

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

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ABSTRACT

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

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

INTRODUCTION

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

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

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

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

Engelmann spruce (*Picea engelmannii* Parry ex Engelmann) and subalpine fir (*Abies 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

explanations for the discrepancy in dominance between seedling banks and the main canopy composition of old-growth spruce-fir forests.

The current study quantifies vital rates for Engelmann spruce and subalpine fir in six permanent forest plots (>2,500 trees) monitored from 1982-2017 and seedling age and growth rates from > 950 destructively sampled spruce and fir seedlings (< 1 m in height) in the Colorado Front Range (CFR; Fig. 1). Using comparisons of vital rates, we offer a new perspective on a long-standing question: Do species differences in juvenile tree growth rates and adult tree vital rates explain the shift from seedling bank dominance by subalpine fir (*Abies lasiocarpa*) to more equal dominance of the main canopy by subalpine fir and Engelmann spruce (*Picea engelmannii*)? For juvenile trees in the seedling and sapling size class (<4 cm dbh), we hypothesize that spruce seedlings grow faster and are more likely to transition into the tree size class (> 4cm dbh) than fir. For subcanopy (4-20 cm dbh) and main canopy trees (> 20 cm dbh), we hypothesize that spruce exhibits lower mortality rates and longer persistence in the main canopy size class (> 20 cm dbh).

METHODS

Study Area

We resurveyed 6 permanent forest plots to assess differences in demographic rates between Engelmann spruce and subalpine fir (hereafter *permanent plots*), and at 10 sites we destructively sampled spruce and fir seedlings to determine dates of seedling establishment and annual height growth rates (hereafter *seedling plots*). All sites are located in subalpine forests in the Arapaho-Roosevelt National Forest on the eastern slope of the Colorado Front Range (Fig. 1). Both plot types span the full range of subalpine, spruce-fir forest types [*Picea-Abies* bogs (E-2), wet *Picea-Abies* (E-3), mesic *Picea-Abies* (E-4), xeric *Picea-Abies* (E-5), and subalpine

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 (hydric, 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

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

Field Methods

Permanent forest plot installation and remeasurement protocol: Permanent plots were installed in summer 1982 or 1983, and subjectively located in areas not disturbed by logging (i.e. lacking cut stumps, Veblen 1986b). Two sizes of permanent plots were included in this study. The four large permanent forest plots (hereafter ‘large plots’) range in size from 0.19 to 0.29 ha. Size was determined by the area necessary to include > 400 trees. Twenty-four smaller permanent forest plots (size range: 60 to 336 m^2) were located beneath canopy openings adjacent to two of the large permanent plots (c. 50 m separation between plot types). Each smaller plot includes c. 40 trees per plot. Canopy openings did not originate from timber cutting, rather they were created by small natural openings in the forest or treefalls. In the current study, data from each cluster of smaller permanent plots (hereafter “gap plots”) was aggregated to produce one sampling unit, which was approximately the same size as the larger permanent plots. To justify including gap plots and large permanent plots in our analyses, we demonstrate similarity in patterns of stand dynamics and vital rates for both plot types (‘gap’ and ‘large’) in Supplement B⁴.

