Solar radiation drives potential demographic collapse in a perennial bunchgrass via dramatically reduced seedling establishment

Timothy H. Parker[a,d]
Alex Gerber[a]
Erin Campbell[a]
Molly Simonson[a]
Robert K. Shriver[b]
Lyman Persico[c]

[a] Biology Department, Whitman College, Walla Walla, WA 99362 USA
[b] Department of Natural Resources and Environmental Sciences, University of Nevada, Reno, Nevada 89557 USA
[c] Geology Department, Whitman College, Walla Walla, WA 99362 USA
[d] Corresponding author: parkerth@whitman.edu

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Abstract

Many perennial plants in semi-arid rangelands have experienced population declines, and understanding the ecological and demographic processes behind these declines is important to slowing or reversing them. Although anthropogenic disturbances drive many declines, other sorts of environmental variability, such as the differences in solar radiation with aspect, may impact population success locally. We experimentally assessed the role of solar radiation in driving an apparent decline in a common perennial bunchgrass, bluebunch wheatgrass (*Pseudoroegneria spicata*), on south-facing slopes at a site in the Columbia Basin of North America. Across three separate experiments on south-facing slopes, we observed dramatically (5 to 36 times) higher seedling success in plots shaded to approximate the solar radiation of north-facing slopes relative to adjacent open (unshaded) plots. When we applied the rates of seedling success from these experiments to demographic models from this site, we found that seedling success in unshaded plots was often too low to allow a stable population on south-facing slopes, but that seedling success in shaded plots was often high enough to allow a stable or increasing population on north-facing slopes. We originally hypothesized that the primary mechanism driving this effect was water stress caused by greater evaporation from hotter open plots. However, despite soils in open plots being consistently hotter than soils in shaded plots, we did not observe a clear pattern of greater soil moisture in shaded plots. Therefore, it appears that higher solar radiation or higher temperatures on south-facing slopes may be sufficient to dramatically reduce seedling survival, and that the higher density of bluebunch wheatgrass on north-facing slopes relative to south-facings slopes may be driven primarily by this low survival of seedlings. As climate warms, the reduced seedling survival that threatens our bluebunch wheatgrass population may be expected to threaten many other species of perennials in similar rangelands.

Introduction

Perennial plants, including grasses, forbs, and shrubs, have declined dramatically in some semi-arid rangeland ecosystems over the past century or more, especially where precipitation falls mostly in winter, and these declines have been of great concern to rangeland managers, ranchers, and conservationists. Many of these declines in perennials are well understood at certain spatial scales, and can often be attributed to disturbances such as increasing fire frequency, over-grazing, herbicide use, and plowing (O'Connor, 1991; Knapp, 1996; Knick & Rotenberry, 1997; DiTomaso, 2000; Keeley *et al.*, 2003; Keeley, 2006; Kulmatiski, 2006; Young & Clements, 2007; Davies *et al.*, 2011; Svejcar *et al.*, 2017). However, perennial success can also vary substantially within a landscape even when disturbance history is similar throughout (Sternberg & Shoshany, 2001; Shriver *et al.*, 2021). Understanding what drives variability in success of perennial rangeland plants in the absence of differences in disturbance is important for understanding how these communities will continue to respond to ongoing environmental change and how management practices might be adjusted.

One of the most striking drivers of variability in the success of plants within some landscapes is aspect (Armesto & Martinez, 1978; Nobel & Linton, 1997; Sternberg & Shoshany, 2001; Ackerly *et al.*, 2002; Scherrer & Körner, 2010; Shriver *et al.*, 2021). In the Northern Hemisphere, south-facing slopes receive more solar radiation than north-facing slopes, and thus are typically the warmest and driest sites on the landscape (Nobel & Linton, 1997; Bennie *et al.*, 2008). In rangelands of Northwestern North America, these south-facing slopes often have lower perennial plant biomass and more invasive annual cover than do north-facing slopes (Harrison, 1999; Gelbard & Harrison, 2003; Shriver *et al.*, 2021). The lower biomass of perennials may result directly from abiotic effects on the demographic rates of perennials (Shriver *et al.*, 2021), but may also be influenced by competition from invasive annuals (Aguirre & Johnson, 1991). The demographic impacts of competition from annuals are expected to primarily impact young perennials that are not yet established (Aguirre & Johnson, 1991), but abiotic stresses could impact an array of demographic rates from seedling establishment to growth, reproduction, and survival at any stage (Dalgleish *et al.*, 2011; James *et al.*, 2011; James *et al.*, 2019; Shriver *et al.*, 2021).

