.

250 **RESULTS**

251 *Seedling bank age and seedling recruitment*

252 Recruitment into the seedling bank was episodic and variable through time (1910-2010),
253 resulting in a multi-aged seedling bank (Fig. 2; Supplement C⁵). Across all plots and for both
254 Engelmann spruce and subalpine fir, > 60% of seedling establishment (germination and survival)
255 occurred during c. 15 episodes (i.e. pulses) of establishment (≥ 10 seedlings establishing per
256 year) after 1950 (Fig. 2). Both species endured long periods of suppression in the seedling bank
257 as evidenced by the lengthy record of recruitment and persistence in the seedling bank. For
258 example, many spruce (47.4% of samples) and fir (41.5% of samples) seedlings were older than
259 c. 50 y, but the median age of spruce (45 y, range 7-184 y) was greater than fir (40 y, range 7 –
260 122 y). When only considering seedlings from 50 to 100 cm in height, spruce (62 y) and fir (63.5
261 y) had a similar median age.

262 *Seedling height growth rates and sapling recruitment rates*

263 The upper 10th percentile of seedling height growth rates indicate that spruce and fir
264 seedlings grow very slowly (c. 1.25 cm/yr) and often do not reach a height of 75 cm until c. 60 yr
265 after germination (Fig. 3). Spruce seedlings reached a greater height in fewer years (Fig. 3A) by
266 growing faster than fir (Fig. 3B). Age was a good predictor of height for both species ($P <$
267 0.001 , $r^2 > 0.94$) and the greater coefficient of spruce ($\beta = 1.36$ cm, ± 0.03) than fir ($\beta = 1.2$ cm,
268 ± 0.02) indicates that spruce attains a greater height in fewer years (linear model in Fig. 3A).
269 Across all plots, spruce had a 0.1 cm/year faster median growth rate than fir (Mann-Whitney U:
270 $P < 0.001$, Fig. 3B); producing a 5 cm taller spruce seedling over 50 yr at median growth rates.
271 This relationship occurred in all seedling growth plots (Supplement D⁶). Additionally, the
272 annualized recruitment rate out of the sapling size class (1.4 m in ht to < 4 cm dbh) and into the

⁵ Supplement C

⁶ Supplement D

273 subcanopy (SC2) in the permanent plots was greater for spruce (1.00%) than fir (0.93%, Fig.
274 3C). This pattern was consistent across two-thirds of the permanent plots.

275 *Changes in stem density 1982-2017*

276 Total stem density (number of stems per hectare) across all permanent plots decreased
277 24% (median) from 1982 to 2017 (Fig. 4), with greater population losses for spruce (median loss
278 34%) than fir (median loss 18%). Only one of six plots showed a population increase. For both
279 species, the greatest decrease in stem density occurred in the seedling and sapling size class
280 (SC1, total median loss -27.1%), the size-class with the largest population⁷. Spruce lost a greater
281 percent of its population (median loss 50%) than fir (median loss 19%) in the seedling and
282 sapling size class and this trend was consistent in all but one plot. In the subcanopy (SC2), stem
283 density declined in all plots, but percent losses of fir (median loss 23%) were greater than spruce
284 (median loss 20%). In contrast, total stem density increased in the main canopy (SC3) by 12%
285 (increase in 4 of 6 plots), with greater gains for spruce (median 9.2%) than fir (median gain
286 5.3%).

287 Despite changes in stem density in all size classes, subalpine fir was significantly more
288 abundant than spruce in the seedling bank, while species dominance in the main canopy favored
289 spruce or equal dominance between species⁷. For example, in the 2016/2017 remeasurement, fir
290 was on average 7 times (range of ratio between fir and spruce 3.4-14.8x) more abundant than
291 spruce in the seedling bank and spruce was on average 1.6 times (range of ratio between spruce
292 and fir, 0.64-2.6x) more abundant than fir in the main canopy.

