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

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Abstract

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

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

Introduction

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

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

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

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

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

Because bluebunch population persistence varies with aspect over small spatial scales, demographic processes must vary over these scales, but we still lack an accounting of this variability. Variation in demography with aspect likely results from the divergent temperature and moisture conditions on different aspects. Variation in temperature and moisture correlate with variation in phenology and morphology of bluebunch wheatgrass across larger spatial scales (St. Clair et al. 2013). Further, within a single site, long-term data from this species suggest that annual variation in temperature and moisture drive annual variation in demographic variables including growth and survival (Dalgleish et al. 2011). Other demographic variables may also be impacted by microclimatic variation in bluebunch wheatgrass. For instance, experimental manipulation of soil moisture influenced seed quality and offspring fitness (Drenovsky et al. 2016). Thus, we have strong a priori expectations for demographic variability with aspect over small spatial scales in this species.

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

Methods

Field Data Collection

We monitored individual bluebunch wheatgrass plants growing on steep hillsides in Spring Gulch on Whitman College's Wallula Gap Biological Station in the Columbia Basin of Washington (46° 00' N, 118° 54' W, 360-420 m elevation). Spring Gulch runs primarily east to west, and so most hillsides face either approximately north or south. On the north-facing slopes there is no exposed bedrock and the silty loam soil is free of rocks and appears >2 m deep. The soil is similarly textured on south-facing slopes and is often >2m deep, but in places is shallower, and bedrock is exposed rarely. However, there was no exposed bedrock on our monitoring locations. North-facing slopes are primarily vegetated by perennial bunchgrasses (besides *P. spicata*, also *Festuca idahoensis*, several species of *Poa*, and others) though rabbitbrush (*Ericameria nauseosa* and *Chrysothamnus viscidiflorus*) is common. Big sagebrush (*Artemisia tridentata*) is rare on both slopes due to recent (2007, 2011, 2015) and presumably less-recent fires. South-facing slopes are dominated by annuals, especially cheatgrass (*Bromus tectorum*), annual fescue (*Vulpia sp*.), and yellow star-thistle (*Centaurea solstitialis*), in most places. However, bluebunch wheatgrass stands ranging from 0.03 ha to 0.17 ha are scattered across the south-facing slopes and cover approximately 5-10% of the surface of these hillsides. Within these south-facing stands of bluebunch wheatgrass, cheatgrass is less common and yellow star-thistle is rare. Only one other large bunchgrass, needle and thread grass (*Hesperostipa comata*), occurs on south-facing slopes, and it is much less common than bluebunch wheatgrass. When measured over approximately 6 months in 2009, soil temperatures at this site were consistently higher on south-facing slopes than on north-facing slopes (Table S1), and soil moisture was consistently higher on north-facing slopes to a depth of 30 cm (Table S2).

In the spring of 2011, we established 14 monitoring sites for bluebunch wheatgrass, seven on north-facing slopes and seven on south-facing slopes. We selected sites where bluebunch wheatgrass was growing. We attempted to locate sites relatively far from other sites on the same slope, and we were able to keep all sites > 140 m distant from the next nearest except for one pair of sites on the south face which we located 20 m apart because of the rarity of bluebunch wheatgrass stands on these slopes (mean distance to adjacent sites on the same slope = 180 ± 75 m (SD), min = 20 m, max = 306 m). Each site was 10 m long and 1 m wide and marked at the corners by rebar stakes. We designated 1 x 1 m sampling areas every other meter within each site, such that sites contained 5 non-adjacent sampling areas. During 2011 and 2012, we experimented with methods of placing the 1 x 1 m quadrats, and methods of relocating individual plants. In 2013, we settled on marking each corner of each 1x1 m quadrat with rebar stakes and marking each bluebunch wheatgrass plant with a small uniquely numbered metal tag held in place by a nail in the soil adjacent to the plant. We used a 1x1 m quadrat consisting of a metal frame with wire forming a grid of 10 x 10 cm cells. We anchored this quadrat with the permanent rebar stakes at each visit to the plot, and used the grid of 10 x 10 cm cells to construct and update maps of the bluebunch wheatgrass plants within the sampling area.

