

1 **Local landscape position impacts demographic rates in a widespread North American**
2 **steppe bunchgrass.**

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32

33 **Abstract**

34 Understanding the environmental drivers of demographic rates and population dynamics over
35 space and time is critical for anticipating how species will respond to climate change. While the
36 influence of temporal environmental variation and large environmental gradients are well
37 recognized, less is known about how local topography and landscape position influence
38 demography over small spatial scales. Here, we investigate how local landscape position (north-
39 vs. south-facing aspects) influence the demographic rates and population growth of a common
40 bunch grass in western North America, bluebunch wheatgrass (*Pseudoroegneria spicata*), using
41 6 years of annual censuses measuring growth, survival, and reproductive output. We found
42 notably lower survival on south facing slopes, particularly among smaller individuals. In
43 contrast, south-facing slopes maintained comparatively high reproductive output in most years,
44 measured both as spikes per plant and spikelets per spike. We also found that lower survival
45 among small individuals and greater reliance on reproduction mean south-facing slopes should
46 also be more sensitive to changes in the recruitment rate, and would generally have to maintain
47 higher recruitment for stable population growth. Taken together, our results highlight the
48 important influence that landscape position and local topography can have in driving
49 populations. As conditions warm and dry with climate change (similar to south facing slopes),

50 bluebunch wheatgrass may become more reliant on reproduction to maintain viable populations
51 and more sensitive to variability in recruitment.

52 **Keywords:** Aspect, Bluebunch Wheatgrass, Columbia Basin, Demography, *Pseudoroegneria*
53 *spicata*, Vital rates

54

55 **Introduction**

56

57 Understanding demographic responses to environmental variation and the consequences of these
58 responses for population dynamics is central to population ecology, evolutionary ecology, and
59 anticipating the response of species and communities to climate change (Donohue et al. 2010,
60 Doak and Morris 2010, Salguero-Gomez et al. 2012, Ehrlén and Morris 2015). The need to
61 understand and anticipate ecological responses to climate change has led to a growing literature
62 linking climate conditions to demographic rates and population dynamics. This work has
63 expanded our knowledge of how plant demographic rates respond to changes in environmental
64 conditions through time (Dagleish et al. 2015, Chu et al. 2016, Shriver 2016, 2017) and across
65 large spatial gradients (Angert 2006, Eckhart et al. 2011, Gelfand et al. 2013, Merow et al.
66 2014). For example, Dagleish et al. (2015) identified temporal variability in both winter and
67 summer climate conditions as critical correlates of inter-annual variation in demographic rates of
68 steppe plants. Similarly, Eckhart et al. (2011) found that spatial variability in temperature and
69 precipitation across a species' range explained differences in population trends in a California
70 annual plant. While most of this work identifying relationships between demographic rates and
71 environmental conditions has focused on temporal variability or large-scale spatial patterns, the
72 influence of local topography and landscape heterogeneity (e.g. < 500 m) on demographic rates
73 is less well understood.

74 The scarcity of analyses on demographic responses to small scale topography is
75 surprising given that it is well known that topographic position can create microclimate
76 conditions that amplify or ameliorate broader spatial and temporal variability in climate
77 (Zellweger et al. 2019). For example, surface temperatures on north- and south-facing slopes
78 have been found to differ up to 20°C in mountainous terrain at ~46° latitude (Scherrer and
79 Körner 2010). However, the effects of local topographic position on environmental conditions
80 are generally not captured by a single weather station or gridded climate datasets (Zellweger et
81 al. 2019). This lack of small-scale climate data may explain why microclimate and local
82 conditions are often not explicitly considered in demographic analyses.

83 However, when demographic analyses do account for microclimate and topographic
84 position, the effects can be striking. For example, Nicolè et al. (2011) found that slope angle was
85 the primary environmental predictor of survival in a rare alpine plant, and hypothesized that soil
86 depth and soil moisture drove this effect. Similarly, Dullinger et al. (2004) found that slope was
87 the most important predictor of adult tree mortality at tree line. Finally, Oldfather and Ackerly
88 (2019) found several significant relationships between microclimate conditions and demographic
89 rates, although this did not lead to consistent trends in population growth across microclimates.
90 These examples make clear that if we want to answer pressing ecological questions across spatial
91 scales understanding how plant demographic rates and population dynamics vary across
92 landscape position and topography will be essential (Gurevitch et al. 2016).

93 Bluebunch wheatgrass (*Pseudoroegneria spicata*) is a large perennial bunchgrass
94 common in and ecologically important to the Columbia Basin and many other low to mid-
95 elevation areas of the Intermountain West of North America (Rodhouse et al. 2014). In these
96 systems, bluebunch wheatgrass often forms a substantial portion of the herbaceous biomass

97 (Rodhouse et al. 2014). However, these semi-arid systems are susceptible to invasion by a
98 number of annual plants, such as cheatgrass (*Bromus tectorum*), that can come to dominate.
99 Conversion from perennial to stable annual systems often follows repeated disturbance from
100 livestock overgrazing and fire (Davies et al. 2012). The loss of perennial grasses, including
101 bluebunch wheatgrass, fundamentally alters the structure and function of steppe ecosystems.
102 Communities dominated by invasives provide less forage for livestock, support less wildlife
103 (DiTomaso 2000), and likely sequester less organic carbon (Verburg et al. 2009, Rau et al.
104 2011). Thus failing to understand how patterns of recruitment, growth, and survival of perennials
105 vary across landscapes in these systems has important applied implications (Brooks and
106 Chambers 2011, Davies et al. 2011). However, in some locations bluebunch wheatgrass can be
107 resilient to disturbances, and when bluebunch wheatgrass or other large deep-rooted perennial
108 bunchgrasses persist at sufficient densities, they can exclude invasive annuals (Rodhouse et al.
109 2014). The spatial configuration of persistent bluebunch wheatgrass may depend on local
110 topography, with north-facing slopes often supporting robust remnant stands of perennials
111 (Rodhouse et al. 2014). Thus understanding the divergent demographic processes at work in
112 bluebunch wheatgrass on north-facing and south-facing slopes is important to understanding how
113 perennial grasslands can resist long-term conversion to invasive annual communities.

114 Because bluebunch population persistence varies with aspect over small spatial scales,
115 demographic processes must vary over these scales, but we still lack an accounting of this
116 variability. Variation in demography with aspect likely results from the divergent temperature
117 and moisture conditions on different aspects. Variation in temperature and moisture correlate
118 with variation in phenology and morphology of bluebunch wheatgrass across larger spatial scales
119 (St. Clair et al. 2013). Further, within a single site, long-term data from this species suggest that

120 annual variation in temperature and moisture drive annual variation in demographic variables
121 including growth and survival (Dalglish et al. 2011). Other demographic variables may also be
122 impacted by microclimatic variation in bluebunch wheatgrass. For instance, experimental
123 manipulation of soil moisture influenced seed quality and offspring fitness (Drenovsky et al.
124 2016). Thus, we have strong a priori expectations for demographic variability with aspect over
125 small spatial scales in this species.

126 Here, we use six years annual censuses (four demographic transitions) of bluebunch
127 wheatgrass populations from north and south-facing aspects from a site in eastern Washington to
128 explore how local landscape position influences demographic rates (survival, growth, and
129 reproductive output) and rates of population growth. Specifically we addressed the following
130 questions: How does aspect influence rates of individual growth, survival, and reproductive
131 output? What are the consequences of these vital rate differences for annual population growth?
132 Finally, because we lack detailed estimates of recruitment (seed to seedling transition) from our
133 plots we estimate the recruitment rate required for stable population growth on both north and
134 south aspects and compare this result to available estimates from the literature.

135

136 **Methods**

137 *Field Data Collection*

138 We monitored individual bluebunch wheatgrass plants growing on steep hillsides in
139 Spring Gulch on Whitman College's Wallula Gap Biological Station in the Columbia Basin of
140 Washington (46° 00' N, 118° 54' W, 360-420 m elevation). Spring Gulch runs primarily east to
141 west, and so most hillsides face either approximately north or south. On the north-facing slopes
142 there is no exposed bedrock and the silty loam soil is free of rocks and appears >2 m deep. The

143 soil is similarly textured on south-facing slopes and is often >2m deep, but in places is shallower,
144 and bedrock is exposed rarely. However, there was no exposed bedrock on our monitoring
145 locations. North-facing slopes are primarily vegetated by perennial bunchgrasses (besides *P.*
146 *spicata*, also *Festuca idahoensis*, several species of *Poa*, and others) though rabbitbrush
147 (*Ericameria nauseosa* and *Chrysothamnus viscidiflorus*) is common. Big sagebrush (*Artemisia*
148 *tridentata*) is rare on both slopes due to recent (2007, 2011, 2015) and presumably less-recent
149 fires. South-facing slopes are dominated by annuals, especially cheatgrass (*Bromus tectorum*),
150 annual fescue (*Vulpia sp.*), and yellow star-thistle (*Centaurea solstitialis*), in most places.
151 However, bluebunch wheatgrass stands ranging from 0.03 ha to 0.17 ha are scattered across the
152 south-facing slopes and cover approximately 5-10% of the surface of these hillsides. Within
153 these south-facing stands of bluebunch wheatgrass, cheatgrass is less common and yellow star-
154 thistle is rare. Only one other large bunchgrass, needle and thread grass (*Hesperostipa comata*),
155 occurs on south-facing slopes, and it is much less common than bluebunch wheatgrass. When
156 measured over approximately 6 months in 2009, soil temperatures at this site were consistently
157 higher on south-facing slopes than on north-facing slopes (Table S1), and soil moisture was
158 consistently higher on north-facing slopes to a depth of 30 cm (Table S2).

159 In the spring of 2011, we established 14 monitoring sites for bluebunch wheatgrass,
160 seven on north-facing slopes and seven on south-facing slopes. We selected sites where
161 bluebunch wheatgrass was growing. We attempted to locate sites relatively far from other sites
162 on the same slope, and we were able to keep all sites > 140 m distant from the next nearest
163 except for one pair of sites on the south face which we located 20 m apart because of the rarity of
164 bluebunch wheatgrass stands on these slopes (mean distance to adjacent sites on the same slope
165 = 180 ± 75 m (SD), min = 20 m, max = 306 m). Each site was 10 m long and 1 m wide and

166 marked at the corners by rebar stakes. We designated 1 x 1 m sampling areas every other meter
167 within each site, such that sites contained 5 non-adjacent sampling areas. During 2011 and 2012,
168 we experimented with methods of placing the 1 x 1 m quadrats, and methods of relocating
169 individual plants. In 2013, we settled on marking each corner of each 1x1 m quadrat with rebar
170 stakes and marking each bluebunch wheatgrass plant with a small uniquely numbered metal tag
171 held in place by a nail in the soil adjacent to the plant. We used a 1x1 m quadrat consisting of a
172 metal frame with wire forming a grid of 10 x 10 cm cells. We anchored this quadrat with the
173 permanent rebar stakes at each visit to the plot, and used the grid of 10 x 10 cm cells to construct
174 and update maps of the bluebunch wheatgrass plants within the sampling area.