The role of aspect in driving population trajectories in perennial plants in semi-arid landscapes is important not only because variation in aspect is common, but because ongoing climate change will impact different aspects differently (Bennie *et al.*, 2008; Scherrer & Körner, 2010; Maclean *et al.*, 2017). South-facing hillsides in the Northern Hemisphere, already hotter and drier than north-facing hillsides, are likely to become even hotter (Ashcroft *et al.*, 2009; Dobrowski, 2011; Maclean *et al.*, 2017), and quite possibly to develop abiotic conditions without a current local analog (Ackerly *et al.*, 2010). Perennial populations that are marginally persistent on south-facing slopes at this time due to heat or drought may be unlikely to persist on these slopes in a warmer world. The loss of perennial plants on south-facing hillsides could have long-term implications for soil persistence and carrying capacity (Persico *et al.*, 2021). Conditions on north-facing slopes may also deteriorate for some plant species due to warming, even dramatically, though the lower levels of solar radiation on those slopes may limit the severity of the impact and provide local microclimate refugia (Scherrer & Körner, 2010; Dobrowski, 2011; Maclean *et al.*, 2017).

Bluebunch wheatgrass (*Pseudoroegneria spicata*) is a large perennial bunchgrass with a wide distribution in the semi-arid rangelands of the interior of Western North America, but this species has declined dramatically in concert with changing land use and the spread of invasive annual weeds (Harris, 1967; Pyke, 1990; Rodhouse *et al.*, 2014; Shriver *et al.*, 2021). At our low-elevation study site in the Columbia Basin of Washington State, bluebunch wheatgrass is one of the most abundant large bunchgrasses, and the only large bunchgrass common on both north and south-facing slopes (Shriver *et al.*, 2021). However, bluebunch wheatgrass may be declining on south-facing slopes and is already much less common on south-facing than north-facing slopes. Further, north and south-facing populations differ in important components of demography (Shriver *et al.*, 2021). For instance, among established plants, small individuals experience somewhat lower annual survival rates on south-facings slopes than on north-facing slopes, but average size of established plants is larger on south-facing slopes, and reproductive output averages higher on south-facing slopes, even when controlling for plant size (Shriver *et al.*, 2021). However, these observed demographic differences may not be sufficient to explain the dramatic difference in population densities between north and south-facing slopes. Instead, it may be that differences in seed and seedling success due to differences in temperature and moisture drive the observed differences in abundance between the aspects. Work from other sites is consistent with this hypothesis. For instance, in a study of bluebunch wheatgrass spanning an extensive portion of the Great Basin (James *et al.*, 2019), warmer soil temperatures, as we find on south facing slopes at our site (Shriver *et al.*, 2021), were associated with reduced seed germination, and greater water stress was associated with reduced seedling survival (James *et al.*, 2019). Further, an experiment that reduced solar radiation through shading by both sagebrush and artificial means found that a 40% reduction in solar radiation, which is only modestly more than the annual difference in solar radiation between south and north-facing slopes at our site, reduced bluebunch wheatgrass seedling mortality (Huber-Sannwald & Pyke, 2005). Thus, further examination is merited of the role of solar radiation on north and south-facing slopes causing differences in seed and seedling success, and so driving demographic differences in our study population.

With the current project, we sought to evaluate the role of solar radiation in demographic differences in bluebunch wheatgrass populations between north and south-facing slopes at Wallula Gap Biological Station in the Columbia Basin. We hypothesized that higher solar radiation, and thus higher temperatures and lower soil moisture, on south-facing slopes drives reduced seed germination, seedling emergence, and seedling survival relative to north-facing slopes. If this hypothesis were correct, we predicted that experimentally shading locations on south-facing slopes to approximate annual rates of solar radiation on north-facing slopes would increase the number of surviving seedlings relative to open (unshaded) plots and that soil in shaded plots would be cooler and moister than soil in open plots. After seeing the results of these experiments, we also predicted that incorporating seed and seedling success rates from open plots in demographic models from the local unmanipulated bluebunch wheatgrass population on south-facing slopes would generate rates of population growth below replacement, but that using seed and seedling data from shaded plots in demographic models from bluebunch wheatgrass on north-facing slopes would indicate stable or growing populations.

Methods

We manipulated solar radiation with shading on steep south-facing 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). This site receives approximately 200-300 mm of precipitation annually (PRISM.Climate.Group, 2022), primarily between October and April. Spring Gulch runs mostly east to west, and so most hillsides face approximately north or south. In the areas where we established our experimental plots, the soil is a silty loam well over 1 m deep. North facing slopes in Spring Gulch are typically vegetated by perennial bunchgrasses (besides *P. spicata*, also *Festuca idahoensis*, *Poa secunda*, and others) though rabbitbrush (*Ericameria nauseosa* and *Chrysothamnus viscidiflorus*) is common. 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 less common than bluebunch wheatgrass.