From 2013 through 2018, a group of two or three researchers visited each plot at least once between late May and late June. During that visit, we searched for every bluebunch wheatgrass plant we could find throughout each plot as well as specifically for bluebunch individuals that had been tagged and mapped on previous visits. We marked any new plants we discovered, and we removed tags for any plants that had disappeared. Bluebunch wheatgrass at our site is entirely cespitose, and so all the stems of a given individual grow in close proximity to each other. Typically, the separation between individuals is clear, but when the distinction between individuals was unclear we likely sometimes lumped two or more individuals together as a single individual. Unfortunately we had no way to confirm plant identity without causing serious harm to the plant. For each bluebunch plant we located, we noted survival, counted the number of living culms and the subset of culms that were flowering (spikes). Both of these counts were highly repeatable (culms: R = 0.88, Fig. S1; spikes: R = 0.88, Fig. S2, See supplementary materials for further details). For all flowering individuals, we haphazardly selected five spikes on which to count the number of spikelets. If there were fewer than five spikes, we counted the spikelets on all spikes. Average number of spikelets per spike was moderately repeatable (R = 0.64, Fig S3). We also measured the height of the tallest culm, but because this measurement changes over the course of our study season due to growth and damage to plants, we decided not to use this measurement in our analyses. Flowering bluebunch wheatgrass is not easily confused with other species at our site, but observers on this project occasionally misidentified small non-flowering individuals of other bunchgrass species as bluebunch wheatgrass. We therefore chose to include only individuals that were flowering, or had been observed to flower in a past or future year, in our analyses to minimize the chance of misidentification errors. As a result we do not have direct, reliable estimates of the seed to seedling transition from our observation plots. Finally, observers occasional failed to observe a plant that was present. In plots visited twice to assess sampling reliability, 6.2% of plants detected in at least one of two visits were not detected on the other visit (supplementary materials). Therefore, we only noted mortality when an individual was absent for 2 or more years, and thus no survival data are available from the final transition and we only estimate vital rates for four transitions over six years.

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

Population Modeling

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

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

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 describing the transition of size *x* individuals to size *y*. In our case plant size in *ln(Number of Culms)*. $K(y, x, t, a)$ itself is made up of vital rate functions,

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

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

Vital rate modeling

We estimated vital rates with generalized linear mixed effect models in a Bayesian framework using Stan and the ‘rstan’ package (Stan Development Team 2020). We parameterized $G(y, x, t, a)$ as a normal kernel, fit to the data with a normal likelihood where the kernel parameters were fit using measured size transitions as

$$G(y, x, t, a) = Normal(y|\mu_g(x, t, a), \sigma^2)$$

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

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 an indicator variable for aspect, *I=1* when the aspect is south-facing and 0 when north-facing. $\gamma_g(t)$ is a random effect intercept that varies by year, $\delta_g(t)$ random effect for aspect that also varies by year, and β_1 and β_2 are fixed effects for size and aspect, respectively.

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

$$logit(s(x, t, a)) = \beta_3 + \beta_4 x + \beta_5 I(a) + \gamma_s(t) + \delta_s(t)\, I(a)$$

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

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

$$F(x, t, a) = Spike(x, t, a) * Spikelets(t, a) * Seeds$$

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

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

$$Seeds = \beta_{11}$$

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

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

Model Analyses

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

Additionally we inferred possible seed to seedling recruitment rates using two approaches. First, we determined how λ_t varied across a range of recruitment rates. Second we identified the absolute recruitment that would be needed for both the northern and southern aspects to achieve $\lambda_t = 1$ (i.e. a stable population) in each year by calculating λ_t across a range of recruitment rates (seed transitioning to plants in the first size class). To determine confidence intervals for recruitment rates, we iterated this process over the entire posterior MCMC chains for all vital rates.

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

Results

Vital Rates

Model results indicate that survival and reproductive output differed between north and south aspects, while individual growth did not (Table 1, Fig. 1-2). Both the number of spikes per plant and the number of spikelets per spike were higher on south-facing slope, although the posterior 95% CI for β_8 (average difference in spikes per plant on south slopes) did overlap with zero. Survival of existing, established plants was lower on south-facing slopes. Differences in survival between aspects were most notable in small plants (<20 culms), where the smallest plants on south-facing slopes show about 50% annual survival and the smallest plants on north-facing slopes showed 70 to 80% survival. However, large plants survival approached 100% on both aspects (Fig. 1). Although spikes per plant also increased with size, it was in large plants where we observed the greatest difference between aspects. On average, large plants produced about 15-25 more spikes per plant on south-facing aspects than north aspects. Yet, greater reproductive output on south facing slopes did not occur in all years with individuals on north facing aspects producing slightly more spikes in 1 of the 4 years (Fig. 2). Growth declined on average with size, but showed no consistent differences across sites. Vital rates also varied substantially from year to year. Most notably, the number of spikes produced per plant tripled on average from 2014-2015 to 2015-2016 (Fig. 3).