175

176 From 2013 through 2018, a group of two or three researchers visited each plot at least once
177 between late May and late June. During that visit, we searched for every bluebunch wheatgrass
178 plant we could find throughout each plot as well as specifically for bluebunch individuals that
179 had been tagged and mapped on previous visits. We marked any new plants we discovered, and
180 we removed tags for any plants that had disappeared. Bluebunch wheatgrass at our site is entirely
181 cespitose, and so all the stems of a given individual grow in close proximity to each other.
182 Typically, the separation between individuals is clear, but when the distinction between
183 individuals was unclear we likely sometimes lumped two or more individuals together as a single
184 individual. Unfortunately we had no way to confirm plant identity without causing serious harm
185 to the plant. For each bluebunch plant we located, we noted survival, counted the number of
186 living culms and the subset of culms that were flowering (spikes). Both of these counts were
187 highly repeatable (culms: $R = 0.88$, Fig. S1; spikes: $R = 0.88$, Fig. S2, See supplementary
188 materials for further details). For all flowering individuals, we haphazardly selected five spikes

189 on which to count the number of spikelets. If there were fewer than five spikes, we counted the
190 spikelets on all spikes. Average number of spikelets per spike was moderately repeatable ($R =$
191 0.64 , Fig S3). We also measured the height of the tallest culm, but because this measurement
192 changes over the course of our study season due to growth and damage to plants, we decided not
193 to use this measurement in our analyses. Flowering bluebunch wheatgrass is not easily confused
194 with other species at our site, but observers on this project occasionally misidentified small non-
195 flowering individuals of other bunchgrass species as bluebunch wheatgrass. We therefore chose
196 to include only individuals that were flowering, or had been observed to flower in a past or future
197 year, in our analyses to minimize the chance of misidentification errors. As a result we do not
198 have direct, reliable estimates of the seed to seedling transition from our observation plots.
199 Finally, observers occasionally failed to observe a plant that was present. In plots visited twice to
200 assess sampling reliability, 6.2% of plants detected in at least one of two visits were not detected
201 on the other visit (supplementary materials). Therefore, we only noted mortality when an
202 individual was absent for 2 or more years, and thus no survival data are available from the final
203 transition and we only estimate vital rates for four transitions over six years.

204 In the summer of 2014, we collected spikes from 60 bluebunch wheatgrass individuals
205 after seed set to determine the typical number of seeds per spike. We collected five spikes from
206 each target plant, and so did not sample from plants with fewer than five spikes. Half of all
207 sampled plants were from north-facing slopes and half were from south-facing slopes. For each
208 plant, we counted the number of spikelets across all five spikes, and the number of seeds
209 produced by those spikelets.

210 *Population Modeling*

211 To understand how individual vital rates combined to influence population growth and
212 dynamics, we developed integral projection models for north and south-facing slopes. Integral
213 projection models are discrete-time, continuous-state structured population models that allow us
214 to explore how differences in vital rates across aspects impact population growth (Easterling et
215 al. 2000). The model is formulated as

$$216 \quad n(y, t + 1, a) = \int_{\Omega} K(y, x, t, a) n(x, t, a) dx$$

217 Where $n(x, t, a)$ is the density of size x individuals at time t on aspect a , $K(y, x, t, a)$ is a kernel
218 describing the transition of size x individuals to size y . In our case plant size in $\ln(\text{Number of}$
219 *Culms*). $K(y, x, t, a)$ itself is made up of vital rate functions,

$$220 \quad K(y, x, t, a) = G(y, x, t, a) * S(x, t, a) + F(x, t, a)$$

221 Where $G(y, x, t, a)$ is a kernel describing the size transition of existing individuals, $S(x, t, a)$ is
222 a function of survival rates for individuals of size x , and $F(x, t, a)$ is a function of reproductive
223 output of individuals (i.e. new plants produced per individual). Although $F(x, t, a)$ can include
224 data on both individual reproductive output (seeds produced) and the germination and survival of
225 seedlings (recruitment of seeds to plants), as noted above we do not have field data on
226 recruitment from our plots. Thus, our $F(x, t, a)$ include only the seeds produced per plant. As
227 outlined below, we also attempt to estimate likely recruitment rates.

228 *Vital rate modeling*

229 We estimated vital rates with generalized linear mixed effect models in a Bayesian
230 framework using Stan and the ‘rstan’ package (Stan Development Team 2020). We

231 parameterized $G(y, x, t, a)$ as a normal kernel, fit to the data with a normal likelihood where the
 232 kernel parameters were fit using measured size transitions as

$$233 \quad G(y, x, t, a) = \text{Normal}(y|\mu_g(x, t, a), \sigma^2)$$

$$234 \quad \mu_g(x, t, a) = \beta_0 + \beta_1 x + \beta_2 I(a) + \gamma_g(t) + \delta_g(t) I(a)$$

235 Where $\mu_g(x, t, a)$ is the average size of individual of size x at time t transition to at $t+1$. $I(a)$ is
 236 an indicator variable for aspect, $I=1$ when the aspect is south-facing and 0 when north-facing.
 237 $\gamma_g(t)$ is a random effect intercept that varies by year, $\delta_g(t)$ random effect for aspect that also
 238 varies by year, and β_1 and β_2 are fixed effects for size and aspect, respectively.

239 We estimated survival using a Bernoulli likelihood to observed survival data where the
 240 probability of survival, $s(x, t, a)$, is

$$241 \quad \text{logit}(s(x, t, a)) = \beta_3 + \beta_4 x + \beta_5 I(a) + \gamma_s(t) + \delta_s(t) I(a)$$

242 Similar to the size model, $\gamma_s(t)$ is a random effect intercept that varies by year, $\delta_s(t)$ random
 243 effect for aspect that also varies by year, and β_4 and β_5 are fixed effects for size and aspect,
 244 respectively.

245 Finally we estimated reproductive output (i.e. seed production) as three parts: 1) the
 246 number of seed spikes produced per plant, $\text{Spike}(x, t, a)$; 2) the average number of spikelets per
 247 spike, $\text{Spikelets}(t, a)$; 3) the average number of seeds per spikelet, Seeds .

$$248 \quad F(x, t, a) = \text{Spike}(x, t, a) * \text{Spikelets}(t, a) * \text{Seeds}$$

$$249 \quad \text{log}(\text{Spike}(x, t, a)) = \beta_6 + \beta_7 x + \beta_8 I(a) + \gamma_{\text{spike}}(t) + \delta_{\text{spike}}(t) I(a)$$

250
$$\log(\text{Spikelets}(t, a)) = \beta_9 + \beta_{10}I(a) + \gamma_{\text{spikelet}}(t) + \delta_{\text{spikelet}}(t)I(a)$$

251
$$\text{Seeds} = \beta_{11}$$

252 Once again, $\gamma_{\text{spike}}(t)$ & $\gamma_{\text{spikelet}}(t)$ are random effects intercept that varies by year, $\delta_{\text{spike}}(t)$
253 & $\delta_{\text{spikelet}}(t)$ are random effects for aspect that also varies by year, and β_7 and β_8/ β_{10} are
254 fixed effects for size and aspect, respectively. Because data on the number of seeds per spikelet
255 was not available in each year, we used a single average value for this parameter, β_{11} . The
256 number of spikes per plant was fit to the field data using a negative binomial likelihood, while
257 the average spikelets per spike and were fit using a log-normal likelihood. We modelled seeds
258 per spikelet using a normal distribution, truncated at zero. All random effects were normally
259 distributed with mean 0 and a fit variance parameter.

260 To implement the integral projection model, we discretized vital rates into 100 size bins
261 using the midpoint rule (Easterling et al. 2000). Because data on the size distribution of new
262 recruits were unavailable we assumed all new plants entered the smallest size class.

263 *Model Analyses*

264 We quantified the expected annual population growth rate (λ_t) (excluding seed to
265 seedling recruitment) by calculating the dominant eigenvalue of the discretized integral project
266 models for each year. Because we carried through all of the uncertainty in parameter estimates
267 from our vital rate models to the integral projection model, we present values as posterior
268 distributions of λ_t .

269 Additionally we inferred possible seed to seedling recruitment rates using two
270 approaches. First, we determined how λ_t varied across a range of recruitment rates. Second we

271 identified the absolute recruitment that would be needed for both the northern and southern
272 aspects to achieve $\lambda_t = 1$ (i.e. a stable population) in each year by calculating λ_t across a range
273 of recruitment rates (seed transitioning to plants in the first size class). To determine confidence
274 intervals for recruitment rates, we iterated this process over the entire posterior MCMC chains
275 for all vital rates.

276 To allow transparency in the process of developing our analyses, we pre-registered our
277 analysis plan prior to examination of the data in aggregate (Parker and Shriver 2018). We outline
278 deviations from this plan in the supplementary materials.

279

280 **Results**

281 *Vital Rates*

282 Model results indicate that survival and reproductive output differed between north and south
283 aspects, while individual growth did not (Table 1, Fig. 1-2). Both the number of spikes per plant
284 and the number of spikelets per spike were higher on south-facing slope, although the posterior
285 95% CI for β_8 (average difference in spikes per plant on south slopes) did overlap with zero.
286 Survival of existing, established plants was lower on south-facing slopes. Differences in survival
287 between aspects were most notable in small plants (<20 culms), where the smallest plants on
288 south-facing slopes show about 50% annual survival and the smallest plants on north-facing
289 slopes showed 70 to 80% survival. However, large plants survival approached 100% on both
290 aspects (Fig. 1). Although spikes per plant also increased with size, it was in large plants where
291 we observed the greatest difference between aspects. On average, large plants produced about
292 15-25 more spikes per plant on south-facing aspects than north aspects. Yet, greater reproductive

293 output on south facing slopes did not occur in all years with individuals on north facing aspects
294 producing slightly more spikes in 1 of the 4 years (Fig. 2). Growth declined on average with size,
295 but showed no consistent differences across sites. Vital rates also varied substantially from year
296 to year. Most notably, the number of spikes produced per plant tripled on average from 2014-
297 2015 to 2015-2016 (Fig. 3).

298 *Population growth rate and Recruitment*

299 If we assume that all seeds lead to new recruits, the higher rates of reproductive output on south-
300 facing slopes than on north-facing slopes leads to much higher estimates of population growth
301 rates (λ) on south-facing slopes in 3 of 4 years (all transitions except 2015-2016) (Fig. 4). Inter-
302 annual variability in vital rates drove up to an almost 4-fold variation in population growth rates
303 within aspect across years (Fig. 4).

304

305 Despite generally higher rates of reproductive output on the south aspect (both spikes per plant
306 and spikelets per spike) and a higher population growth rate assuming 100% recruitment in three
307 of four years, population growth rate on south-facing slope was lower for a given recruitment
308 rate in three of four years (Fig. 5). As a result, south-facing slopes may need to maintain higher
309 rates of recruitment to maintain stable populations ($\lambda=1$) than north-facing slopes (Fig. 5). The
310 recruitment rate required to maintain stable populations varied from year-to-year from <0.001 to
311 ~ 0.01 . However, the recruitment rates required on the south facing slopes to maintain stable
312 populations were also considerably more uncertain than north facing slopes.

