

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 =  $180 \pm 75$  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  $\beta_1$  and  $\beta_2$  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  $\beta_4$  and  $\beta_5$  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,  $\text{Seeds}$ .

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

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

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

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

252 Once again,  $\gamma_{spike}(t)$  &  $\gamma_{spikelet}(t)$  are random effects intercept that varies by year,  $\delta_{spike}(t)$   
253 &  $\delta_{spikelet}(t)$  are random effects for aspect that also varies by year, and  $\beta_7$  and  $\beta_8/ \beta_{10}$  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,  $\beta_{11}$ . 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 ( $\lambda_t$ ) (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  $\lambda_t$ .

269 Additionally we inferred possible seed to seedling recruitment rates using two  
270 approaches. First, we determined how  $\lambda_t$  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  $\lambda_t$  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  $\beta_8$  (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 ( $\lambda$ ) 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  $\sim 0.01$ . 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

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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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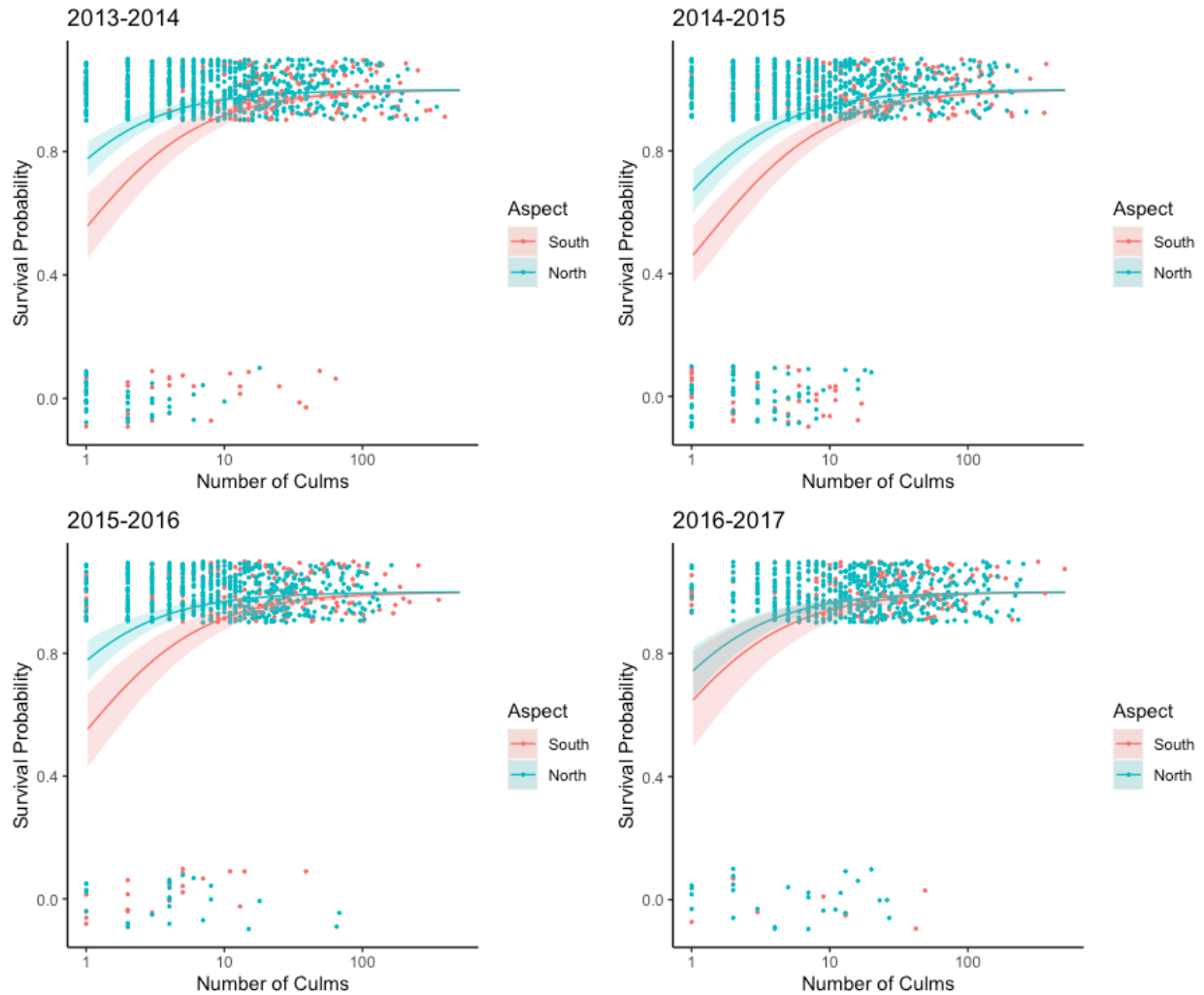
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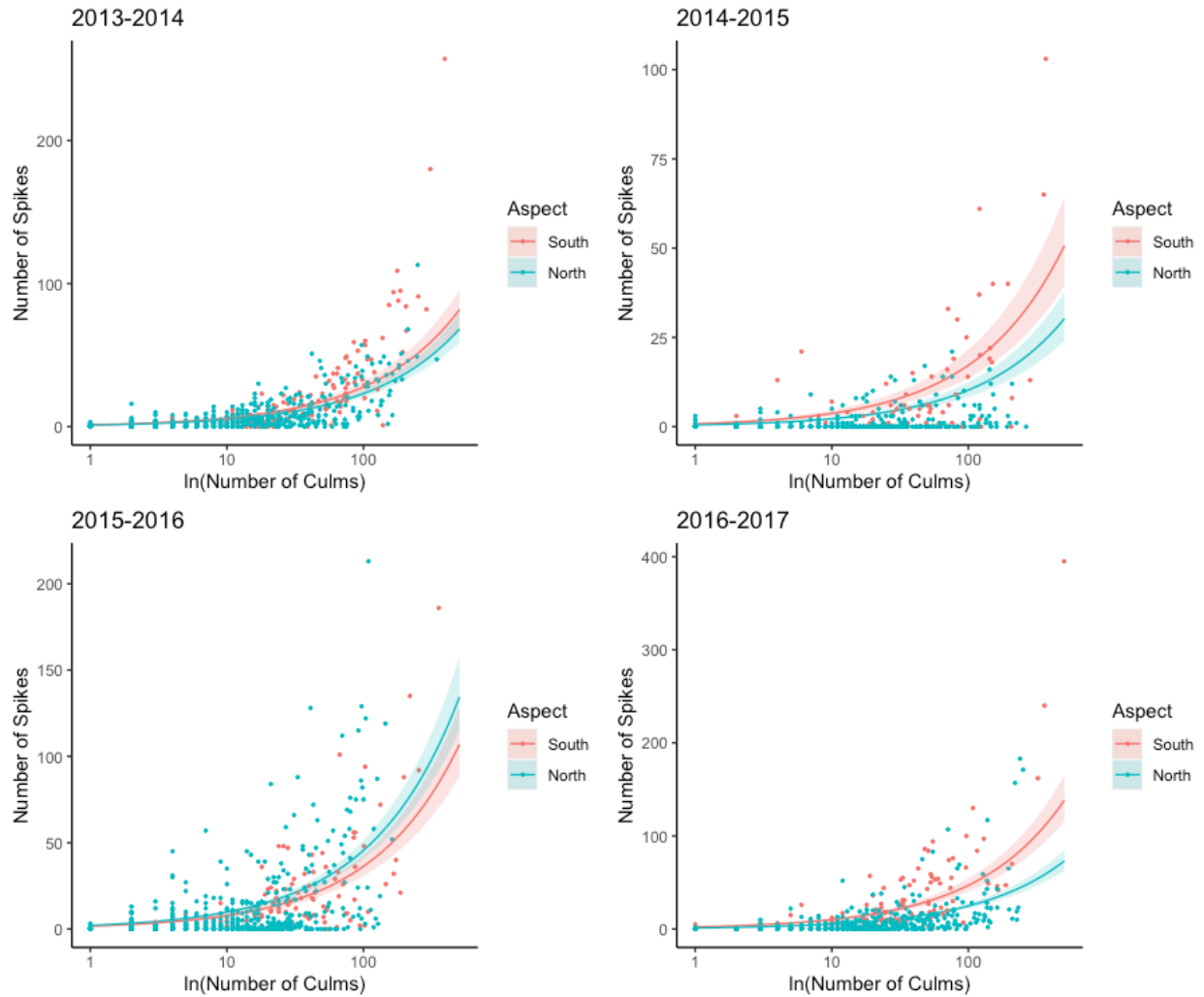
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573 Fig 1. Survival probability of bluebunch wheatgrass on north and south aspects across all annual  
 574 transitions at the Wallula Gap Biological Station, WA, USA. Points indicate measured field data.  
 575 Lines represent posterior mean estimate 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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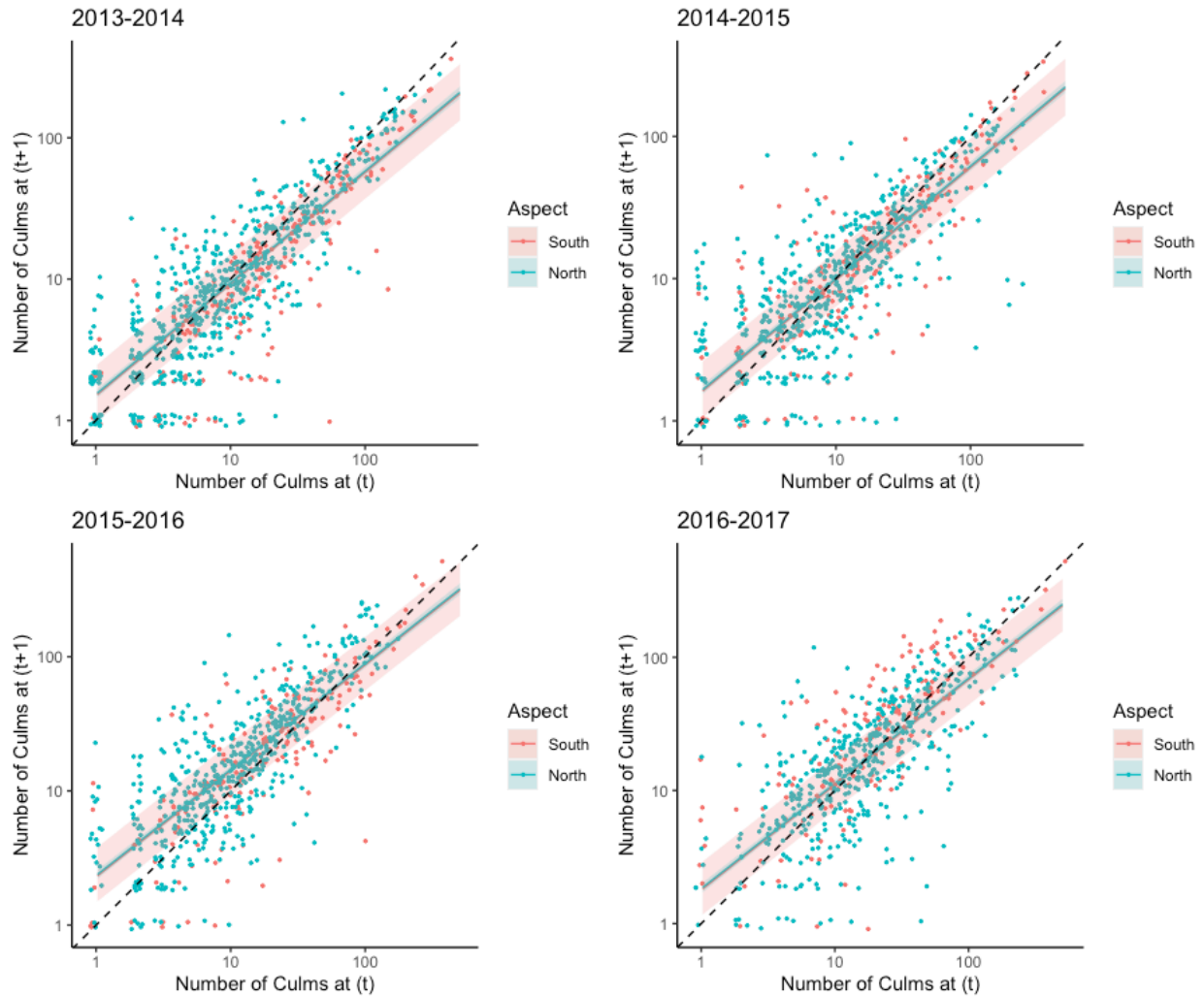