293 *Adult tree vital rates*

⁷ Supplement E

294 For all trees ('total stems'), subalpine fir recruited at higher rates (0.18% greater median
295 recruitment, Fig. 5A) and died at higher rates (0.10% higher median mortality, Fig. 5B) than
296 Engelmann spruce, resulting in a slight net increase in total fir populations (0.05% greater
297 median net change, Fig. 5C) (see Supplement E⁷ for plot-level vital rate figures). Lower spruce
298 mortality and recruitment rates than fir resulted in higher rates of spruce persistence within a size
299 class (0.12% higher median persistence, Fig. 5D). These trends in vital rates occurred in most
300 plots⁷. However, findings differed by size class, with much greater disparity in median vital rates
301 between species in the main canopy than subcanopy. Considerably higher fir than spruce
302 recruitment rates in main canopy (0.54% greater median recruitment, Fig. 5A) were offset by
303 slightly higher fir mortality rates (0.62% higher median mortality, Fig. 5B). Consequently,
304 spruce populations exhibited greater net increase (0.14% greater median net change, Fig. 5C) and
305 persistence than fir in main canopy (0.53% higher median persistence, Fig. 5D). In the main
306 canopy, trends in recruitment, mortality and persistence rates were consistent with the pattern in
307 vital rates in all but one plot⁷. We found no pattern in net change in population within plots. In
308 the subcanopy, fir and spruce recruited at the same rate (median 0.5% and no trend across plots).
309 Trends in mortality, persistence, and net change in subcanopy were generally consistent with
310 main canopy, but the magnitude of the difference between spruce and fir vital rates was minimal.

311 **DISCUSSION**

312 Differences in vital rates between subalpine fir and Engelmann spruce, quantified from
313 35 years of monitoring permanent forest plots and from destructively sampling seedlings,
314 elucidate the mechanisms behind a shift from seedling bank dominance by fir to codominance of
315 spruce and fir in the main canopy. Consistent with our hypothesis for juvenile trees (< 4 cm dbh),

⁷ Supplement E

316 we found that spruce seedlings grow faster and are more likely to transition out of the sapling
317 size class than fir, which may be advantageous for outcompeting fir and attaining a position in
318 the main canopy. Although we found relatively minimal differences in vital rates for subcanopy
319 trees, considerably lower spruce mortality rates and higher persistence rates than fir in the main
320 canopy support our hypothesis that differences in vital rates favor codominance of spruce and fir.
321 Our results show variability in recruitment rates into the seedling bank, seedling growth rates, in-
322 growth into larger size classes, and mortality between species and across size classes that lead to
323 differences in species persistence (i.e. canopy residence time). Projecting future forest
324 trajectories from seedling bank composition (i.e. understory/overstory correspondence) is
325 therefore problematic for spruce-fir forests, because key assumptions of the correspondence
326 framework are not supported (e.g. that the target species have similar vital rates; White et al.
327 1985, Veblen 1992).

328 **Seedling bank dynamics**

329 Both Engelmann spruce and subalpine fir seedlings recruited episodically, but at different
330 abundances into the seedling bank. Across multiple plots in different watersheds, broad-scale
331 establishment (germination and survival) occurred as frequently as every two years, but there
332 were also much longer intervals (21 yr for fir and 24 yr for spruce) between broad-scale
333 establishment events (Andrus et al. 2018). This is to be expected for species that infrequently
334 produce abundant seed crops (Woodward et al. 1994; Buechling et al. 2016), experience high
335 rates of seed predation (Johnson and Fryer 1996), and require alignment of abundant seed
336 availability with favorable climate conditions for germination and survival (Kueppers et al. 2017;
337 Andrus et al. 2018). The presence of spruce and fir in the seedling bank strongly suggests that
338 the biophysical conditions, including sites beneath individual and clusters of tree mortality and
339 canopy gaps, are suitable for the regeneration of both species in mature spruce-fir forests.

340 However, the greater relative abundance of fir in the seedling bank implies that slight differences
341 in the regeneration niche, such as fir's larger seed size, greater ability to penetrate deeper litter
342 layers and survive at low light levels under a dense forest canopy (Knapp and Smith 1982), play
343 an important role in structuring seedling bank composition.