313

314 **Discussion**

315 We found strong evidence that demographic rates in bluebunch wheatgrass, a common
316 bunchgrass in western steppe ecosystem, differed over small spatial scales between north and
317 south-facing slope. While small plants on north-facing slopes survived at much higher rates than
318 those on adjacent south-facing slopes, plants on south-facing slopes had far more reproductive
319 output per plant in most years. Despite generally higher seed production per plant on south-
320 facing slopes, the lower survival of small plants means that attaining higher recruitment rates
321 appears necessary for the south-facing populations to remain stable. This requirement for
322 elevated recruitment may have major implications for population persistence in the face of
323 climate change given that in semi-arid ecosystems, recruitment may be particularly sensitive to
324 increasing temperature and aridity (e.g., James et al. 2019). Although we expect temperature and
325 moisture to be important direct drivers of demographic process, other differences between
326 slopes, such as the degree of competition with invasive annuals, may also have contributed to the
327 divergent demographic patterns we observed. Regardless of the ecological mechanisms driving
328 these patterns, our demonstration of demographic variation over small spatial scales contributes
329 to the growing body of work establishing the importance of local topography and landscape
330 position in influencing vital rates and demographic inference.

331 Our observation that changing slope position influenced different demographic variables
332 in different ways is consistent with other recent work on small-scale variability in demographic
333 rates. For example, Oldfather and Acklery (2019) found notable differences in demographic rates
334 including survival and reproductive output across microclimate conditions. Similarly other work
335 has found declines in survival with changing slope and aspect, most notably lower survival on
336 steeper, drier slopes (Dullinger et al. 2004, Nicolè et al. 2011). Still, in some systems different

337 demographic rates between sites may not lead to different population growth trends if there is
338 compensation among vital rates (Oldfather and Ackery 2019). However, in our system we think
339 this is unlikely despite our inability to compare population growth rates directly between aspects.
340 As we describe below, recruitment rates would likely need to be higher on south-facing slopes
341 than on north-facing slopes to maintain a stable population, but we have reason to expect that
342 bluebunch wheatgrass actually recruits at lower rates on south-facing slopes.

343 Although we lack precise estimates of recruitment rate, we do have evidence that
344 changes in recruitment rates could strongly impact population growth. This insight helps us
345 understand current differences in abundance of bluebunch wheatgrass at our site and has
346 important implications for the future of these populations. When we assumed all seed led to new
347 recruits (i.e. the recruitment rate was 1), estimates of population growth were notably higher for
348 south-facing slopes than north. But, assuming all seed becomes new recruits is unrealistic,
349 ongoing experimental work suggests recruitment rates are actually substantially lower on south-
350 facing slopes, where bluebunch wheatgrass is also much less abundant and survival of small
351 plants is lower. Further, based on models in which we systematically varied recruitment rate,
352 point estimates for the level of recruitment needed to maintain stable populations on south-facing
353 slopes were higher in three of four years than the level of recruitment needed on north-facing
354 slopes, though estimates for south-facing slopes were highly uncertain. What was clearer from
355 these models, however, is that differences in recruitment rates between slopes could be sufficient
356 to stabilize population growth on the two slopes, or even drop population growth on south-facing
357 slopes below that of north-facing slopes. For example, when we increased recruitment rates
358 three-fold from 0.005 to 0.015 recruits per seed in our models, this increased population growth
359 estimates by up to 50% (depending on year and aspect). Given that our ongoing experimental

360 work suggests that the difference in actual recruitment rate could be 10-fold or larger between
361 aspects, the impact of recruitment rate on population growth could be substantial. This sort of
362 sensitivity of population growth rates to recruitment is consistent with previous work which has
363 established recruitment as a critical process controlling the recovery and restoration of dryland
364 plants and perennial bunch grasses (James et al. 2011), and our estimates of recruitment rates
365 required to maintain stable population are consistent with published rates. For example, James et
366 al. (2019) found consistent probabilities of transitioning from seed to establishment of ~0.04.
367 Boyd and James (2013) found similar, but more variable rates. They estimated that germination
368 varied from 20-80%, emergence of these germinates was 5-20%, and initial establishment of
369 those that emerged was 20-80%. This would yield recruitment rates ranging from 0.002 to 0.128,
370 which correspond well with our estimated range from 0.001-0.01 to maintain stable populations
371 on average. Given this possibility for substantial variability in recruitment rates, and the likely
372 sensitivity of recruitment in semi-arid systems to increasingly hotter, drier conditions (James et
373 al. 2011), and invasion of non-native species (Aguirre and Johnson 1991), we expect that
374 variation in recruitment will increasingly impact demography and long-term population
375 persistence of bluebunch wheatgrass in these systems.

376 Although we do not have detailed measurements of differences in temperature and soil
377 moisture conditions associated with each sample location, other data (Table S1 and S2) and
378 ongoing experiments from this site as well as other studies indicate that increased temperatures
379 and reduced soil moisture availability, driven by increased solar radiation, may be responsible
380 for vital rate differences. Ongoing experiments performed at this site indicate that when
381 incoming solar radiation is reduced on south-facing slopes (using shade cloth), temperatures
382 decrease and germination and survival of young bluebunch wheatgrass plants increase

383 dramatically (TH Parker unpublished data). Additional studies have also indicated that soil
384 moisture and temperature conditions can substantially alter vital rates of bluebunch wheatgrass.
385 For example, James et al. (2019) found that warmer soil temperatures and reduced precipitation
386 limit the germination, emergence, and early survival of steppe bunchgrasses including bluebunch
387 wheatgrass. Similarly, in a system where snowmelt is an important source of moisture, greater
388 snowpack is associated with greater survival of bluebunch wheatgrass (Dalglish et al. 2011).
389 Our finding that plot level demographic performance may be quite variable across microsites,
390 even in nearby locations that share similar areal climate conditions, suggests that quantifying
391 microsite climate variation at the scale of plots could provide exciting opportunities to expand
392 our understanding of the relationships between climate and demographic performance across
393 landscapes. Even in the absence of detailed field measurements, models that scale areal climate
394 conditions to local microclimates based on topography are an exciting possibility (Zellweger et
395 al. 2019).

396 Although north and south aspects differ in temperature and soil moisture, they also
397 support different plant communities, and these community differences are also plausible drivers
398 of demographic performance of bluebunch wheatgrass. One of the most obvious differences in
399 plant communities is the higher density of annuals, including cheatgrass and yellow star-thistle,
400 on south-facing slopes. Cheatgrass, in particular, may outcompete bluebunch wheatgrass
401 seedlings and thus hinder its growth (Aguirre and Johnson 1991) and survival, apparently by
402 reducing moisture availability (Harris 1967). In contrast to seedlings, established bunchgrasses
403 apparently outcompete cheatgrass (Rodhouse et al. 2014), thus the negative effects of increased
404 cheatgrass abundance should be most pronounced on smaller, establishing bluebunch wheatgrass
405 individuals that must compete for water in the shallow rootzone used by cheatgrass (Young et al.

406 1987). This scenario is in line with our finding of reduced survival only in smaller individuals on
407 south-facing aspects, although our ongoing shading experiments suggest that direct effects of
408 temperature may be most important. Still, both increased competition and an already warmer
409 drier climate on south-facing aspects could interact to limit the competitive ability of young
410 bluebunch individuals (Larson et al. 2018).

411 Although higher temperatures and greater density of invasive annuals may explain the
412 lower survival of small bluebunch wheatgrass plants on south-facing slopes relative to north
413 facing slopes, the higher reproductive output on south-facing slopes is more difficult to explain.
414 It could be that the lower density of perennial bunchgrasses on south-facing slopes reduces the
415 intensity of competition for soil moisture among well-established individuals and that greater
416 access to resources leads to greater reproductive output. However, various ongoing studies
417 examining the possibility that competition among established bluebunch plants influences the
418 size or distribution of individual plant at this site have revealed little evidence of such
419 competition. Therefore, the driver of higher reproductive output on south-facing slopes remains
420 uncertain.

421 One of the most striking features of our study site to the casual observer is the lower
422 density of perennial plants, especially bunchgrasses, on south-facing slopes relative to north-
423 facing slopes, and so the differences we observed in bunchgrass demographic rates between
424 these slopes is not a surprise. However, because we lack detailed measurements of recruitment
425 we remain uncertain whether these differences in population density result from ongoing
426 differences in population growth rate between the two slopes. What we do know, however, is
427 that the hotter, drier conditions on south-facing slopes are associated with reduced survival of
428 small plants on these slopes, and that experimental reduction of temperature on south-facing

429 slopes dramatically increases seedling emergence and survival. Further, our models demonstrate
430 that plausibly low levels of recruitment on south-facing slopes could cause the bluebunch
431 wheatgrass population on those slopes to decline. These observations, combined with published
432 observations that recruitment limits other populations of plants in semi-arid rangelands (James et
433 al. 2011), leads us to hypothesize that lower survival of small individuals coupled with
434 recruitment limitation may be leading to a decline of bluebunch wheatgrass on south-facing
435 slopes and help explain the lower density of bluebunch wheatgrass on these slopes. Further,
436 given predictions of increasingly warm and dry conditions in the North American steppe regions
437 with climate change (Bradford et al. 2020), we hypothesize that the population decline will
438 worsen, and that as north-facing slopes warm bluebunch wheatgrass populations vital rates there
439 may come to resemble what we currently find on south facing slopes. Future work should focus
440 on better understanding plant demography in steppe, bunchgrass systems, especially the role of
441 temperature and moisture in influencing recruitment.

442

443 **Acknowledgments**

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447 of Food and Agriculture.

448 **Author Contributions**

449 THP designed the study and collected data with assistance from EC, HG, AH, SK, MMB, KM,
450 RM, EO, DR, MS, AW. RKS performed analyses. RKS and THP wrote the manuscript.