Population growth rate and Recruitment

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

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

Discussion

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

Our observation that changing slope position influenced different demographic variables in different ways is consistent with other recent work on small-scale variability in demographic rates. For example, Oldfather and Acklery (2019) found notable differences in demographic rates including survival and reproductive output across microclimate conditions. Similarly other work has found declines in survival with changing slope and aspect, most notably lower survival on steeper, drier slopes (Dullinger et al. 2004, Nicolè et al. 2011). Still, in some systems different demographic rates between sites may not lead to different population growth trends if there is compensation among vital rates (Oldfather and Ackery 2019). However, in our system we think this is unlikely despite our inability to compare population growth rates directly between aspects. As we describe below, recruitment rates would likely need to be higher on south-facing slopes than on north-facing slopes to maintain a stable population, but we have reason to expect that bluebunch wheatgrass actually recruits at lower rates on south-facing slopes.

Although we lack precise estimates of recruitment rate, we do have evidence that changes in recruitment rates could strongly impact population growth. This insight helps us understand current differences in abundance of bluebunch wheatgrass at our site and has important implications for the future of these populations. When we assumed all seed led to new recruits (i.e. the recruitment rate was 1), estimates of population growth were notably higher for south-facing slopes than north. But, assuming all seed becomes new recruits is unrealistic, ongoing experimental work suggests recruitment rates are actually substantially lower on south-facing slopes, where bluebunch wheatgrass is also much less abundant and survival of small plants is lower. Further, based on models in which we systematically varied recruitment rate, point estimates for the level of recruitment needed to maintain stable populations on south-facing slopes were higher in three of four years than the level of recruitment needed on north-facing slopes, though estimates for south-facing slopes were highly uncertain. What was clearer from these models, however, is that differences in recruitment rates between slopes could be sufficient to stabilize population growth on the two slopes, or even drop population growth on south-facing slopes below that of north-facing slopes. For example, when we increased recruitment rates three-fold from 0.005 to 0.015 recruits per seed in our models, this increased population growth estimates by up to 50% (depending on year and aspect). Given that our ongoing experimental work suggests that the difference in actual recruitment rate could be 10-fold or larger between aspects, the impact of recruitment rate on population growth could be substantial. This sort of sensitivity of population growth rates to recruitment is consistent with previous work which has established recruitment as a critical process controlling the recovery and restoration of dryland plants and perennial bunch grasses (James et al. 2011), and our estimates of recruitment rates required to maintain stable population are consistent with published rates. For example, James et al. (2019) found consistent probabilities of transitioning from seed to establishment of ~0.04. Boyd and James (2013) found similar, but more variable rates. They estimated that germination varied from 20-80%, emergence of these germinates was 5-20%, and initial establishment of those that emerged was 20-80%. This would yield recruitment rates ranging from 0.002 to 0.128, which correspond well with our estimated range from 0.001-0.01 to maintain stable populations on average. Given this possibility for substantial variability in recruitment rates, and the likely sensitivity of recruitment in semi-arid systems to increasingly hotter, drier conditions (James et al. 2011), and invasion of non-native species (Aguirre and Johnson 1991), we expect that variation in recruitment will increasingly impact demography and long-term population persistence of bluebunch wheatgrass in these systems.

Although we do not have detailed measurements of differences in temperature and soil moisture conditions associated with each sample location, other data (Table S1 and S2) and ongoing experiments from this site as well as other studies indicate that increased temperatures and reduced soil moisture availability, driven by increased solar radiation, may be responsible for vital rate differences. Ongoing experiments performed at this site indicate that when incoming solar radiation is reduced on south-facing slopes (using shade cloth), temperatures decrease and germination and survival of young bluebunch wheatgrass plants increase dramatically (TH Parker unpublished data). Additional studies have also indicated that soil moisture and temperature conditions can substantially alter vital rates of bluebunch wheatgrass. For example, James et al. (2019) found that warmer soil temperatures and reduced precipitation limit the germination, emergence, and early survival of steppe bunchgrasses including bluebunch wheatgrass. Similarly, in a system where snowmelt is an important source of moisture, greater snowpack is associated with greater survival of bluebunch wheatgrass (Dalgleish et al. 2011). Our finding that plot level demographic performance may be quite variable across microsites, even in nearby locations that share similar areal climate conditions, suggests that quantifying microsite climate variation at the scale of plots could provide exciting opportunities to expand our understanding of the relationships between climate and demographic performance across landscapes. Even in the absence of detailed field measurements, models that scale areal climate conditions to local microclimates based on topography are an exciting possibility (Zellweger et al. 2019).