344 Following establishment, individuals of both species grew very slowly in height (1-1.5
345 cm/yr) and endured long-periods of suppression in the seedling bank (> 70 yr), a finding
346 supported by other seedling bank studies in spruce-fir forests in south-central British Columbia
347 (Antos et al. 2000) and the intermountain western United States (McCaughey and Schmidt
348 1982). Indeed, many seedlings were of sufficient age to be canopy trees under different growing
349 conditions (e.g. at open post-fire sites) or in other forest types. The present study and others
350 averaging seedling growth rates from basal tree-ring estimates of age (instead of bud-scar
351 counts) and height have found that spruce seedlings generally grow at the same rate or faster than
352 fir (e.g. McCaughey and Schmidt 1982, Antos et al. 2000). In the context of spruce-fir forest
353 dynamics where release of suppressed individuals into canopy gaps is the main source of canopy
354 replacement (Veblen 1986b, Parish et al. 1999), spruce's greater performance (i.e. height growth
355 rate) reduces its residence time in the seedling bank and helps to explain the understory/overstory
356 discordance typical of old-growth spruce-fir forests (Antos et al. 2000). However, canopy
357 replacement and the composition of the forest canopy is equally or more strongly influenced by
358 trends in adult-tree mortality and recruitment as well as the length of canopy residence time (i.e.
359 persistence) during later life stages (Lertzman 1995).

360 **Adult tree vital rates explain shift in composition**

361 Despite changes in stand density across size classes in the permanent plots from 1982-
362 2017, subalpine fir maintained greater densities in the seedling bank, while Engelmann spruce
363 either dominated the main canopy or was codominant with fir at the stand-scale. This is the

364 expected trend for spruce-fir stands in *compositional equilibrium* (Whipple and Dix 1979; Aplet
365 et al. 1988; Antos and Parish 2002). We found that higher rates of fir recruitment into the main
366 canopy were balanced by equally high rates of mortality, which lead to a slightly higher net
367 increase in spruce populations and considerably longer canopy residence time of spruce. As
368 identified by the present and previous studies, fir appears more susceptible to the interannual
369 effects of climate on mortality than spruce in old-growth forests (Smith et al. 2015), likely from
370 endemic-level western balsam bark beetle [*Dryocoetes confusus* (Swaine)] attack and *Armillaria*
371 *sp.* root rot (Parish et al. 1999; Maclauchlan 2016). Additionally, the quantified difference in
372 mortality rates is clear evidence for the lower mortality rate of spruce inferred from lower
373 frequency of treefalls and greater longevity in stand structure analysis in Rocky Mountain
374 spruce-fir forests (Oosting and Reed 1952; Veblen 1986a; Antos and Parish 2002) and in
375 Appalachian (White et al 1985) and montane Northeastern China (Okitsu et al. 1995) spruce-fir
376 forests.

377 **Implications for studies of forest dynamics**

378 Differences in species vital rates are one of many factors influencing changes (or lack
379 thereof) in forest community composition and structure over time (Peet and Christensen 1980).
380 By monitoring permanent plots through time, it is possible to address assumptions commonly
381 applied in studies of forest dynamics and expectations based on models (e.g. transition
382 probability matrices) and stand structure analysis (Lertzman 1995). The traditional concept of
383 correspondence between the seedling bank and main canopy relies on many assumptions, namely
384 that species survivorship curves are similar across species, constant through time, and that
385 species' have similar longevity (White et al. 1985; Veblen 1992). If one were to apply the
386 correspondence framework to stand structure data from spruce-fir forests, they would likely

387 conclude that fir will become the dominant species in the main canopy, because of its greater
388 abundance in the seedling bank and similarity in longevity. However, differences in vital rates,
389 as illustrated by fir's greater fecundity and mortality, and spruce's greater persistence, do not
390 support this assumption in spruce-fir forests. Instead, we show that differences in vital rates are
391 critical for allowing species to coexist and maintaining similar composition and structure in old-
392 growth spruce-fir forests over time, a phenomenon also observed in old-growth *Fagus-Abies*
393 forests in Bosnia-Herzegovina (Nagel et al. 2010), old-growth *Abies-Picea* forests in northern
394 Japan (Takahashi 1997), and subalpine *Abies-Betula* forests in China (Taylor and Zisheng 1988).