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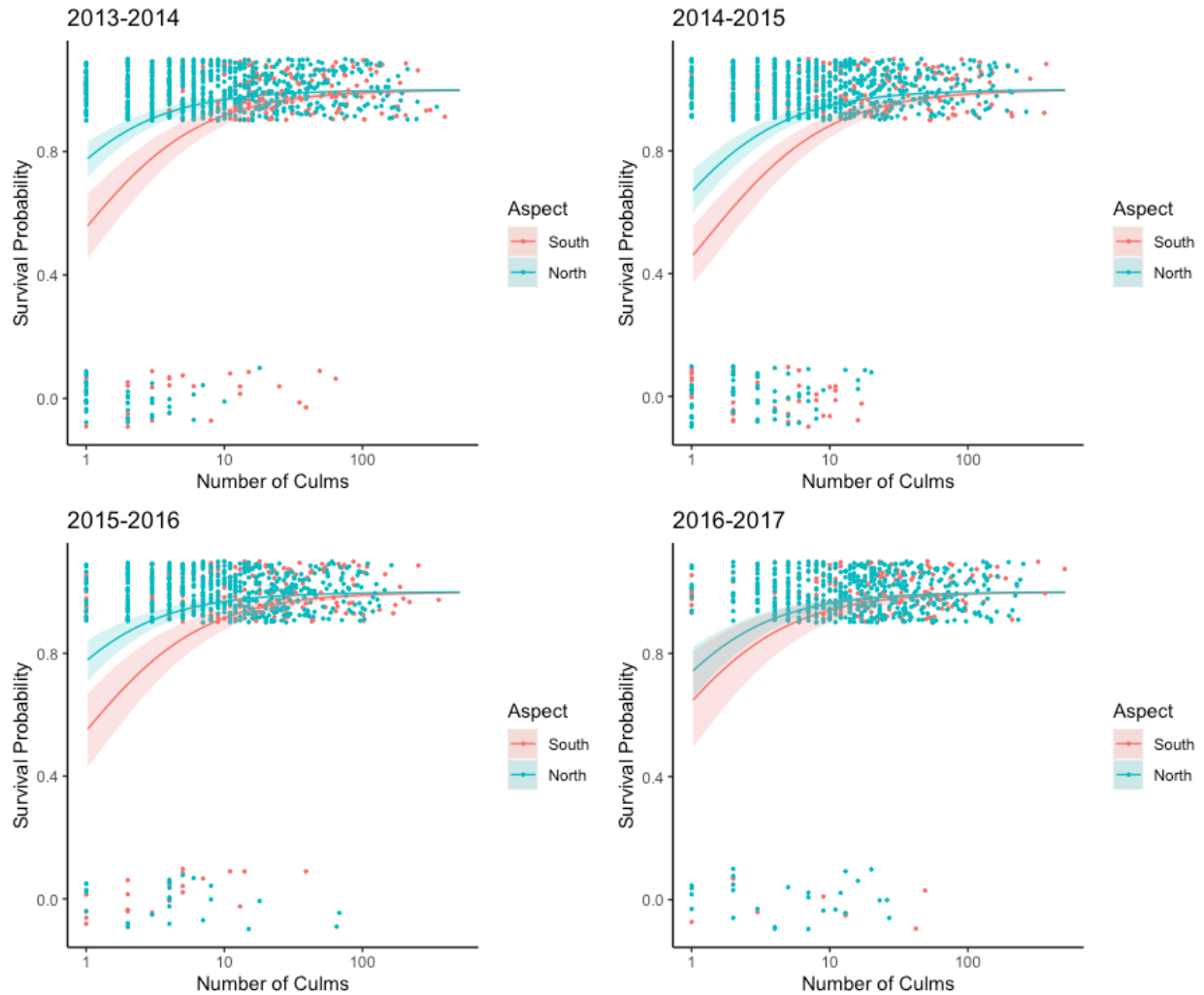
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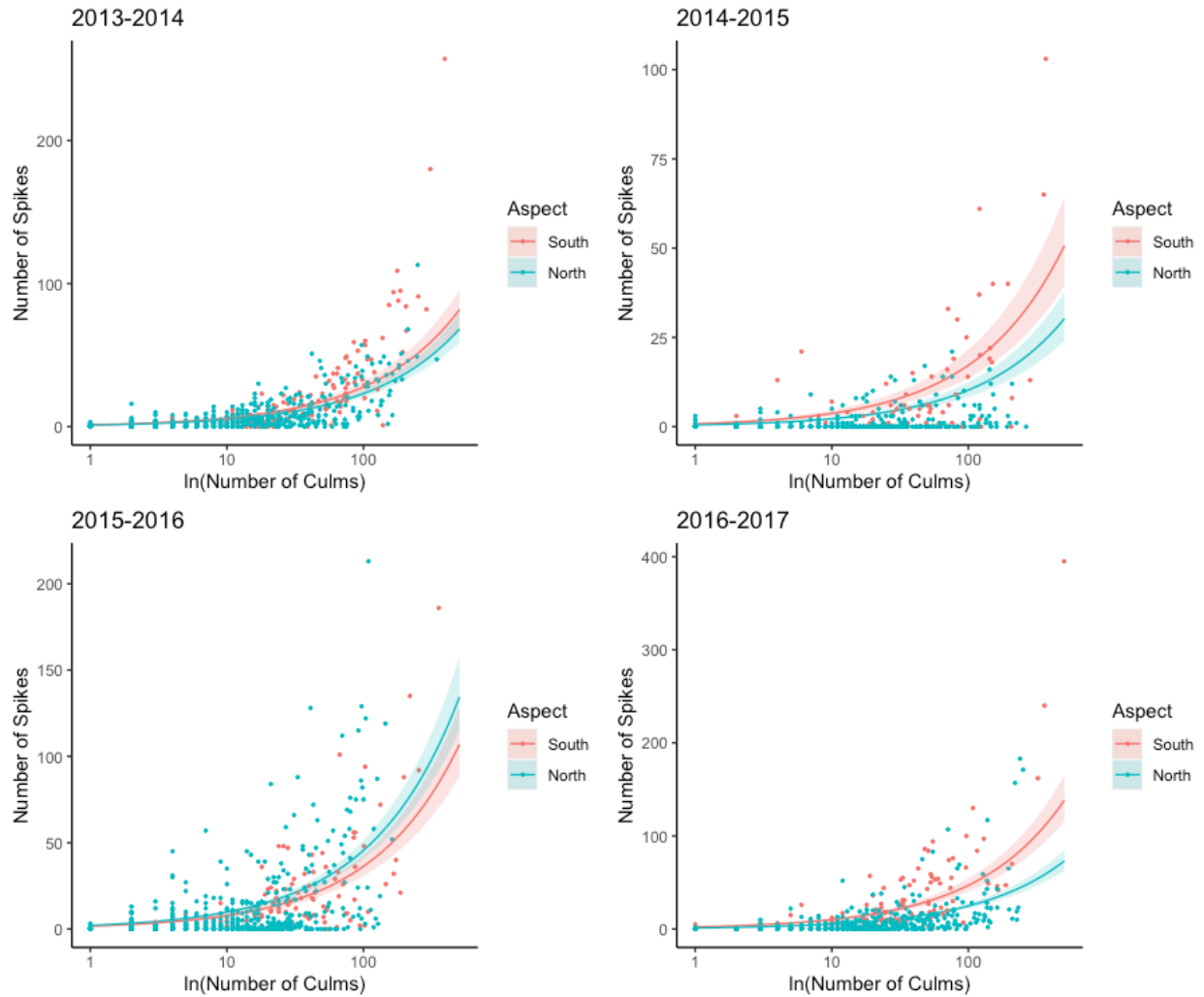
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573 Fig 1. Survival probability of bluebunch wheatgrass on north and south aspects across all annual
 574 transitions at the Wallula Gap Biological Station, WA, USA. Points indicate measured field data.
 575 Lines represent posterior mean estimate for the average individual survival, with 95% CI shaded
 576 region. For smaller individuals, survival rates were higher on north-facing slopes than on south-
 577 facing slopes. Note, points are jittered on y-axis to make it easier to view overlapping points.

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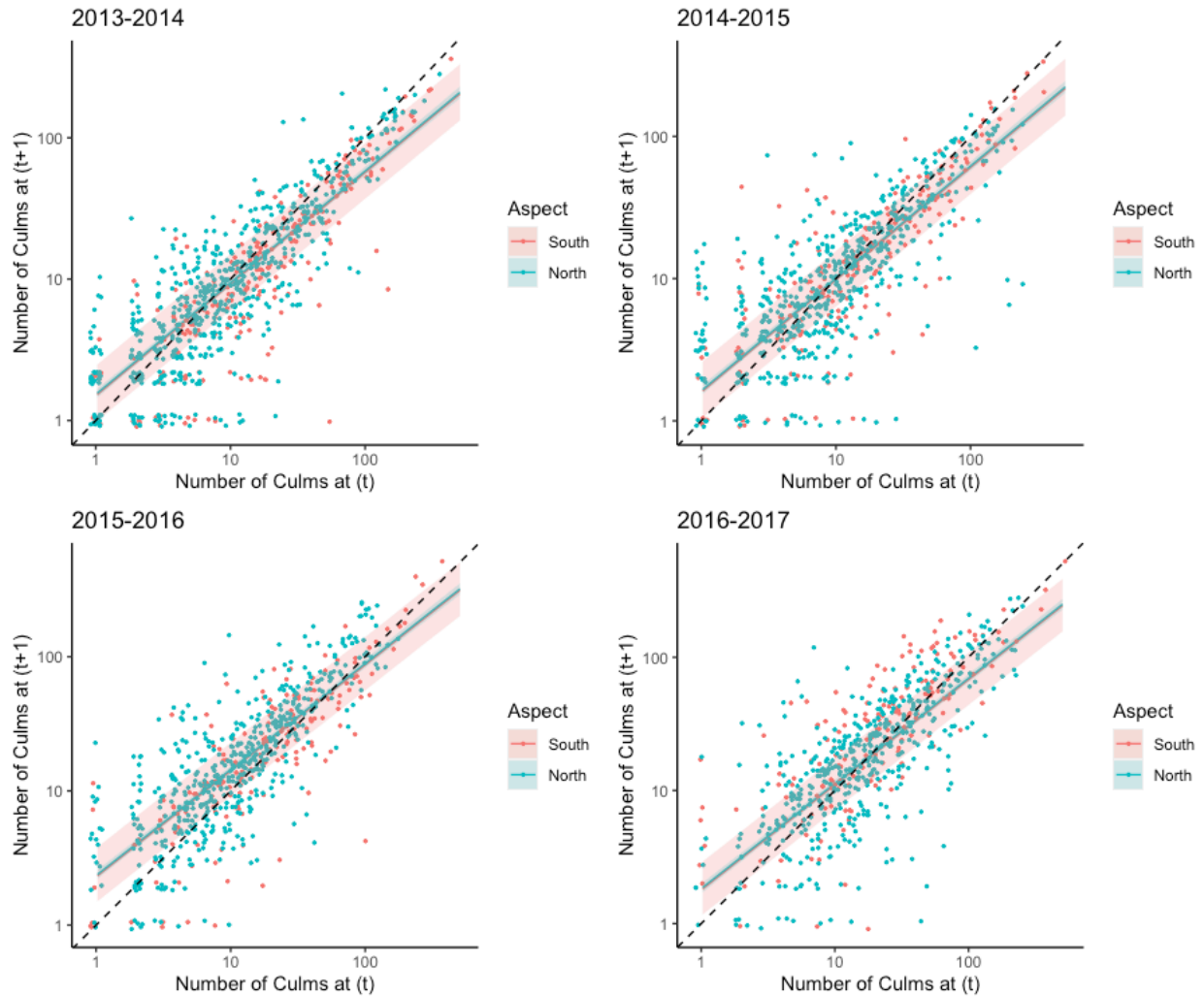


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583 Fig 2. Spikes produced per bluebunch wheatgrass plant across all annual transitions on north and
 584 south aspects at the Wallula Gap Biological Station, WA, USA. Points indicate measured field
 585 data. Lines represent posterior mean estimate for the average individual spikes produced, with
 586 95% CI shaded region. Especially among larger plants (those with more culms), the number of
 587 spikes (culms with flowers) increased more rapidly on south-facing than on north-facing slopes
 588 in most years.