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583 Fig 2. Spikes produced per bluebunch wheatgrass plant across all annual transitions on north and  
 584 south aspects at the Wallula Gap Biological Station, WA, USA. Points indicate measured field  
 585 data. Lines represent posterior mean estimate 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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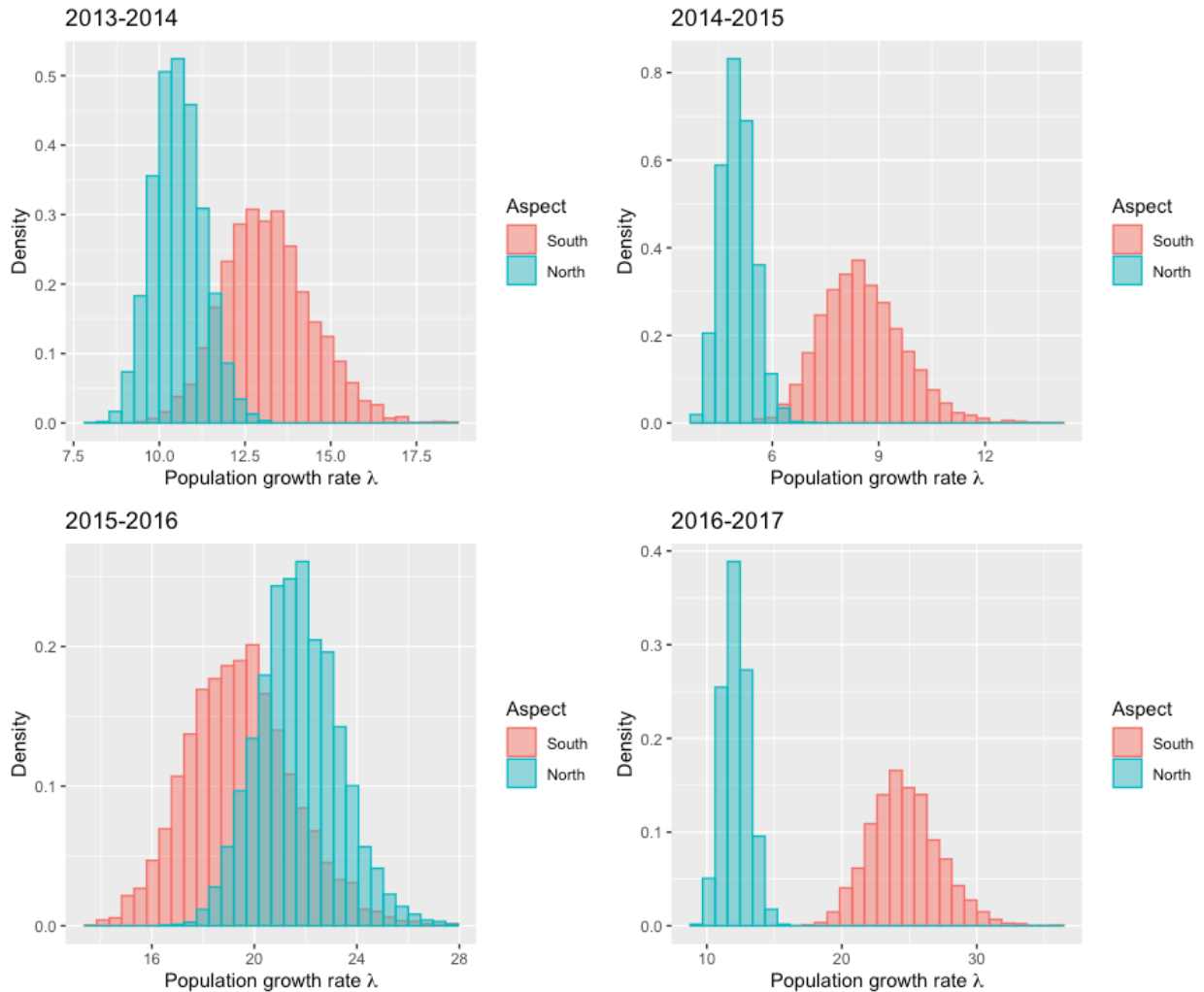