395 In addition to explaining the discordance between understory/overstory composition, our
396 results apply more generally to assumptions and interpretations of stand structure analysis. For
397 example, a common practice in interpreting static age structure data is to assume individuals of
398 older age classes are survivors of initially equal-sized cohorts (Knowles and Grant 1983), which
399 implies constant input into populations (Veblen 1992; Johnson et al. 1994). In the present study,
400 recruitment into the seedling bank and larger size classes varied considerably over time. Thus,
401 assumptions of equal sized cohorts, necessary for computing mortality rates from static age
402 structure, would lead to erroneous mortality rates. Interpretation of vital rates from static age
403 structure has also led to speculation about general trends in mortality with tree size and age (e.g.
404 constant or U-shaped). Our findings support the concept that intermediate size classes can exhibit
405 lower mortality rates than larger size classes (Fraver et al. 2008). This phenomenon directly
406 counters expectations of constant or declining rates of mortality in larger size classes as
407 interpreted from stand structure data that fit inverse-J and Deevey (II and III) curves (*sensu*
408 Harcombe 1987), or constant transition or mortality probabilities through time in transition
409 probability models (Lertzman 1995).

410

CONCLUSION

411 In Engelmann spruce and subalpine fir forests, species-specific differences in life history
412 traits, as expressed through tree population vital rates, strongly affect forest community
413 composition and structure. Slight differences in the regeneration niche affect structure and
414 composition of the seedling bank, whereas differences in vital rates of adult-trees influence the
415 structure and composition of the forest canopy. Differences in vital rates across tree size classes
416 for two species with similar regeneration niches need to be explicitly considered when inferring
417 long-term trends from static age or size structures. Using permanent plots, we demonstrate that
418 differences in vital rates can result in the transition from fir dominance in the seedling bank to
419 dominance by spruce or codominance by spruce and fir in the main canopy. Our results
420 underscore the importance of explicitly considering potential differences in tree population vital
421 rates when comparing seedling banks to forest canopy composition and when inferring future
422 trajectories of forest stand dominance.

423

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- 559

560

FIGURE LEGENDS

561 **Figure 1:** Study area map A) Extent of Engelmann spruce and subalpine fir from southwestern
562 USA to central British Columbia, Canada (dark gray) in North America. B) Location of study
563 area in Colorado and extent of spruce-fir forest in Colorado, USA. C) Location of permanent
564 plots (tree) and destructively sampled seedling plots (circle with dot) on the eastern slope of the
565 Colorado Front Range in the Arapaho-Roosevelt National Forest. Seedling plot sampling areas:
566 (1) BL - Brainard Lakes Recreation Area, (2) MRS - University of Colorado's Mountain
567 Research Station, (3) BW - Boulder watershed, and (4) RP - Rollins Pass.

568

569 **Fig. 2:** Proportion of Engelmann spruce (A) and subalpine fir (B) seedlings (< 1 m in height)
570 establishing by year from 10 sites in the Colorado Front Range based on destructive sampling of
571 976 stems (after Andrus et al. 2018). The oldest spruce (establishment year 1831) and fir
572 (establishment year 1893) seedlings were omitted from the graph to improve interpretability.

573

574 **Fig. 3:** A) Seedling height (length of main stem) vs. age for the upper 10th percentile of seedling
575 growth rates in each plot for Engelmann spruce (black) and subalpine fir (gray). The regression
576 line is forced through the zero origin and the shaded region is the 95% confidence interval. B)
577 Comparison of upper 10th percentile of growth rates (GR, cm/year) from each plot for spruce (n
578 = 49) and fir (n = 51). Statistical significance between species was tested with a Mann-Whitney
579 test (***) = <0.001). C) Annualized sapling recruitment rate year⁻¹ for spruce and fir. Annualized
580 recruitment rate is the number of saplings (1.4 m in height to < 4 cm dbh) transitioning to
581 subcanopy (> 4 cm to < 20 cm dbh) between 1982 and 2016 divided by the total initial sapling
582 population. The thick horizontal line within the box is the median, the box represents the

583 interquartile range (25th-75th percentiles; IQR) of the distribution, and the whiskers extend no
584 further than ± 1.5 times the IQR.