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

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

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

One of the most striking features of our study site to the casual observer is the lower density of perennial plants, especially bunchgrasses, on south-facing slopes relative to north-facing slopes, and so the differences we observed in bunchgrass demographic rates between these slopes is not a surprise. However, because we lack detailed measurements of recruitment we remain uncertain whether these differences in population density result from ongoing differences in population growth rate between the two slopes. What we do know, however, is that the hotter, drier conditions on south-facing slopes are associated with reduced survival of small plants on these slopes, and that experimental reduction of temperature on south-facing slopes dramatically increases seedling emergence and survival. Further, our models demonstrate that plausibly low levels of recruitment on south-facing slopes could cause the bluebunch wheatgrass population on those slopes to decline. These observations, combined with published observations that recruitment limits other populations of plants in semi-arid rangelands (James et al. 2011), leads us to hypothesize that lower survival of small individuals coupled with recruitment limitation may be leading to a decline of bluebunch wheatgrass on south-facing slopes and help explain the lower density of bluebunch wheatgrass on these slopes. Further, given predictions of increasingly warm and dry conditions in the North American steppe regions with climate change (Bradford et al. 2020), we hypothesize that the population decline will worsen, and that as north-facing slopes warm bluebunch wheatgrass populations vital rates there may come to resemble what we currently find on south facing slopes. Future work should focus on better understanding plant demography in steppe, bunchgrass systems, especially the role of temperature and moisture in influencing recruitment.

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Author Contributions

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

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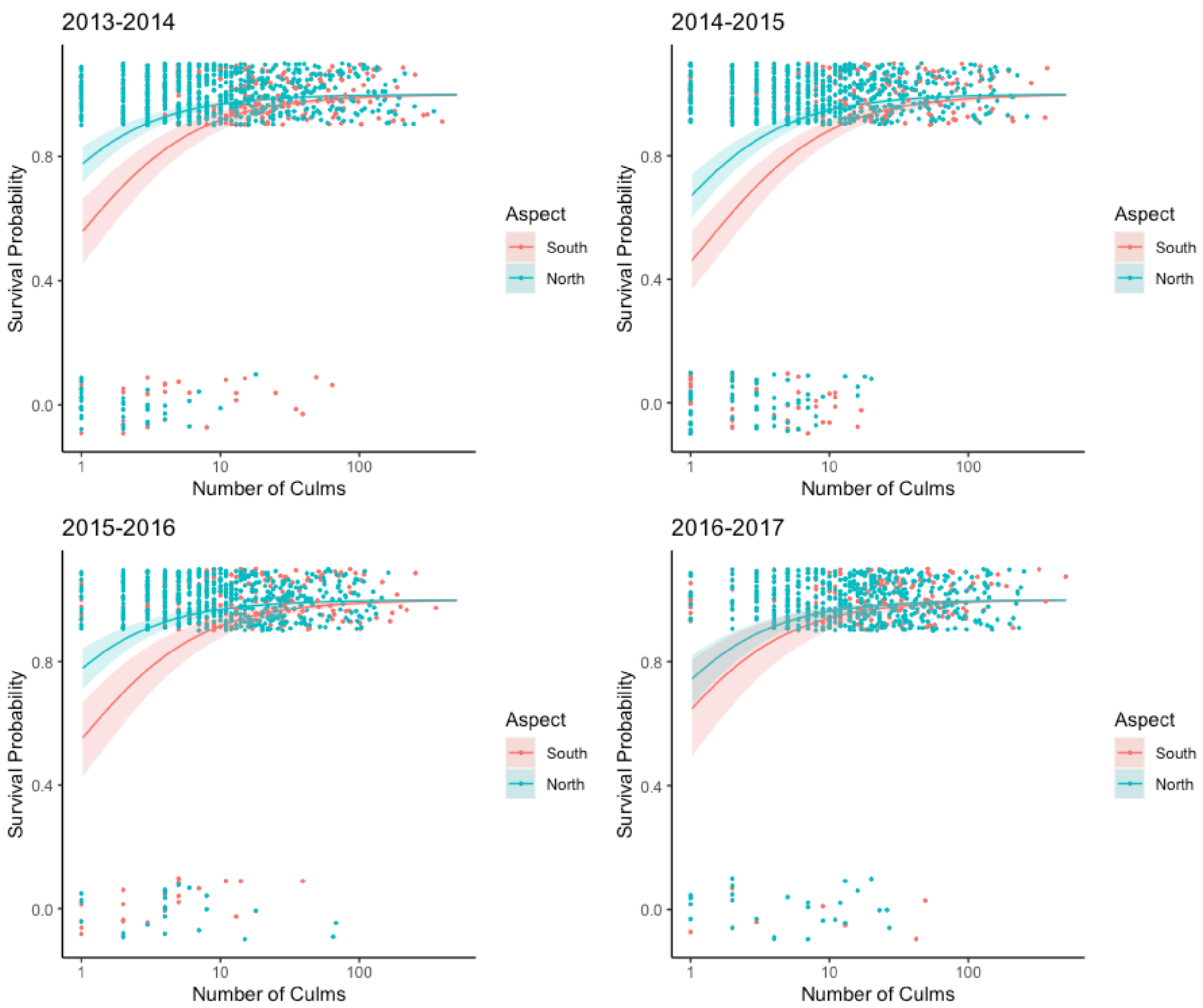