In three separate experiments, we established shaded plots on south-facing slopes to reduce the solar radiation level to approximate, on an annual basis, the solar radiation level on north-facing slopes. In all three experiments, each shade plot was paired with an adjacent open (unshaded) control. Both shade and control structures were 2 x 2 m and enclosed by 1.5 m tall welded wire fence. In 2011, we used a digital elevation model to estimate the difference in solar radiation between north and south-facing slopes. At that time, we estimated that solar radiation on north-facing slopes at Spring Gulch is approximately 70% of solar radiation on south-facing slopes annually, and we based our experimental treatment on this value. Unfortunately, we lost those original analyses, but that provided an opportunity to re-run solar radiation analyses in more detail. When we ran new analyses, we found similar results, with an estimate that north-facing slopes receive approximately 40-70% of the solar radiation of south-facing slopes on an annual basis, and 50-80% of the solar radiation of south-facings slopes in June when rates of radiation are highest (Fig. 1, S1-S3). Thus, our shade treatments, which reduced solar radiation to approximately 70% of the values typical on south-facing slopes, approximates summer levels of north-facing slopes, and is less of a reduction than is typical in winter on north-facing slopes. Our treatment was therefore conservative and did not reduce solar radiation as much as the typical difference between north and south-facing slopes. To implement our shading treatment, we covered the top and the east, south, and west sides of each shade plot with shade cloth designed to reduce solar radiation by 40%. We cut holes removing ~20% of the shade cloth on top and on the side to allow wind to pass through and to prevent snow from building up on top. Accounting for these holes, the shade cloth reduced solar radiation to ~70% of the level on south-facing slopes. In practice, we reduced solar radiation by <30% because the holes in the shade cloth increased in size over time, rips formed, and material was lost.

In December 2011, we established six pairs of shade and open plots in areas with no established bluebunch wheatgrass plants within 10 m. Within each shade and open plot, we evenly scattered approximately 9600 bluebunch wheatgrass seeds, which we collected from south-facing bluebunch plants the previous July, in a 1 x 1 m square central plot in each shade and unshaded structure. The entire 2 x 2 m area contained no perennial plants. Before and after seeding, we raked the ground surface to improve seed-soil contact. We uniquely marked (with blue laboratory tape and marker pen) and mapped each bluebunch wheatgrass seedlings in late May 2012 and we visited again in late June of 2012, noting how many remained green and how many had turned brown and presumably died. We noted and mapped the live bluebunch plants again in June 2013. However, later examination of the data demonstrated that some of the plants that were recorded as brown and presumed dead in 2012 appeared to be alive at the time of 2013 survey. Thus, possibly we were not able to reliably identify which plants were dying in June, or our method of marking, which did not facilitate re-identification across years, led us to misidentify some plants in 2013 when relying only on the map for identification. Thus, we chose to use only count data, not individual seedling identity, in our analysis. It was not feasible for observers to remain blind to the hypotheses being tested by this or the following experiments.

In January 2018, we established six pairs of shade and open plots within established stands of bluebunch wheatgrass on south-facing slopes. We chose sites which allowed us to establish a 1 x 1 m survey area containing no existing bluebunch wheatgrass (or other perennial) plants in the center of the shade (or open) plot. We counted the number of bluebunch wheatgrass plants growing within the 1 x 1 m survey areas of these plots in June of 2018-2021 and July 2022. Further, we marked each seedling with a metal tag affixed to the ground with a long nail adjacent to the plant, and mapped the locations of seedlings on a grid in which the plot was divided into 100 10 cm x 10 cm squares.

In December 2018, we initiated another shading experiment by constructing eight pairs of shade and open plots in areas with no established bluebunch wheatgrass plants within 10 m. This experiment was identical to the one established in 2011 except that we scattered approximately 12,500 bluebunch wheatgrass seeds per plot. In May of 2019, prior to gathering data for this project, we pre-registered our data gathering and analysis plans on the Open Science Framework to maximize transparency (https://doi.org/10.17605/OSF.IO/CGXN4). We counted the number of bluebunch wheatgrass seedlings in late May 2019, June 2020, and June 2021. We deviated from the pre-registration in two notable ways. We did not mark individual plants with metal tags, and we visited the plots only once per summer instead of twice. We made these decisions because (a) the large number of germinated seedlings would have made tagging very time-consuming and imprecise (due to proximity of seedlings), and (b) examination of the data from the 2011 experiment showed that determining survival of individuals seedlings within a summer was not reliable.