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

⁴ Supplement B

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

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

Seedling plots and lab procedures

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

³ Supplement A

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

Data analysis

Testing for differences in seedling growth rates and sapling recruitment rates

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

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

⁵ Supplement C

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

Testing for differences in vital rates

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

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

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

RESULTS

Seedling bank age and seedling recruitment

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

Seedling height growth rates and sapling recruitment rates

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

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

Changes in stem density 1982-2017

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

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

Adult tree vital rates

⁷ Supplement E

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

DISCUSSION

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

⁷ Supplement E

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

Seedling bank dynamics

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

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

Implications for studies of forest dynamics

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

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

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

CONCLUSION

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

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FIGURE LEGENDS

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

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

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

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

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

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

FIGURES

Fig. 1

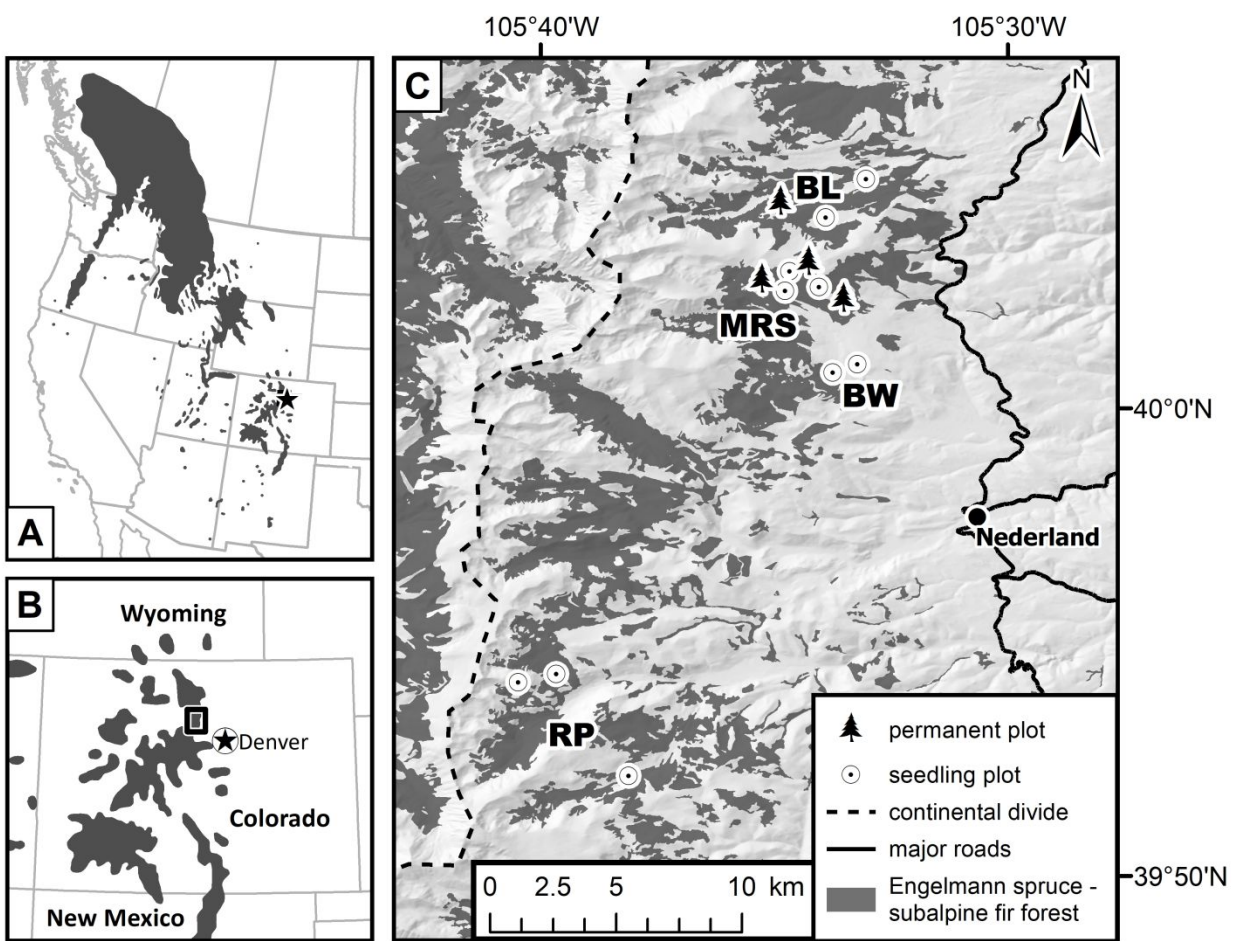


Fig. 2

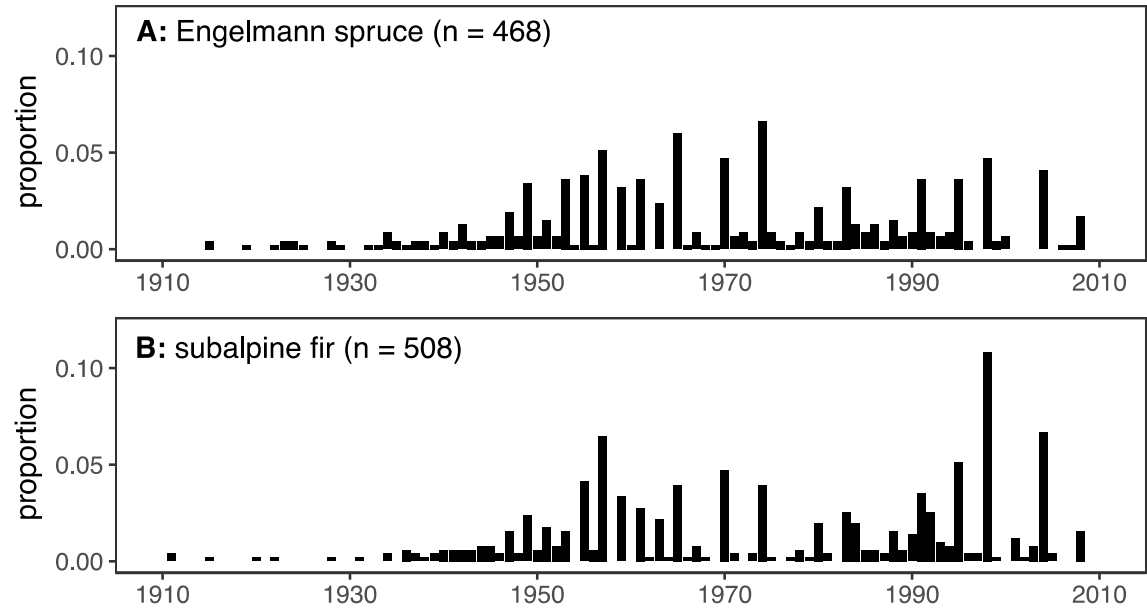


Fig. 3

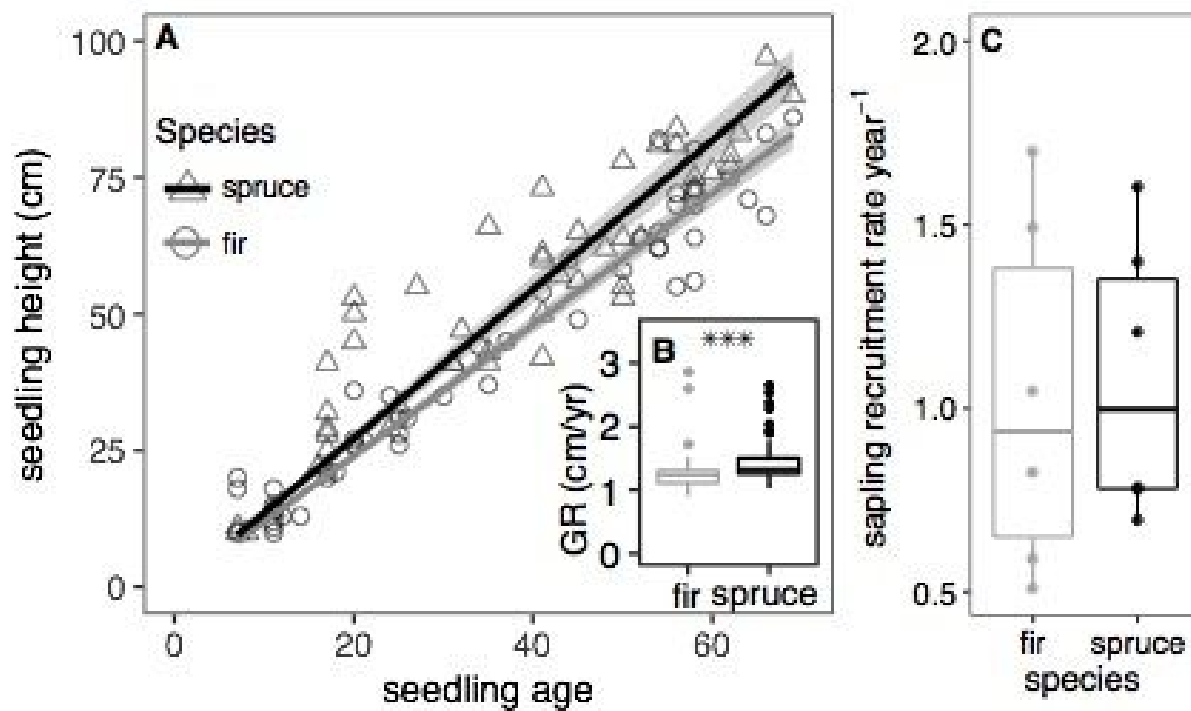
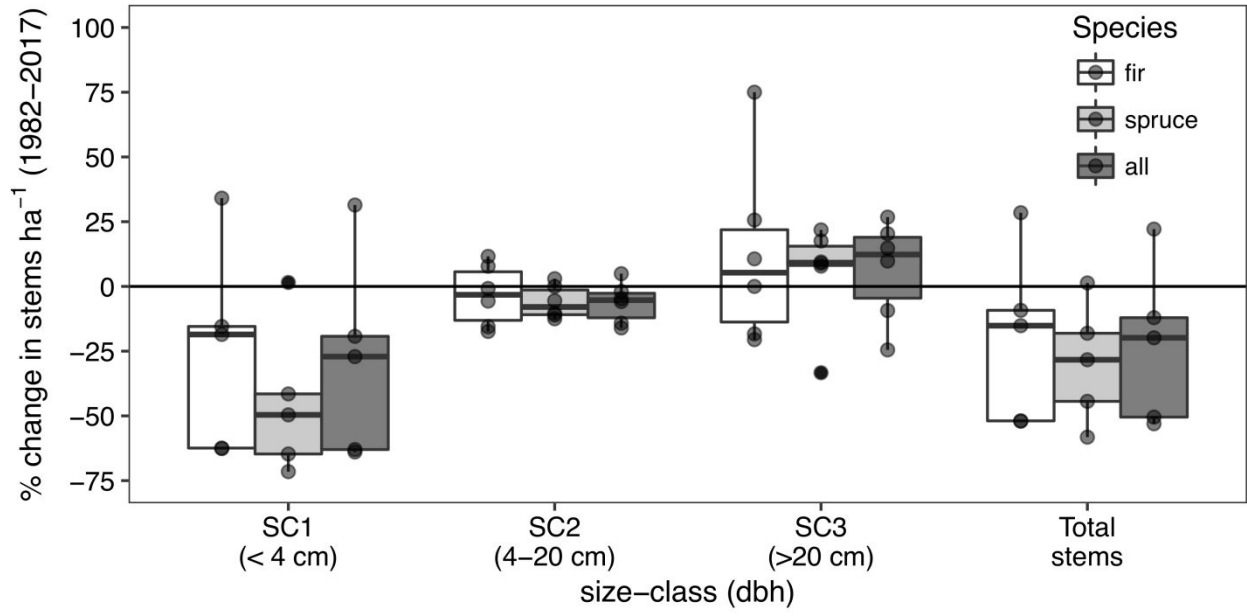
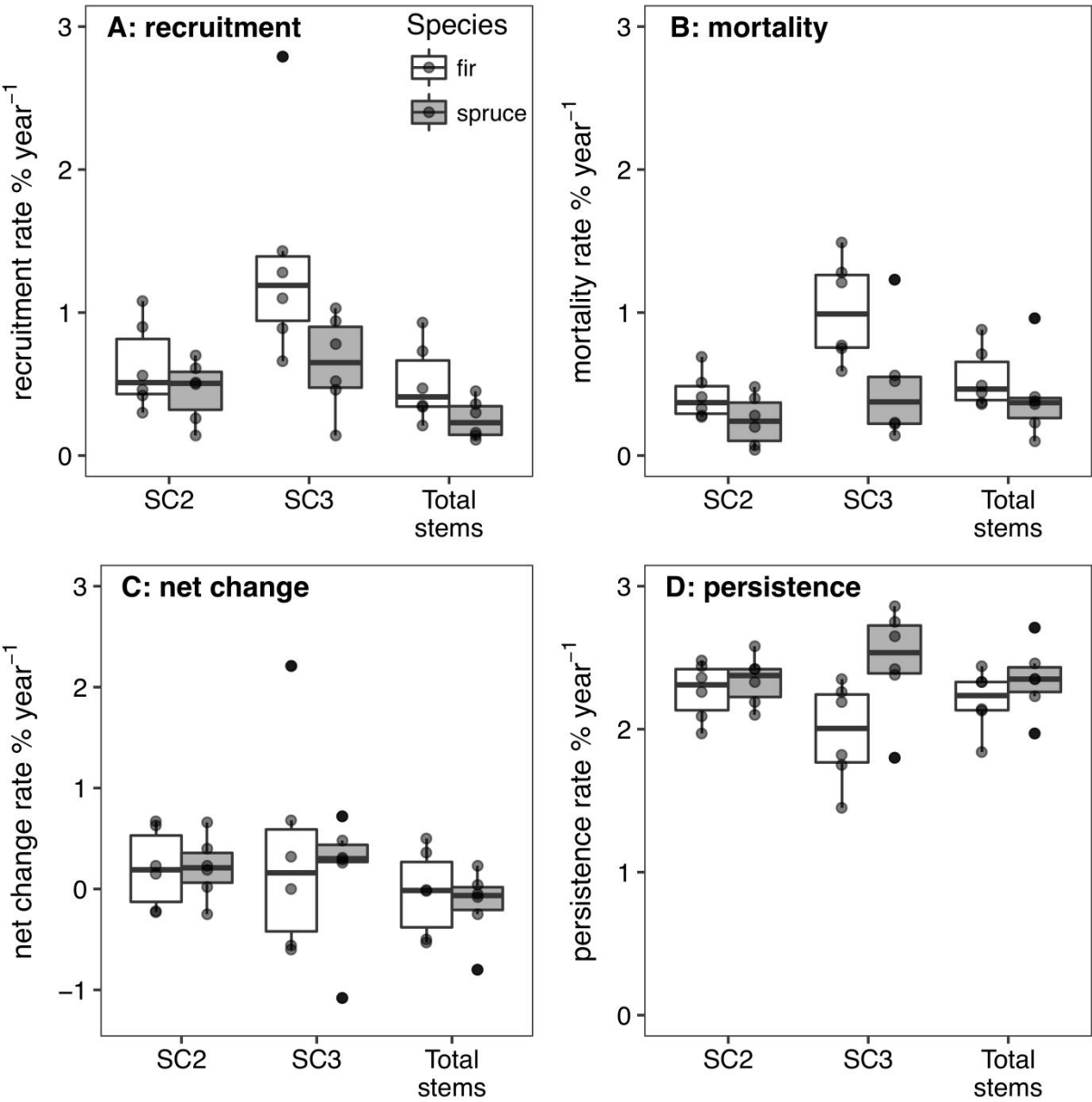


Fig. 4



613 **Fig. 5**



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