Fig 1. Survival probability of bluebunch wheatgrass on north and south aspects across all annual transitions at the Wallula Gap Biological Station, WA, USA. Points indicate measured field data. Lines represent posterior mean estimate for the average individual survival, with 95% CI shaded region. For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

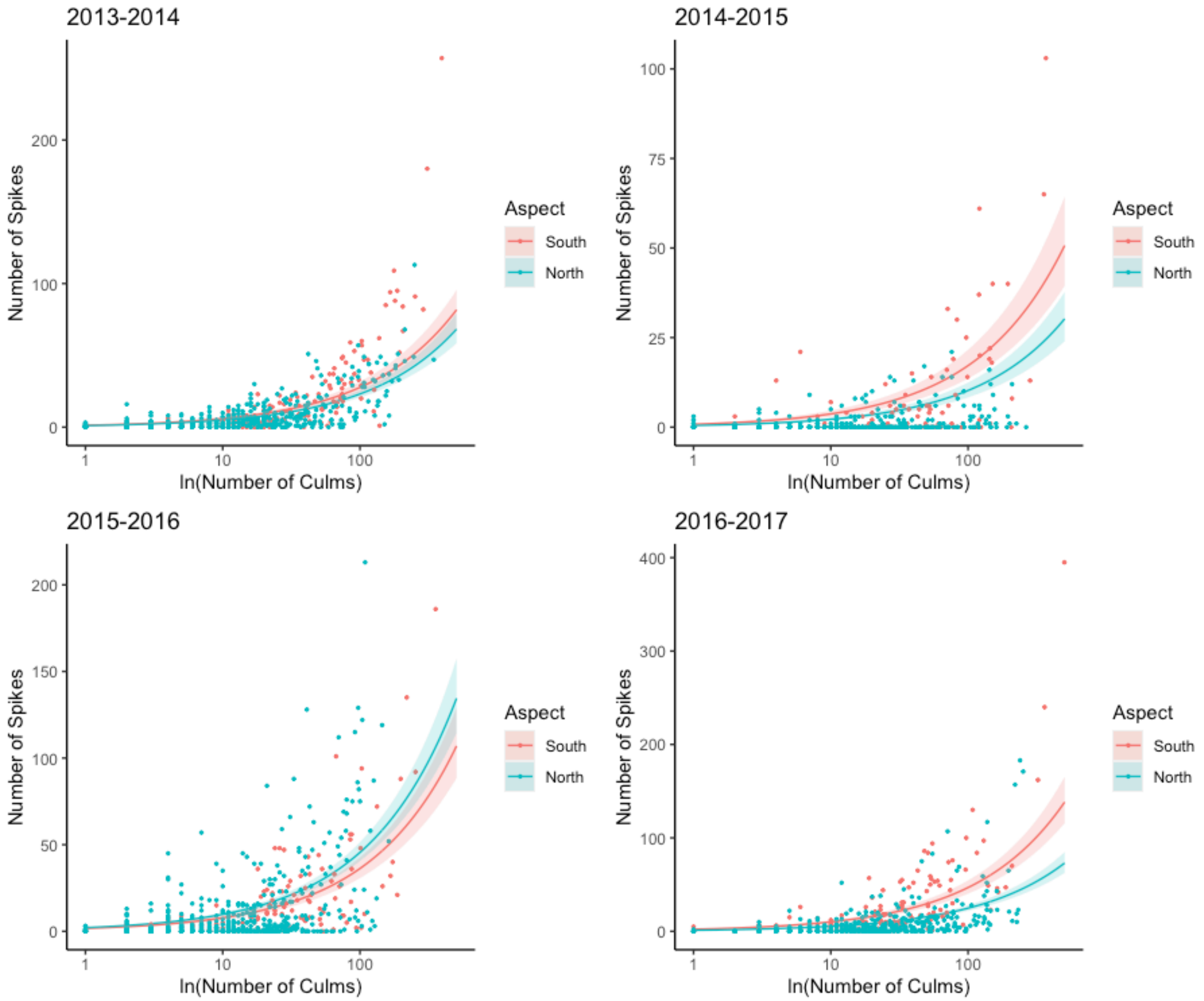

Fig 2. Spikes produced per bluebunch wheatgrass plant across all annual transitions on north and south aspects at the Wallula Gap Biological Station, WA, USA. Points indicate measured