585

586 **Fig 4:** Percent change in stems per hectare by diameter at breast height (dbh) size class for
587 Engelmann spruce and subalpine fir (individually and together) from 1982 to 2017 in six
588 permanent plots in the Colorado Front Range. In the boxplots, the thick horizontal line within the
589 box is the median, the box represents the interquartile range (25th-75th percentiles; IQR) of the
590 distribution, and the whiskers extend no further than ± 1.5 times the IQR. The dots plotted over
591 each boxplot represent an individual plot.

592

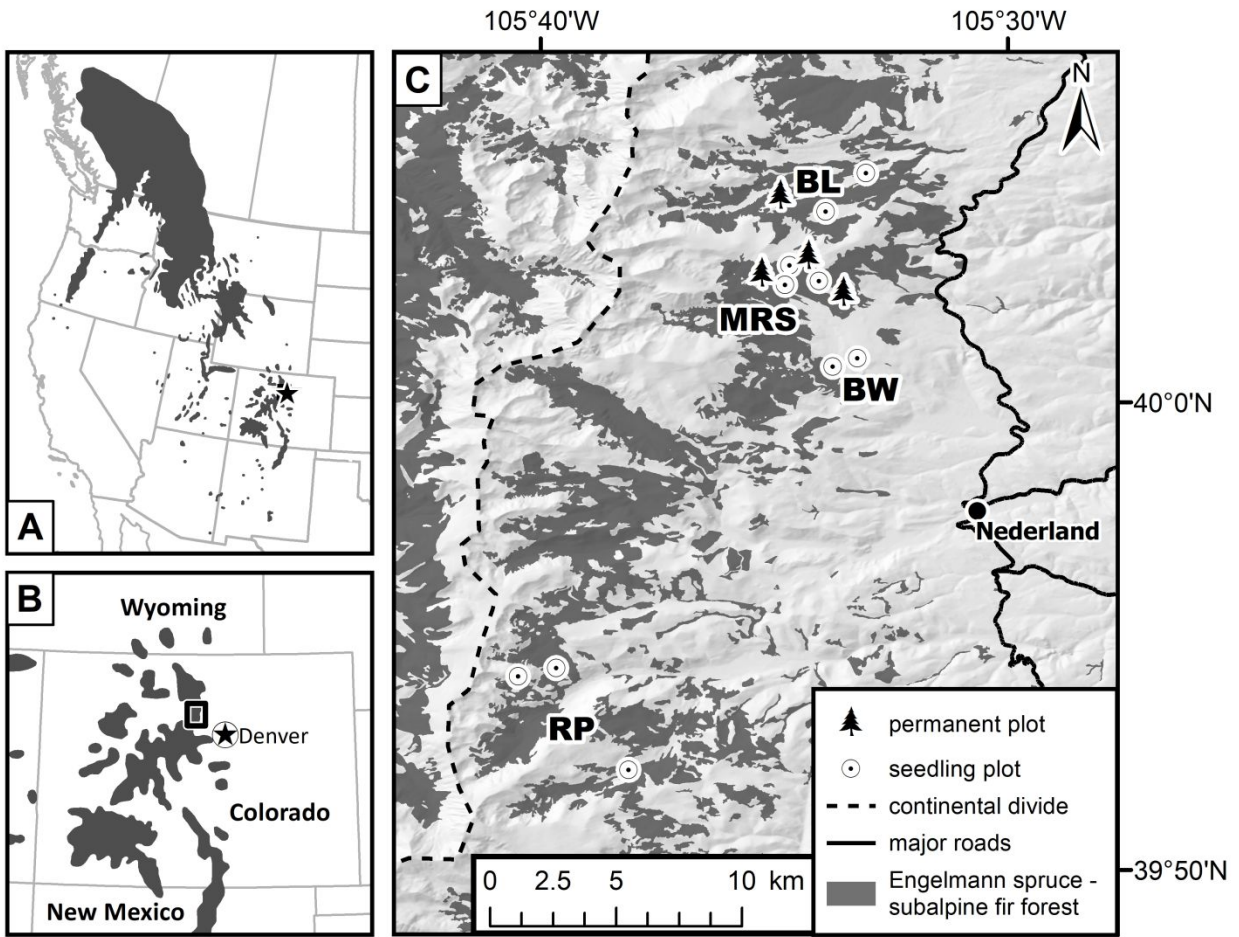
593 **Fig 5:** Annualized recruitment rate (in-growth) (A), mortality (B), net change in population (C),
594 and persistence (D) by size class (SC2: > 4 cm dbh - < 20 cm dbh, SC3: > 20 cm dbh, All: > 4cm
595 dbh) for Engelmann spruce and subalpine fir from 1982 to 2017 in six permanent plots in the
596 Colorado Front Range. In the boxplots, the thick horizontal line within the box is the median, the
597 box represents the interquartile range (25th-75th percentiles; IQR) of the distribution, and the
598 whiskers extend no further than ± 1.5 times the IQR. The dots plotted over each boxplot represent
599 the value for an individual plot by species. See *methods* for details on how each annualized rate
600 was calculated.