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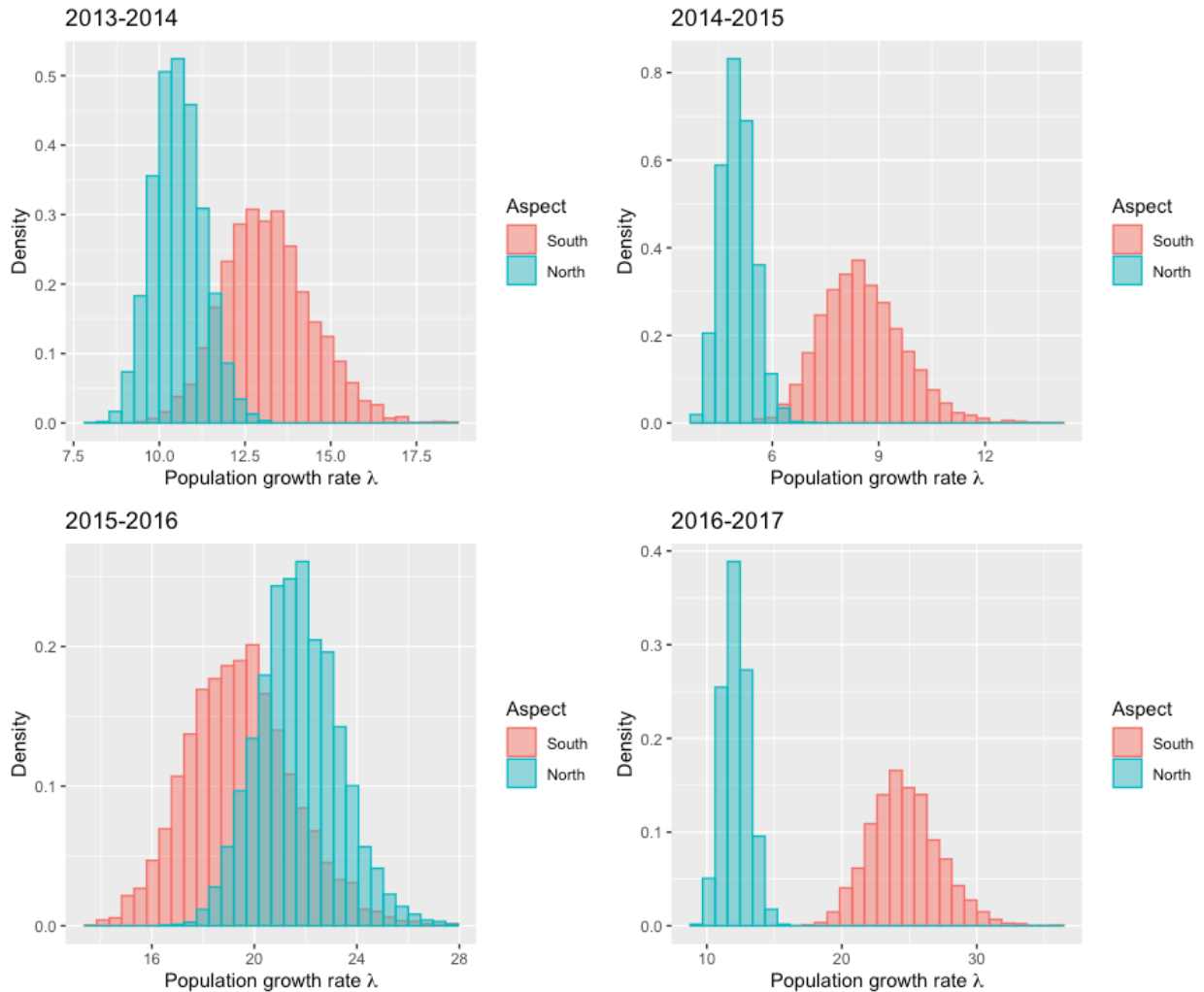


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594 Fig 3. Size changes for bluebunch wheatgrass on north and south aspects at the Wallula Gap
 595 Biological Station, WA, USA across all annual transitions. Points indicate measured field data.
 596 Colored lines represent posterior mean estimate for the average individual size change, with 95%
 597 CI shaded region. Dashed line is 1:1, thus above the dashed line indicates growth, and below the
 598 line indicates a reduction in culm number. The pattern is similar on both slopes, and the best-fit
 599 lines are consistent with regression to the mean, with smaller plants more likely to grow and
 600 larger plants more likely to shrink.

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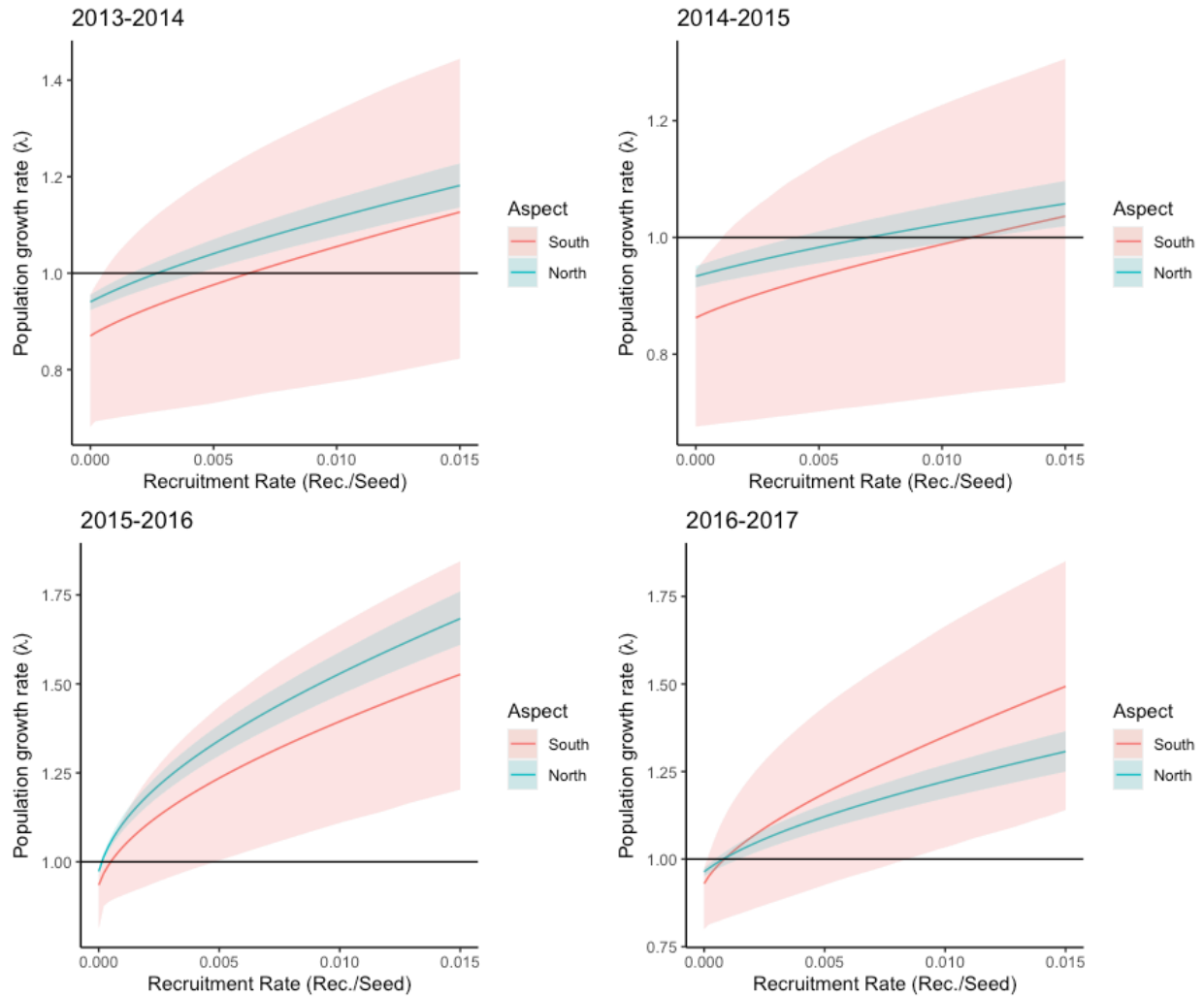
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604 Fig 4. Posterior distributions for estimated population growth rate on north and south-facing
 605 slopes if we assume that every seed becomes 1 plant (i.e. there is no explicit germination and
 606 establishment rate) for bluebunch wheatgrass at the Wallula Gap Biological Station, WA, USA.
 607 Each panel corresponds to an annual transition. The variability in estimates within a year and
 608 aspect derives from carrying through all uncertainty in parameter estimates from our vital rate
 609 models. Estimates of lambda in the absence of germination and establishment data were much
 610 higher on south-facing slopes in three of four years, presumably resulting from higher seed
 611 production on those slopes.

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616 Fig 5. Estimated population growth rate in each year from a range of recruitment rates for
 617 bluebunch wheatgrass on north and south-facing slopes at the Wallula Gap Biological
 618 Station, WA, USA. Lines represent posterior mean estimate for the recruitment rate (new
 619 recruits per seed), with 95% CI shaded region. The confidence intervals for north-facing
 620 slopes were much narrower than for south-facing slopes. Also, in three of the four years, our
 621 population growth estimates for north-facing slopes were higher across the full range of
 622 modelled recruitment rates, although the large uncertainty associated with south-facing
 623 slopes weakens our ability to compare these patterns between aspects.

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632 Table 1. Posterior parameter estimates for effect of aspect on bluebunch wheatgrass at the
 633 Wallula Gap Biological Station, WA, USA.. Values indicate the difference of south-facing
 634 aspects from north-facing ones. Overall fixed effects of aspect for each vital rate (bold) as well
 635 as individual year random effects (i.e. yearly deviations from fixed effect) are shown. Parameter
 636 values show consistent differences in survival and spikelet across aspects, modest differences in
 637 spike production with considerable annual variability, and no differences in size changes.

638

Parameter	Mean	2.5%	97.5%
Surv: β_5	-0.85	-1.46	-0.18
$\delta_s(1)$	-0.17	-0.38	1.27
$\delta_s(2)$	-0.03	-1.84	0.15
$\delta_s(3)$	-0.2	-0.36	1.33
$\delta_s(4)$	0.40	-0.21	1.43
Size: β_2	-0.02	-0.45	0.45
$\delta_g(1)$	-0.16	-0.63	0.27
$\delta_g(2)$	0.007	-0.45	0.44
$\delta_g(3)$	-0.15	-0.63	0.29
$\delta_g(4)$	0.29	-0.17	0.74
Spikes: β_8	0.26	-0.4	0.89
$\delta_{spike}(1)$	-0.08	-0.71	0.58
$\delta_{spike}(2)$	0.25	-0.37	0.96
$\delta_{spike}(3)$	-0.49	-1.13	0.14
$\delta_{spike}(4)$	0.38	-0.25	1.02
Spikelets: β_{10}	0.12	0.01	0.26
$\delta_{spikelet}(1)$	-0.04	-0.21	0.05
$\delta_{spikelet}(2)$	0.03	-0.09	0.2
$\delta_{spikelet}(3)$	-0.003	-0.15	0.12
$\delta_{spikelet}(4)$	0.01	-0.12	0.14

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647 **Supplementary information.**

648 **Shriver et al.**

649 Table S1. Soil temperature data, measured by inserting a 10 cm stainless steel thermometer with
 650 a dial display into soil until temperature equilibration, on 8 north-facing and 9 south-facing
 651 locations in April, May, July, and September 2009 in Spring Gulch, Wallula Gap Biological
 652 Station, WA.