field data. Lines represent posterior mean estimate for the average individual spikes produced, with 95% CI shaded region.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

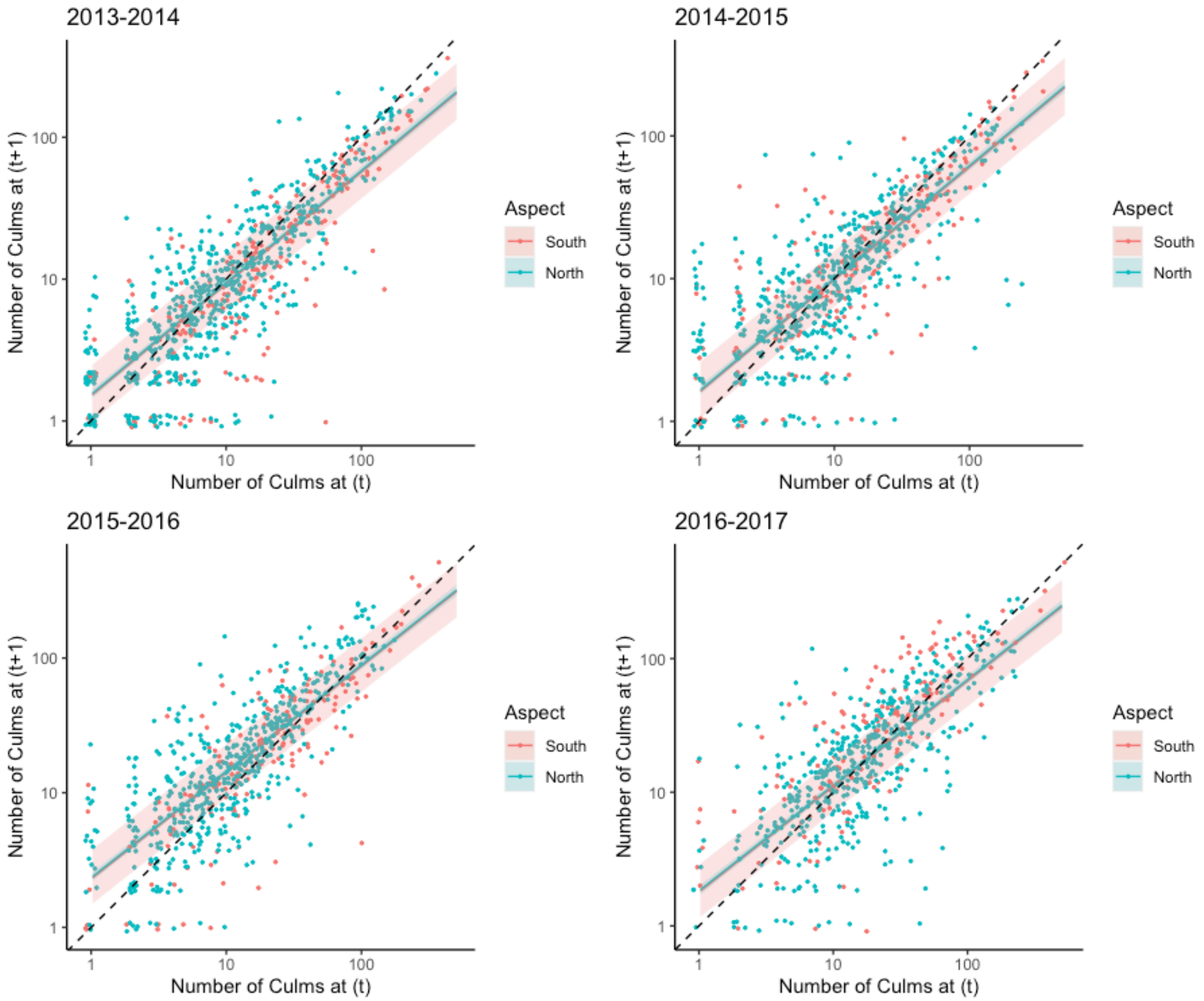

Fig 3. Size changes for bluebunch wheatgrass on north and south aspects at the Wallula Gap Biological Station, WA, USA across all annual transitions. Points indicate measured field data. Colored lines represent posterior mean estimate for the average individual size change, with 95% CI shaded region.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