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594 Fig 3. Size changes for bluebunch wheatgrass on north and south aspects at the Wallula Gap  
 595 Biological Station, WA, USA across all annual transitions. Points indicate measured field data.  
 596 Colored lines represent posterior mean estimate 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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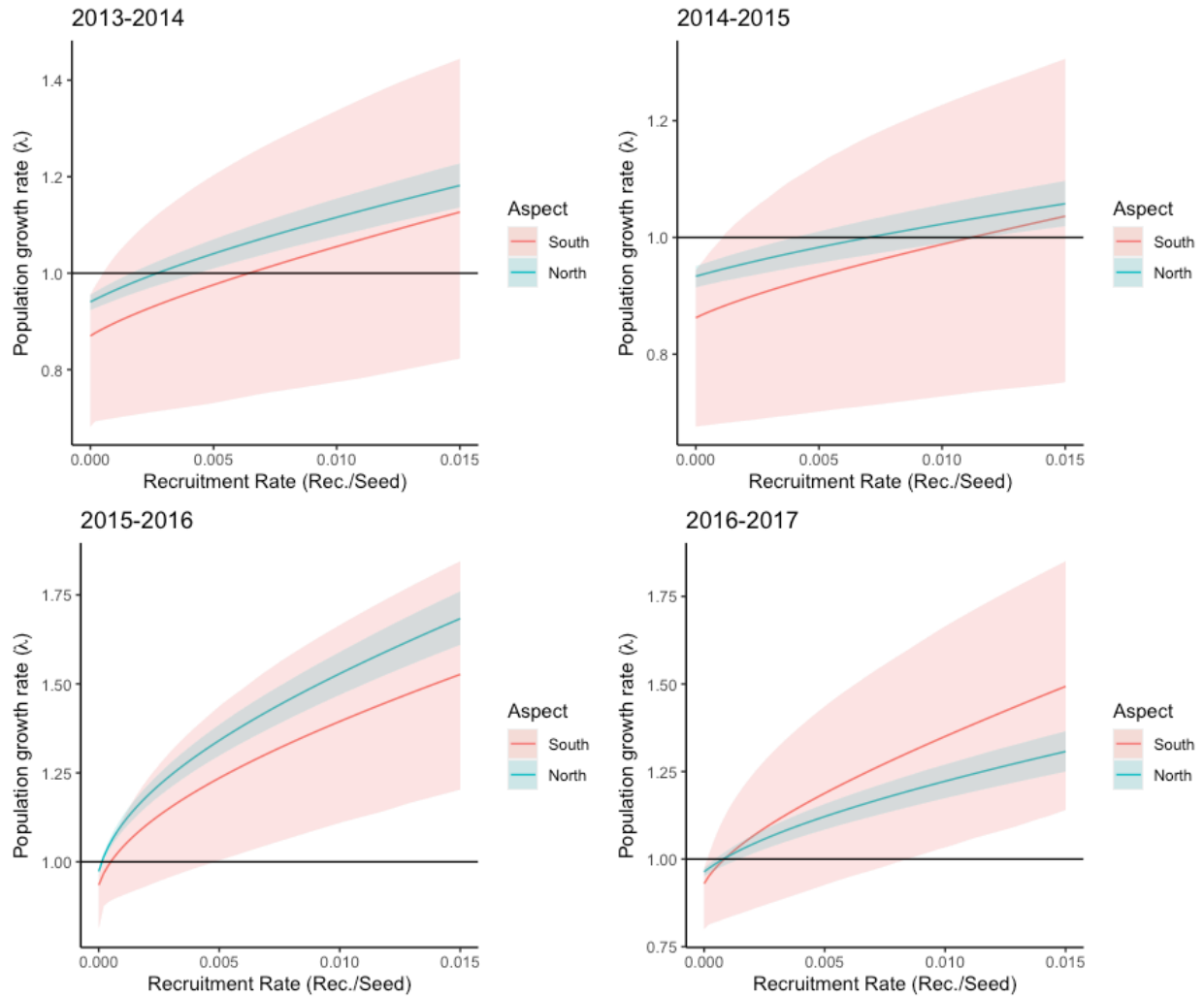
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604 Fig 4. Posterior distributions for estimated population growth rate on north and south-facing  
 605 slopes if we assume that every seed becomes 1 plant (i.e. there is no explicit germination and  
 606 establishment rate) for bluebunch wheatgrass 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%        |
|---|--------------|--------------|--------------|
| <b>Surv: <math>\beta_5</math></b>         | <b>-0.85</b> | <b>-1.46</b> | <b>-0.18</b> |
| $\delta_s(1)$                             | -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         |
| <b>Size: <math>\beta_2</math></b>         | <b>-0.02</b> | <b>-0.45</b> | <b>0.45</b>  |
| $\delta_g(1)$                             | -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         |
| <b>Spikes: <math>\beta_8</math></b>       | <b>0.26</b>  | <b>-0.4</b>  | <b>0.89</b>  |
| $\delta_{spike}(1)$                       | -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         |
| <b>Spikelets: <math>\beta_{10}</math></b> | <b>0.12</b>  | <b>0.01</b>  | <b>0.26</b>  |
| $\delta_{spikelet}(1)$                    | -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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