plot	Aspect (category)	Aspect (degrees)	slope steepness (degrees)	April 18		May 21		July 20		Sept 7, 8	
				temp. (°C)	time	temp. (°C)	time	temp. (°C)	time	temp. (°C)	date ¹
1	north	326	20	8.5	09:20	13.5	09:49	25.0	08:05	18.0	7
4	north	45	29	8.5	09:50	15.0	10:15	24.5	08:33	19.0	7
6	north	19	14	9.5	10:20	15.0	10:44	24.5	08:55	23.5	7
7	north	38	30	8.5	10:40	14.5	10:50	23.0	09:17	20.0	7
9	north	318	30	9.0	11:10	13.5	11:15	.	09:37	26.0	8
10	north	348	24	8.5	11:30	13.0	12:00	.	10:01	19.0	7
11	north	26	44	8.5	11:40	15.0	12:27	.	1:20	20.0	8
12	north	10	14	10.0	11:50	18.5	12:53	.	10:28	21.0	7
north mean ± SE				8.9 ± 0.2		14.8 ± 0.6		24.2 ± 0.3		20.8 ± 0.9	
20	south	164	28	10.5	09:00	16.0	09:38	29.0	08:00	29.0	7
19	south	147	18	12.5	09:30	19.0	10:06	31.0	08:20	32.0	7
3	south	190	28	11.0	09:40	16.0	10:11	29.0	08:26	25.5	7
18	south	180	20	11.0	10:00	19.0	10:22	31.0	08:44	40.0	7
5	south	180	50	12.0	10:10	16.0	10:30	27.5	08:47	27.0	7
17	south	198	21	12.0	10:30	19.0	10:37	32.0	09:13	30.0	7
16	south	212	24	12.0	10:50	19.0	10:58	30.0	09:24	39.0	7
15	south	194	21	12.0	11:20	19.0	11:23	.	09:50	36.0	8
14	south	154	28	15.0	12:20	20.5	11:42	.	10:14	31.0	7
south mean ± SE				12.0 ± 0.4		18.2 ± 0.6		29.9 ± 0.6		32.2 ± 1.7	

653 1. In September, all samples were taken between 13:00 and 14:00.

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655 Table S2. Soil moisture at depths of 0-10 cm, 10-20 cm, and 20-30 cm, measured as proportion
 656 of mass lost after heating approximately 15 to 50 g soil to 100°C for 24 hours, from 8 north-facing
 657 and 9 south-facing locations in March, April, May, July, and September 2009 in Spring Gulch,
 658 Wallula Gap Biological Station, WA. For time of day and plot location features, consult Table
 659 S1.

plot	Aspect (category)	March 18	April 18	May 21	July 20	Sept 7, 8
		0-10 cm				
1	north	0.156	0.120	.	0.028	0.036
4	north	0.193	0.132	0.072	0.022	0.027
6	north	0.197	0.150	0.084	0.022	0.029
7	north	0.149	0.147	0.069	0.021	0.037
9	north	0.113	0.105	0.047	0.016	0.027
10	north	0.172	0.099	0.072	0.026	0.031
11	north	0.188	0.154	0.080	0.025	0.027
12	north	0.122	0.096	0.051	0.023	0.021
north mean ± SE		0.161 ± 0.011	0.125 ± 0.008	0.068 ± 0.005	0.023 ± 0.001	0.029 ± 0.002
20	south	0.108	0.166	0.063	0.016	0.017
19	south	0.073	0.054	0.043	0.020	0.015
3	south	0.130	0.119	0.066	0.014	0.016
18	south	0.095	0.054	0.043	0.020	0.019
5	south	0.078	0.058	0.053	0.014	0.012
17	south	0.092	0.047	0.038	0.016	0.017
16	south	0.085	0.049	0.048	.	0.016
15	south	0.118	0.091	0.066	0.016	0.027
14	south	0.083	0.037	0.027	0.013	0.015
south mean ± SE		0.096 ± 0.006	0.075 ± 0.014	0.050 ± 0.004	0.016 ± 0.001	0.017 ± 0.001
10-20 cm						
1	north	0.127	0.115	0.106	0.036	0.037
4	north	0.140	0.128	0.098	0.038	0.034
6	north	0.175	0.162	0.122	0.036	0.032
7	north	0.147	0.154	0.111	0.038	0.039
9	north	0.121	0.110	0.087	0.024	0.031
10	north	0.142	0.148	0.096	0.043	0.038
11	north	0.138	0.142	0.119	.	0.034
12	north	0.143	0.110	0.085	0.024	0.027
north mean ± SE		0.142 ± 0.006	0.134 ± 0.007	0.103 ± 0.005	0.034 ± 0.003	0.034 ± 0.001
20	south	0.094	0.069	0.070	0.024	0.026
19	south	0.099	0.071	0.046	0.018	0.023
3	south	0.137	.	0.086	0.024	0.019
18	south	0.096	0.067	0.061	0.025	0.025
5	south	0.115	0.021	0.073	0.025	0.021
17	south	0.094	0.072	0.049	0.020	0.020
16	south	0.096	0.071	0.063	.	0.019
15	south	0.105	0.105	0.090	.	0.022

14	south	0.085	0.051	0.035	0.019	0.020
south mean ± SE		0.102 ± 0.005	0.066 ± 0.008	0.064 ± 0.006	0.022 ± 0.001	0.021 ± 0.001
20-30 cm						
1	north	0.132	0.125	0.112	0.049	0.048
4	north	0.133	0.126	0.109	0.045	0.041
6	north	0.145	0.149	0.125	0.046	0.040
7	north	0.140	0.147	0.116	0.046	0.044
9	north	0.077	0.109	0.101	0.039	0.037
10	north	0.128	0.112	0.107	0.045	0.043
11	north	0.156	0.130	0.120	0.046	0.035
12	north	0.101	0.123	0.103	0.045	0.038
north mean ± SE		0.127 ± 0.009	0.128 ± 0.005	0.111 ± 0.003	0.045 ± 0.001	0.041 ± 0.001
20	south	0.091	0.070	0.067	0.037	0.029
19	south	0.084	0.070	0.055	0.023	0.026
3	south	0.132	0.127	0.097	0.059	0.028
18	south	0.091	0.086	0.061	0.037	0.038
5	south	.	.	0.083	0.044	0.027
17	south	0.078	0.071	0.054	0.034	0.025
16	south	0.092	0.081	0.063	0.034	0.024
15	south	0.106	0.105	0.105	.	0.028
14	south	0.085	0.062	0.052	0.022	0.019
south mean ± SE		0.095 ± 0.006	0.084 ± 0.008	0.071 ± 0.007	0.036 ± 0.004	0.027 ± 0.002

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664 Repeatability – Methods

665 Each year, we re-surveyed one or more transects or portions of transects (subset of quadrats) to
666 allow estimation of repeatability values for culm number, spike number, and average number of
667 spikelets. We also re-surveyed the first transect surveyed at the start of the field season and
668 considered the first survey a practice round. Thus we excluded these practice rounds from our
669 estimates of repeatability. We estimated repeatability using the method of (Nakagawa and
670 Schielzeth 2010) which accounts for structure in the data while estimating repeatability values of
671 interest so as to avoid overestimating repeatability due to similarities within groups, for instance,
672 of the same experimental treatment. To accomplish this, we fit generalized linear mixed models
673 with the R package rptR (Stoffel et al. 2017, version 9.22 in R version 3.5.1) and ran 1000 bootstrap
674 iterations. To estimate within-year culm and spike count repeatabilities, we used only plants in
675 which the same individual was counted on two separate dates in the same year. If a plant in a twice-
676 surveyed quadrat was not counted in one of the two surveys, we excluded it from this analysis. For
677 our analysis of the number of spikes and the average number of spikelets, we excluded plants with
678 no spikes to avoid biasing upwards our estimates of repeatability by the many cases where there
679 were counts of zero on both visits. Because we wanted to determine repeatability of counts within
680 a single year, we assigned each pair of measurements within a single year a unique pair identifier.
681 Thus plant identity was not linked across years. We set aspect (north vs. south face) as a fixed
682 effect, and year and pair identity as random effects. We did not account for quadrat or transect
683 identity in the model, because we had no expectation that, after accounting for aspect, there would
684 be substantial spatial variability in the count data. For culm number and spike number analyses,
685 we specified Poisson error in rptR, which automatically accounts for overdispersion (Stoffel et al.
686 2017). For analysis of the mean number of spikelets per spike, we specified Gaussian error. We

687 were also interested in the reliability of our detections of individual plants, and so we estimated
688 the proportion of plants detected in only one of the two rounds. We did not conduct a repeatability
689 analysis because plants that were detected in neither survey are not all listed in our database in a
690 given year, and so there is a bias against the presence of a certain type of binomial data (two
691 failures to detect) in the data set.

692

693 Repeatability – Results

694 Our counts of features of individual plants were repeatable for culm count ($n = 260$ count pairs, R
695 $= 0.884 \pm 0.050$ (SE), 95% CI: 0.786-0.968, $p = 7.4 \times 10^{-122}$, Fig S1), spike count ($n = 178$ count
696 pairs, $R = 0.883 \pm 0.057$ (SE), 95% CI: 0.760-0.968, $p = 2.4 \times 10^{-76}$, Fig S2), and mean spikelet
697 count ($n = 178$ count pairs, $R = 0.641 \pm 0.072$ (SE), 95% CI: 0.487-0.769, $p = 1.7 \times 10^{-32}$, Fig S3).
698 In plots visited twice in a single year (excluding practice plots), we detected 93.75% of bluebunch
699 wheatgrass plants on both visits.