601

602

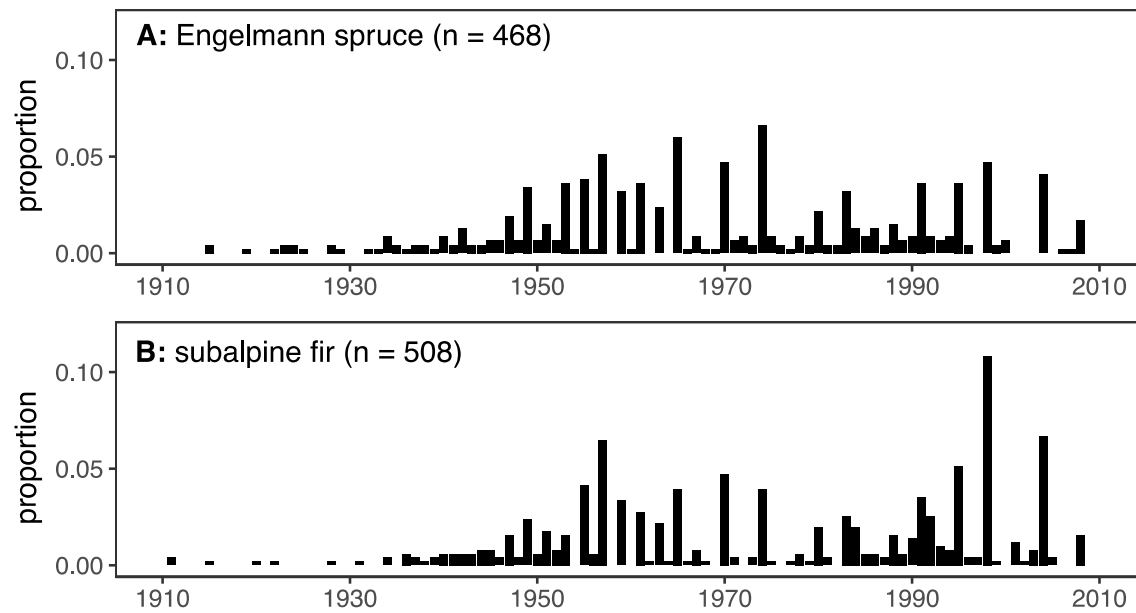
FIGURES

603 Fig. 1



604

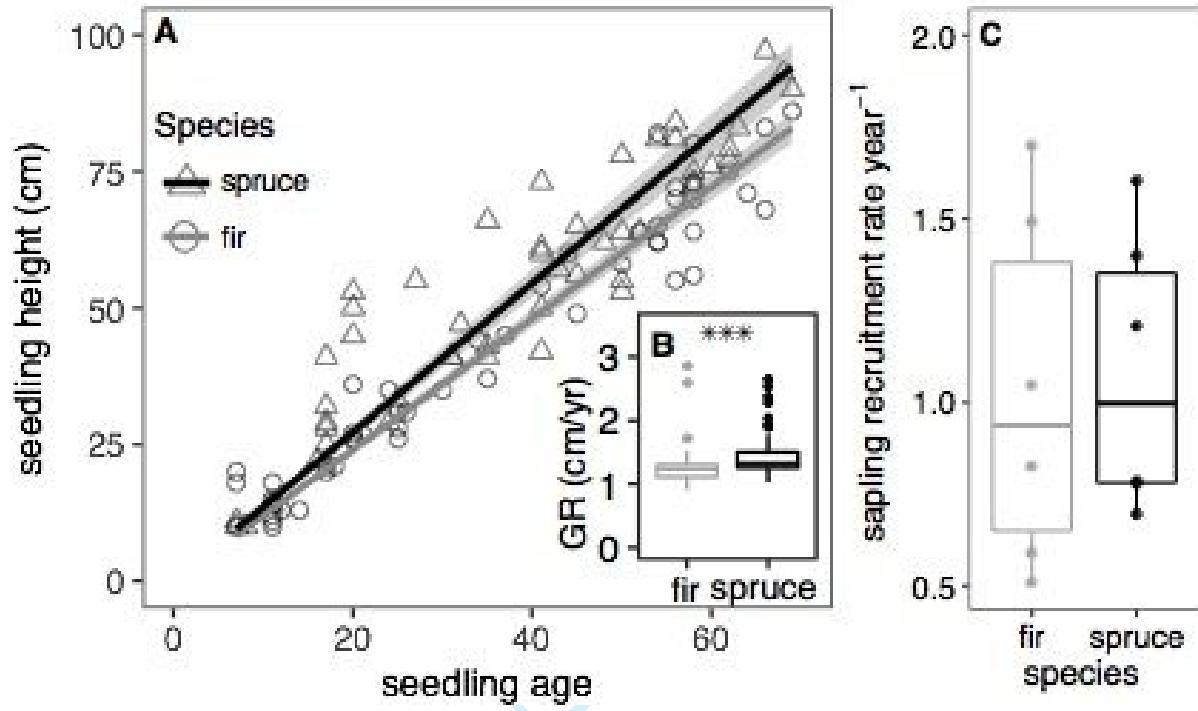
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