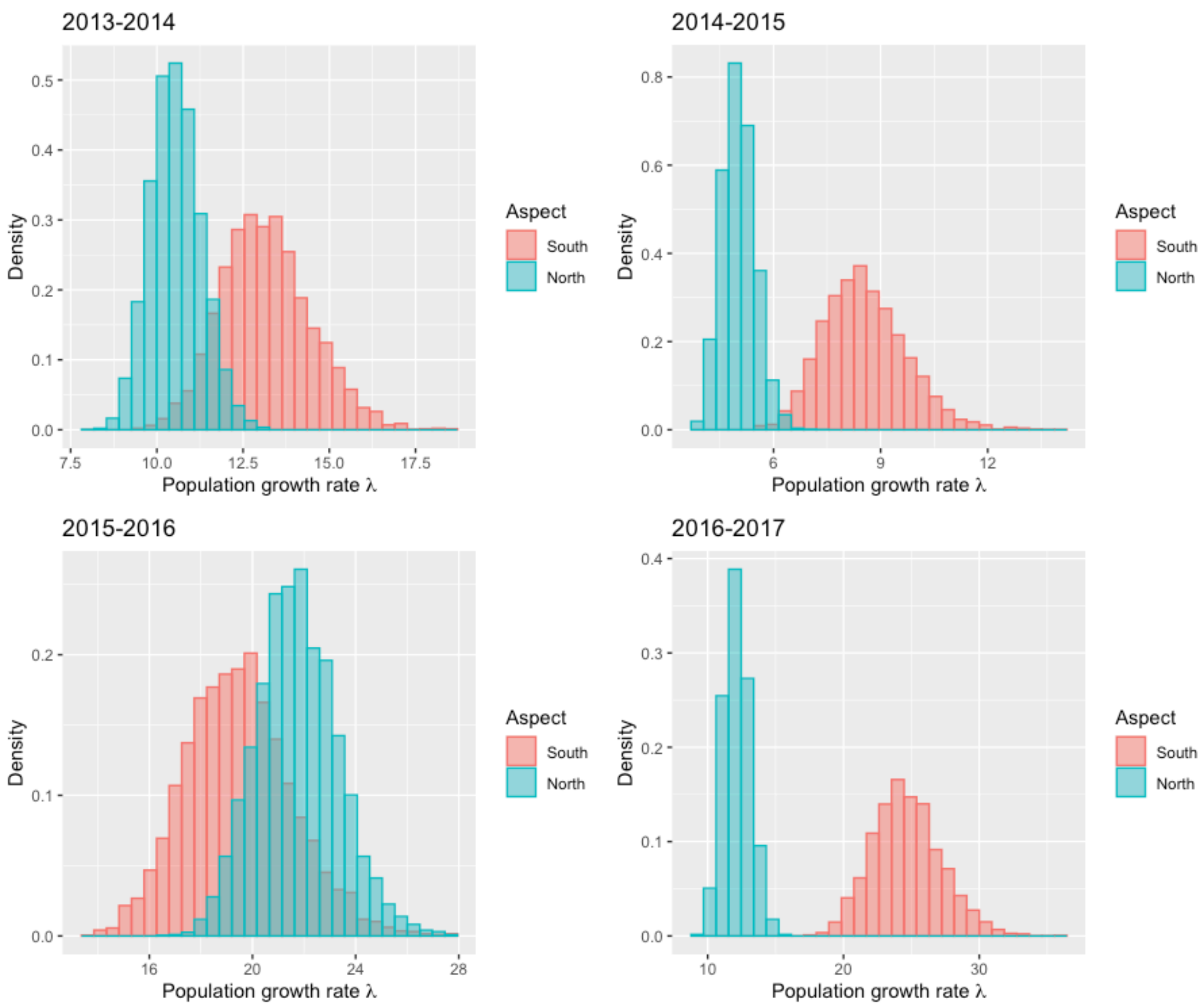

Fig 4. Posterior distributions for estimated population growth rate on north and south-facing slopes if we assume that every seed becomes 1 plant (i.e. there is no explicit germination and establishment rate) for bluebunch wheatgrass at the Wallula Gap Biological Station, WA, USA. Each panel corresponds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