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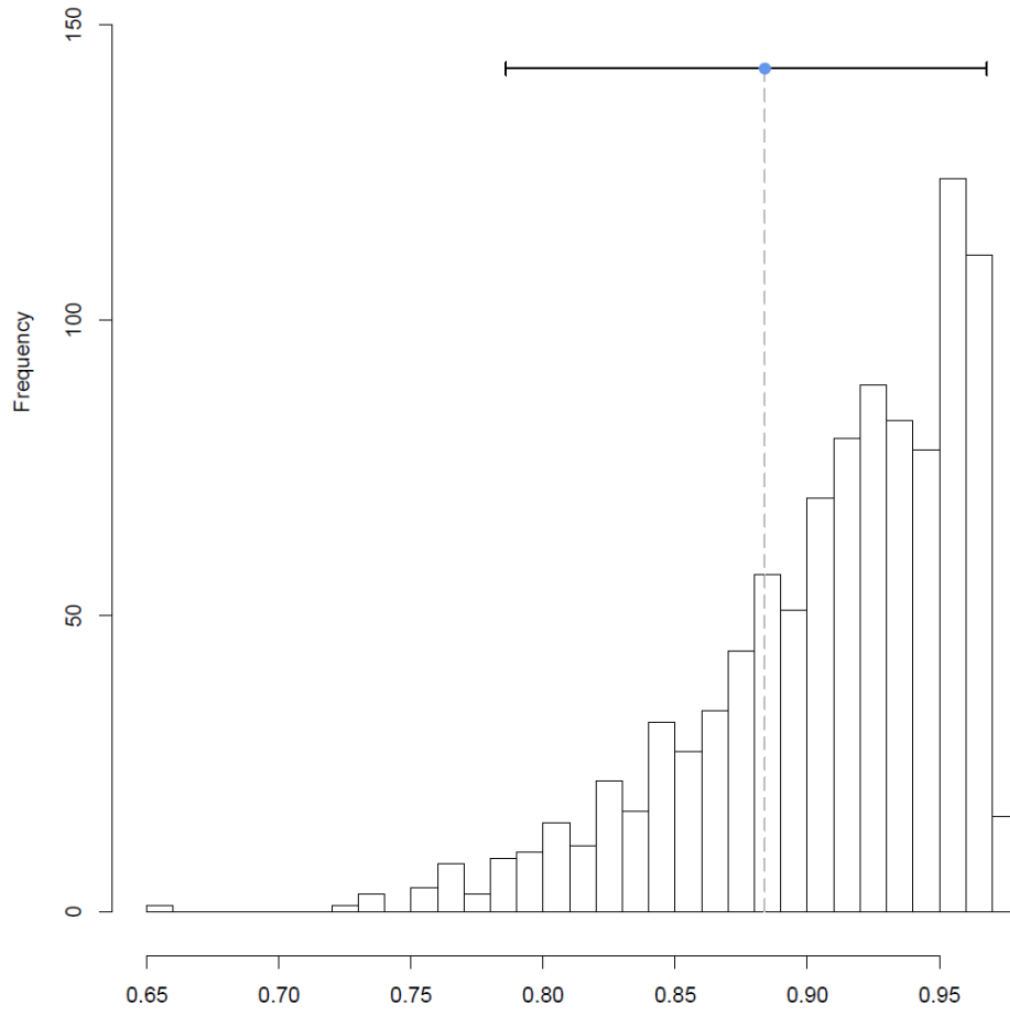
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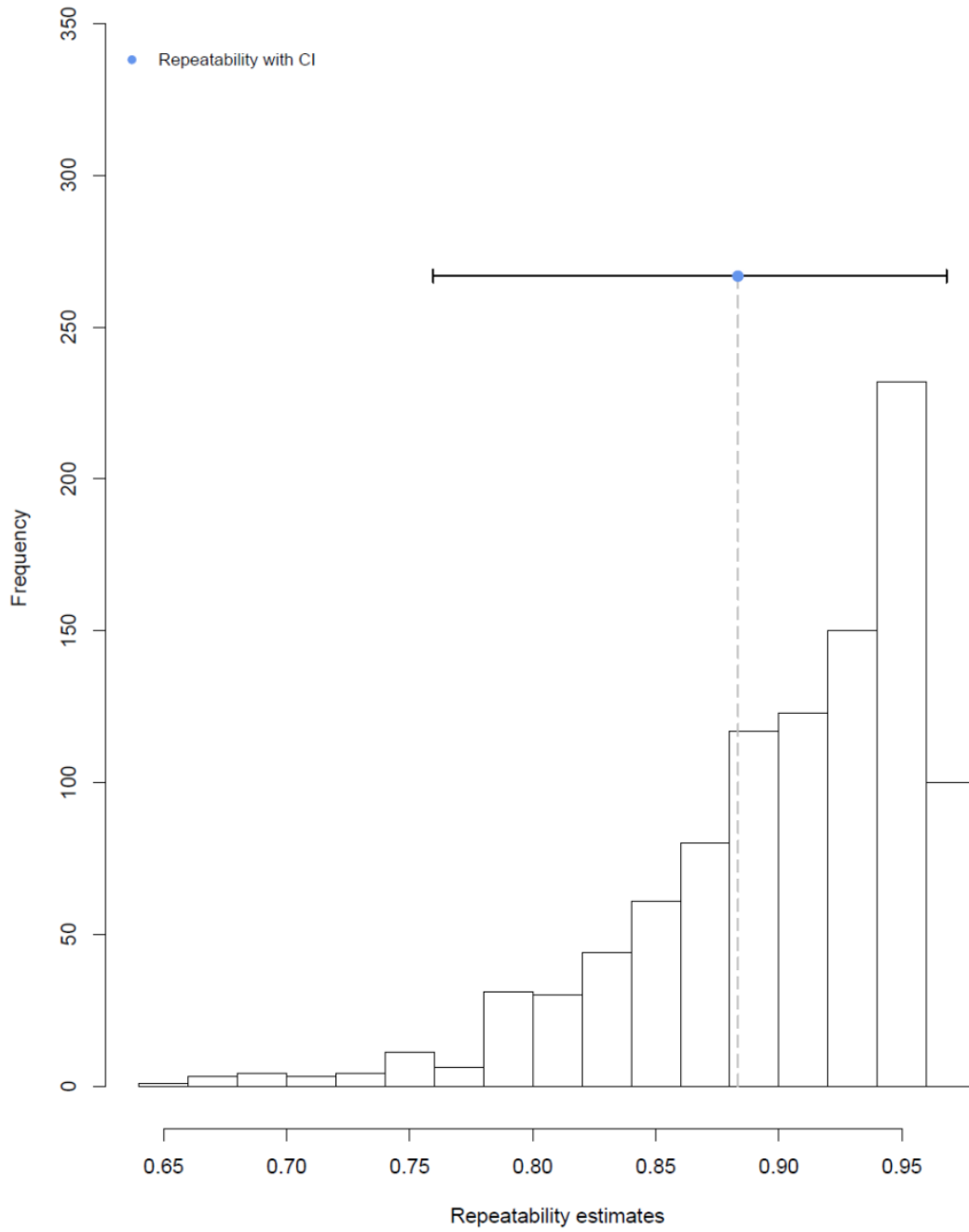


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707 Figure S1. Distribution of bootstrap estimates of repeatability of log-transformed (in the Poisson
 708 GLMM) bluebunch wheatgrass culm counts, along with point estimate and 95% confidence
 709 intervals, from pairs of counts of the same individuals at Spring Gulch, Wallula Gap Biological
 710 Station, WA. Repeatability was high.

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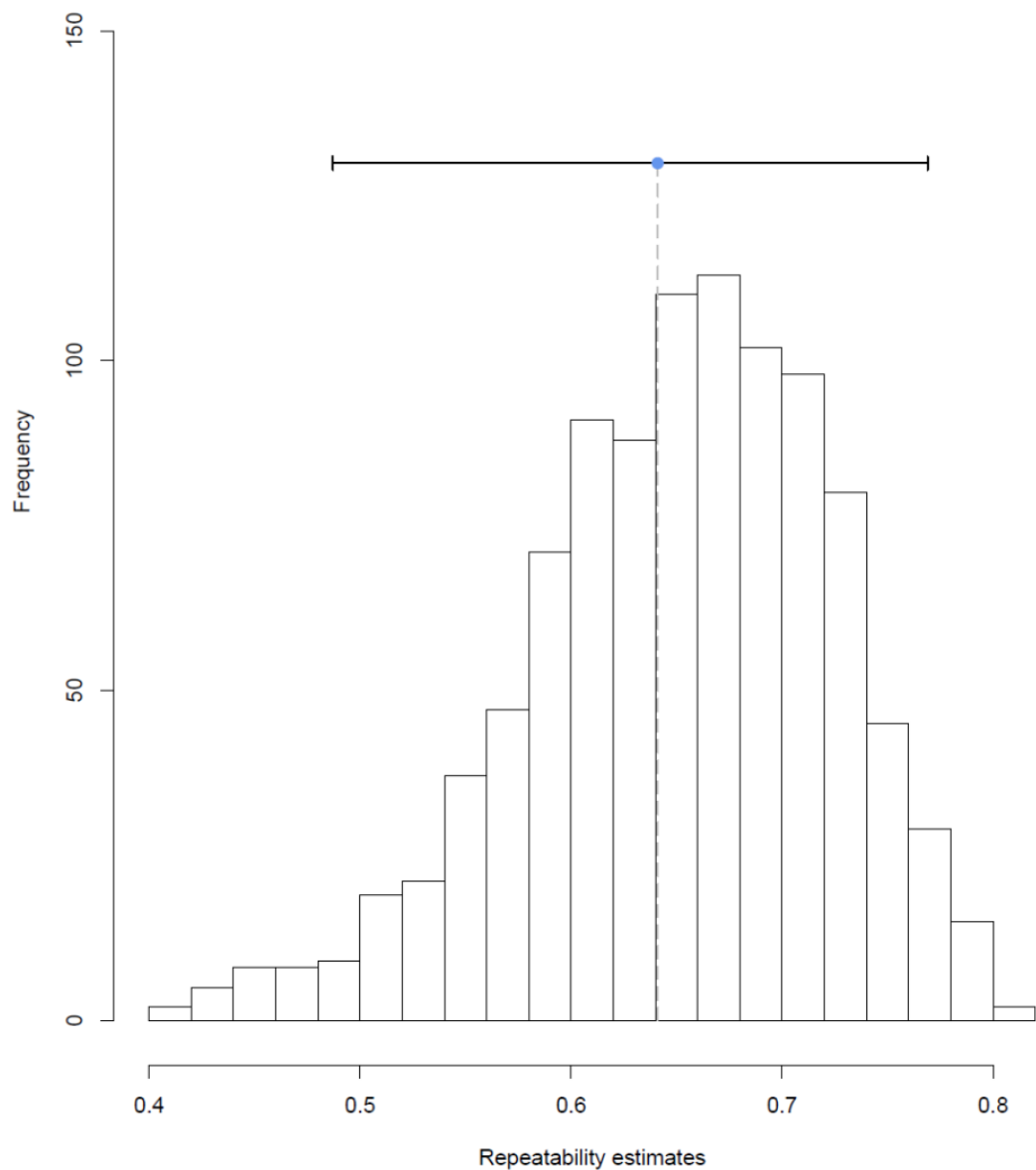
712



715 Figure S2. Distribution of bootstrap estimates of repeatability of (in the Poisson GLMM)
716 bluebunch wheatgrass spike counts, along with point estimate and 95% confidence intervals, from

717 pairs of counts of the same individuals at Spring Gulch, Wallula Gap Biological Station, WA.
718 Repeatability was high.

719



720

721 Figure S3. Distribution of bootstrap estimates of repeatability of mean count of spikelets per spike
722 in bluebunch wheatgrass, along with point estimate and 95% confidence intervals, from pairs of

723 counts of the same individuals at Spring Gulch, Wallula Gap Biological Station, WA.

724 Repeatability was moderate.

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741 Table S3. IPM model posterior parameter values from mixed effects GLMs.