606 **Fig. 2**

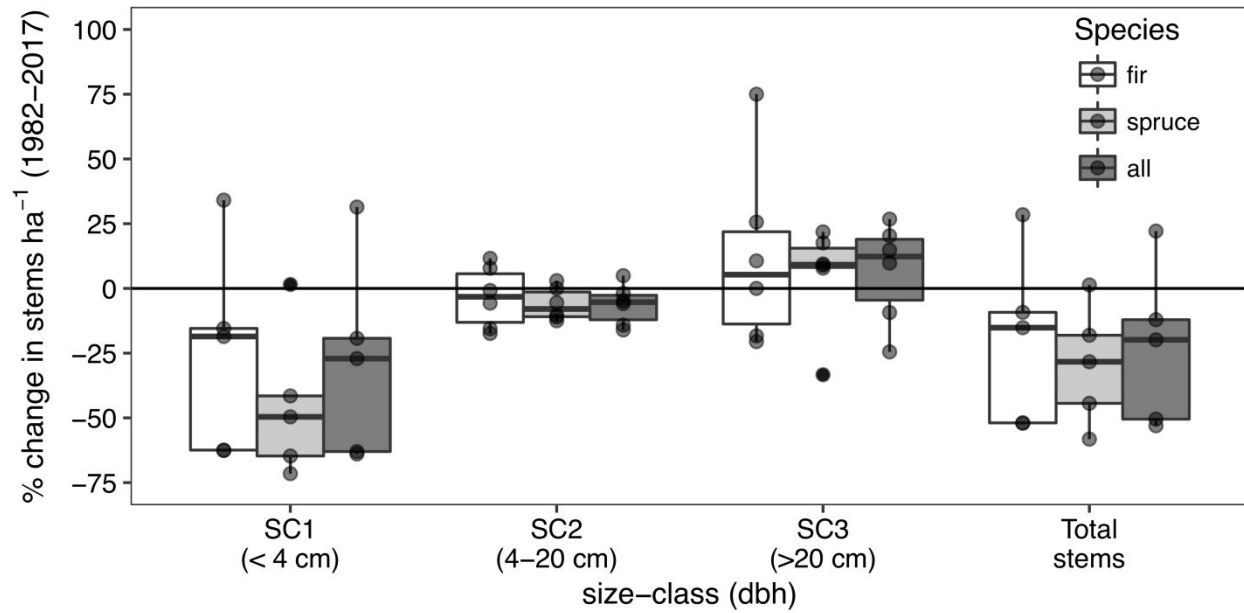
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608 Fig. 3