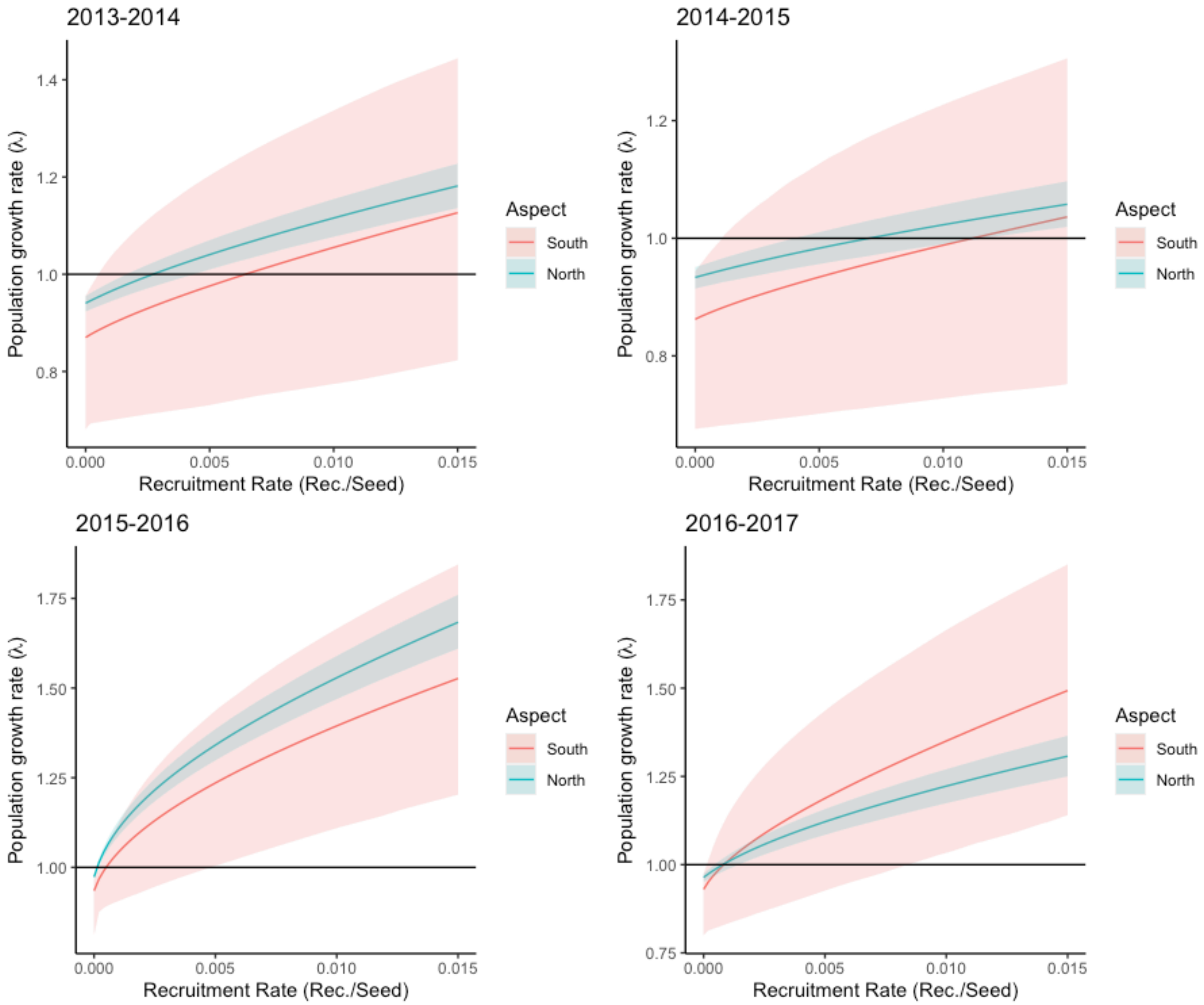

Fig 5. Estimated population growth rate in each year from a range of recruitment rates for bluebunch wheatgrass on north and south-facing slopes at the Wallula Gap Biological Station, WA, USA. Lines represent posterior mean estimate for the recruitment rate (new recruits per seed), with 95% CI shaded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

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

Parameter	**Mean**	**2.5%**	**97.5%**
Surv: $\boldsymbol{\beta_5}$	**-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: $\boldsymbol{\beta_2}$	**-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: $\boldsymbol{\beta_8}$	**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: $\boldsymbol{\beta_{10}}$	**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