Parameter	Mean	2.5% CI	97.5% CI
β_0	0.59	0.16	0.99
β_1	0.79	0.77	0.81
β_2	-0.02	-0.45	0.45
β_3	1.06	0.38	1.67
β_4	0.96	0.83	1.09
β_5	-0.85	-1.46	-0.18
β_6	0.05	-0.81	0.94
β_7	0.67	0.63	0.7
β_8	0.26	-0.4	0.89
β_9	1.83	1.65	1.99
β_{10}	0.12	0.01	0.26
β_{11}	1.42	1.33	1.5
σ	0.72	0.7	0.74
$\gamma_g(1)$	-0.67	-1.88	0.5
$\gamma_g(2)$	-0.42	-1.53	0.64
$\gamma_g(3)$	1.03	-0.24	2.46
$\gamma_g(4)$	0.04	-0.94	1.06
$\gamma_s(1)$	0.47	-0.75	1.8
$\gamma_s(2)$	-0.99	-2.5	0.38
$\gamma_s(3)$	0.49	-0.76	1.83
$\gamma_s(4)$	0	-1.31	1.37
$\gamma_{spike}(1)$	0.02	-0.94	0.97
$\gamma_{spike}(2)$	-1.17	-2.56	0.05
$\gamma_{spike}(3)$	1	-0.17	2.26
$\gamma_{spike}(4)$	0.12	-0.86	1.08
$\gamma_{spikelet}(1)$	-0.21	-1.36	0.83
$\gamma_{spikelet}(2)$	-0.89	-2.39	0.37
$\gamma_{spikelet}(3)$	0.6	-0.53	1.86
$\gamma_{spikelet}(4)$	0.5	-0.58	1.68
$\delta_g(1)$	-0.16	-0.63	0.27
$\delta_g(2)$	0.007	-0.45	0.44
$\delta_g(3)$	-0.15	-0.63	0.29
$\delta_g(4)$	0.29	-0.17	0.74
$\delta_s(1)$	-0.17	-0.38	1.27
$\delta_s(2)$	-0.03	-1.84	0.15
$\delta_s(3)$	-0.2	-0.36	1.33
$\delta_s(4)$	0.40	-0.21	1.43
$\delta_{spike}(1)$	-0.08	-0.71	0.58
$\delta_{spike}(2)$	0.25	-0.37	0.96

$\delta_{spike}(3)$	-0.49	-1.13	0.14
$\delta_{spike}(4)$	0.38	-0.25	1.02
$\delta_{spikelet}(1)$	-0.04	-0.21	0.05
$\delta_{spikelet}(2)$	0.03	-0.09	0.2
$\delta_{spikelet}(3)$	-0.003	-0.15	0.12
$\delta_{spikelet}(4)$	0.01	-0.12	0.14

742

743

744 **References**

745 Nakagawa, S., and H. Schielzeth. 2010. Repeatability for Gaussian and non-Gaussian data: a
 746 practical guide for biologists. *Biological Reviews* 85:935–956.

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761
762 To facilitate transparency in the process of developing our analyses, we pre-registered an analysis plan prior to
763 examining the data in aggregate (Parker and Shriver 2018). The purpose of this supplement is to identify and explain
764 deviations from this pre-registration. We include the full text of the pre-registration below. The original text is in
765 italics, and our post-analysis explanations are in normal text.

766
767 *Summary*

768
769 *Provide a narrative summary of what is contained in this registration, or how it differs from prior registrations.*

770
771 *This summary follow the outline of the preregistration challenge.*

772
773 *Title*

774
775 *Demography of a perennial bunchgrass across a natural aridity gradient*

776
777 -----

778 *Research Questions*

779
780 *How does aspect (north versus south-facing slope, which correspond to higher vs. lower aridity) influence the*
781 *demography of bluebunch wheatgrass at Spring Gulch, Wallula Gap Biological Station, Washington, USA?*

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783 -----

784 *Hypotheses*

785
786 *Aspect (north vs. south-facing) influences lambda (the population growth rate)- non-directional*

787 *Aspect influences plant size – directional (based on examinations 2011 and 2012 data): larger plants on south-facing*
788 *slopes*

789 *Aspect influence plant growth – non-directional*

790 *Plant size influences survival – directional: larger plants survive better*

791 *--This effect differs between aspects – non-directional*

792 *Plant size influences reproductive rate – directional: larger plants reproduce more*

793 *--This effect differs between aspects – non-directional*

794
795 *Consequences of vital rate changes across gradient for lambda.*

796 *Hypotheses*

797 *1) Non-directional changes in vital rates-Increases in one vital rate (e.g. growth) compensate for declines in*
798 *another (e.g. survival) leading to stable populations ($\lambda \geq 1$) on both north and south*

799 *2) Directional change in vital rates- Vital rates are not able to compensate leading one population to be a sink*
800 *($\lambda < 1$) while the other might be a source ($\lambda > 1$).*

801
802 Because we lacked sufficient data on recruitment, our estimates of lambda assumed recruitment of 100%, and
803 therefore are not meant not as absolute estimates of population growth. Instead our estimates of lambda
804 demonstrate the aggregated impact of differences in growth, survival, and reproductive output between north and
805 south-facing slopes.

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808 *Existing Data*

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810 *Registration prior to analysis of the data*

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813 *Explanation of existing data*

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These data are part of a long-term project that began in 2011. We refined the data gathering process in 2011 and 2012, and finally settled on a reliable method for re-locating individual plants (using metal tags in the ground next to plants, and rebar stakes to hold the 1 x 1m sampling grid) in 2013. Thus we will use data from 2013 and later. Undergraduate students have looked at portions of these data for their senior theses, but patterns in data after 2015 have not been examined, and those analyses have been less thorough than what we propose here.

Data collection procedures

In 2011 we identified 14 10m x 1m transects through existing populations of bluebunch wheatgrass. We placed seven transects on south-facing slopes and seven transects on north-facing slopes. We sampled five 1x1m quadrats from each transect, each separated from others by 1 m of unsampled territory. Within each quadrat, researchers identified each bluebunch wheatgrass plant, assigned it an arbitrary number, affixed a metal tag in the ground adjacent to the plant, and mapped the location of the plant using a map with 10cm x 10cm grid cells. For each bluebunch wheatgrass plant, researchers counted the number of live stems (culms) and the number of live stems with flowers (spikes). For any plant with flowers, researchers counted the number of spikelets per spike up to five spikes. If the number of spikes exceeded five, researchers selected five haphazardly for the spikelet counts. Researchers also measure the height of the tallest culm. For a subset of quadrats, we re-visited several days or weeks later to take a 2nd count to allow us to determine repeatability.

Sample size

The sample size is 70 quadrats divided between 14 transects, with half the transects on south-facing and half on north facing slopes. The number of plants per quadrats is highly variable.

Sample size rationale

The sample size was chosen based on the amount of data a pair of students could reasonably gather in three to four weeks.

Stopping rule

We will continue to gather data for the foreseeable future. We will analyze the 2013-2018 data at this time because we have the opportunity to conduct the analysis.

Manipulated variables

not applicable

Measured variables

Within each quadrat, researchers identified each bluebunch wheatgrass plant, assigned it an arbitrary number, affixed a metal tag in the ground adjacent to the plant, and mapped the location of the plant using a map with 10cm x 10cm grid cells.

867 *For each bluebunch wheatgrass plant we gathered the following data:*
868 *-number of live stems (culms)*
869 *-number of live stems with flowers (spikes)*
870 *-For any plant with flowers, the number of spikelets per spike up to five spikes. If the number of spikes exceeded five,*
871 *researchers selected five haphazardly for the spikelet counts.*

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873

874 *Indices*

875
876 *-We will not combine any measures*
877 -----

878 *Study type*

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881 *Observational Study - Data are collected from study subjects that are not randomly assigned to a treatment. This*
882 *includes surveys, "natural experiments," and regression discontinuity designs.*

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886 *Blinding*

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888 *No blinding is involved in this study.*

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892 *Study design*

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895 *The sampling design is described above. It is a demographic study in which all individuals of the target species within*
896 *the study area are measured each year.*

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899 *Randomization*

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901 *not applicable*

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903 -----

904 *Statistical models*

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907 *Annual vital rate analysis will be done using three mixed effects GLMs in a Bayesian framework. There will be a*
908 *separate GLM for each of these three vital rates as the response variable: growth, survival, reproduction*
909 *Fixed effects will include:*

- 910 1) *Plant Size (number of culms)*
911 2) *Aspect (categorical: north-facing, south-facing)*
912 3) *Aspect*Size*

913
914 *Random effects will include:*

- 915 1) *Transect*
916 2) *Year*

917

918 *We will fit the full model and then interpret the importance of each fixed-effect variables based off its posterior (i.e.*
919 *we will ask if the posterior overlaps with zero) and the sensitivity of each of the three vital rate GLMs (growth,*
920 *survival, reproduction) and lambda to each parameter (size, aspect, size*aspect).*

921

922 Modeling was modified to include fixed effects of:

923 1) Plant Size (log number of culms)

924 2) Aspect (categorical: north-facing, south-facing)

925 Aspect*Size interactions were not explored

926

927 Random effects included:

928 1) Year

929 2) Year*Aspect

930 Adding Year*Aspect allowed the effect of aspect to change year to year to account for interactions of environmental
931 conditions and aspect.

932

933

934 *Transformations*

935

936

937 *Size/growth data will be fit using normally distributed, linear effects.*

938 *Survival will be Bernoulli regression using logit link function.*

939 *Spikelets per plant and new recruits per plant will be fit with a Poisson or negative-binomial regression with log link*
940 *function. The distribution with the maximum log-likelihood will be selected for use.*

941

942 Vital rate data were all fit using log number of culms, due to highly right-skewed distribution of culms.

943

944 *Aspect will be coded as 0-1 for North-South respectively*

945

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948 *Follow-up analyses*

949

950 *The student analysis conducted in 2015 on the 2013-2015 data suggested plants were getting smaller. This trend*
951 *could have been driven by inflated counts in 2013 and so if we find evidence of this pattern in the larger data set, we*
952 *will re-run analyses without the 2013 data to see if the pattern continues to hold.*

953

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956 *Inference criteria*

957

958

959 *Lambda for north and south populations will be calculated separately using Integral Projection Models using vital*
960 *rates models. Growth, Survival, and spikelet production (reproduction) data will come from regressions (above). Plant*
961 *sizes will be cutoff at the maximum observed size, and the remaining size distributions will be normalized to sum to*
962 *1. Germination rate will be calculated as seeds (based on supplemental average seed per spikelet dataset) in t that*
963 *turn into plants in t+1. No seedbank will included in the model.*

964

965 *Given sparse data on recruitment we will also infer the recruitment needed for each population to reach lambda=1*
966 *on both the north and south aspects in a Bayesian framework (see methodology in Shriver et al. 2012). The*
967 *recruitment function will be assumed to be a log-linear function of plant size and aspect (similar reproduction function*
968 *fit to data above). Recruitment needed for a stable population will be interpreted as different if the 95% credible*
969 *interval of the difference in recruitment across aspects does not overlap with 0.*

970

971 Because we already had data on reproductive output based on plant size, no relationship between plant size and
972 the number of recruits produced was needed. Recruitment was a rate greater than 0.

973 -----

974 *Data exclusion*

975
976

977 *We will only include bluebunch wheatgrass plants that have been observed to flower in one or more years. This is*
978 *because the students collecting the data have shown some inconsistency in identifying members of this species when*
979 *not flowering.*

980 -----

981 *Missing data*

982

983 *Rows with missing growth and reproduction data will be imputed in a Bayesian framework. Missing data points are*
984 *treated as unknown parameter that are imputed using available data and full parameter and process uncertainty*
985 *from GLM models of growth and reproduction. Plants will be assumed to have survived if survival is not observed in*
986 *a year but it is then observed alive in subsequent year.*

987

988 Missing data was excluded rather than imputed

989 -----

990 *Exploratory analysis (optional)*

991
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994 *Upload an analysis script with clear comments (optional)*

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998 *Other (optional)*

999

1000

1001

1002 *References*

1003 Parker, T. H., & Shriver, R. (2018, December 18). Bluebunch wheatgrass demographic analysis 2013-2018.
1004 <https://doi.org/10.17605/OSF.IO/JQCHW>

1005