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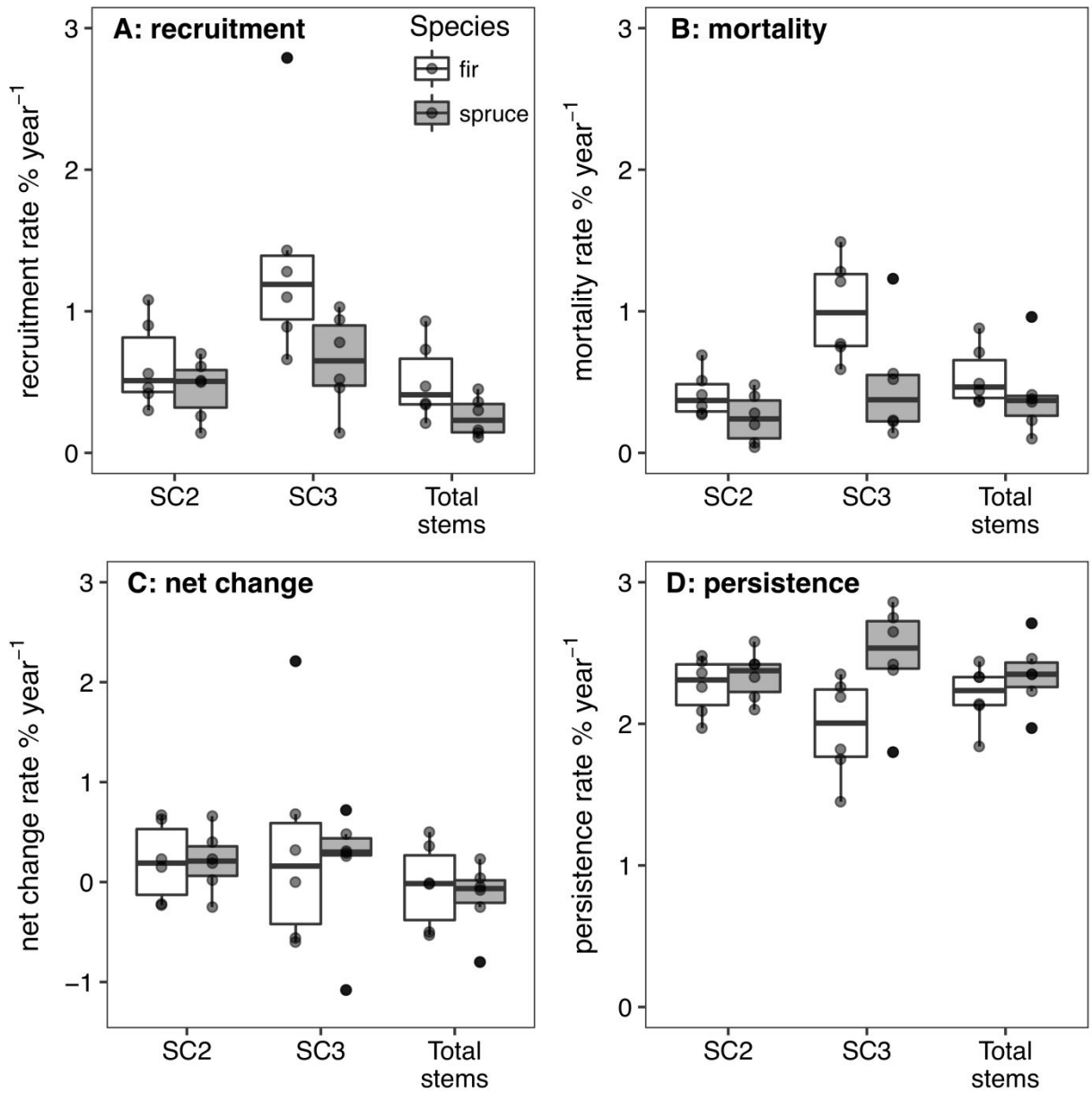
610 **Fig. 4**

611

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613 Fig. 5



614