Because we hypothesized that shade would influence seed and seedling success via temperature and moisture, we measured soil temperature and soil moisture in shade and open plots on multiple occasions from 2016 – 2021. We measured soil temperature (°C) by inserting a digital thermometer 10 cm into the soil in the plot and waiting until the temperature reading stabilized. To measure soil moisture, we took 30cm soil cores from just outside the 1m-by-1m quadrats, but within the fenced and shaded plots. We divided soil cores into 0-10cm, 10-20cm, and 20-30cm depths and sealed them in plastic bags in the field. We then weighed the soil before and after dehydrating in an oven for 24 hours at 100°C. We used the evaporated proportion of the soil sample by mass as our moisture measurement. We always sampled temperature and moisture in the field between 10:00 am and 2:00 pm and sampled paired plots within 5 minutes of each other. We measured soil moisture and temperature in 2016 and 2017 in each of the 12 plots from the first seeding experiment in early season (late May – early June), mid-season (mid to late June), and late season (July). In 2018, we measured soil moisture and temperature in the unseeded plots, in 2019 we measured soil moisture in the second set of experimentally seeded plots, and in 2020 and 2021, we measured soil temperature in the second set of experimentally seeded plots. In 2018 – 2021, we measured moisture and/or temperature only once per year.

Data analysis

For experimentally seeded plots, we compared the success of germination and seedling survival on a per-seed or per-seedling basis using generalized linear mixed models with binomial error in R (version 4.1.1, package lme4 version 1.1-28). We generated treatment means with the emmeans package (version 1.7.2). We analyzed the first experiment (initiated in 2011) separately from the second experiment (initiated in 2018). For comparisons of success on a per-seed basis, for each year of seedling counts, our response variables consisted of a comparison of the number of seedlings observed during the count that year to the number of seeds that did not produce a seedling detectable in that year. The number of seeds that did not produce a seedling was simply the number of seedlings detected in current year subtracted from the estimated number of seeds planted. For comparisons of success on a per-seedling basis, for each year of seedling counts after the first year, our response variables consisted of a comparison of the number of seedlings observed during the count that year to the number of seedlings observed in the previous year that did not survive to the current year. In these cases, the number of seedlings failing to survive was the number of seedlings detected in the current year subtracted from the number of seedlings counted in the prior year. In the assessment of the survival of 2019 seedlings to 2020, in one plot, the number of seedlings tallied in 2020 exceeded the number of seedlings tallied in 2019. We assume that this was a counting error, but we cannot rule out the possibility that some seeds planted in 2018 did not germinate until the 2019-2020 growing season. Regardless of the cause, we excluded the plot pair with the higher seedling count in the second year to allow our binomial GLM to run. Predictor variables in these analyses included a fixed effect of treatment (shaded vs. unshaded) and a random effect of plot pair (since each shaded plot was paired with a nearby unshaded plot).

For the unseeded plots (plots with no seeds added), we did not know the number of seeds falling in each plot, and so we used a count of seedlings present as the response variable in a series of generalized linear (mixed) models. We first attempted to analyze the number of new seedlings detected in each year in a single model with negative binomial error including all years in which we accounted for repeated observations in each plot with random effects (with plot identity nested within treatment) (R version 4.1.1, package lme4 version 1.1-28). However, this model did not converge, and a simpler model excluding the nested random effect, but retaining a random effect of plot pair, also did not converge. Therefore, we ran separate models for each year without a random effect of plot pair. In these models, the number of new seedlings detected in that year was the response variable and the shade treatment was the fixed effect. We attempted to run each model with negative binomial error, but two models (2018 and 2022) would not run without errors, and so in those two cases, we used Poisson error. We also ran a single model with the total number of surviving seedlings (regardless of germination year) in the fifth year (2022) as the response variable with negative binomial error. We generated treatment means with the emmeans package (version 1.7.2).

We analyzed the temperature and moisture data using linear mixed effects models (R version 4.1.1, package lme4 version 1.1-28). Since we sometimes measured temperature and moisture multiple occasions in a single season, over which duration we expected temperature and moisture to be changing (between May and July), we assigned each sample to one of three time periods “late May, early June,” “mid to late June,” and “July.” Some years did not contain data from some time periods. For both temperature and moisture, we first attempted to run relatively complex models that included all measurements and multiple random effects to account for structure in the data and multiple measurements per site and year. However, these complex models had problems with fit and were not suitable for inference. Therefore, for temperature data, we conducted a separate analysis for each time period in each year. For moisture, which was measured at three separate depths, analyses were further divided by depth category. In these analyses, treatment (shade vs open) was the fixed effect and plot pair was a random effect. One of the nine temperature analyses had a problem with fit and thus did not produce reliable results, and nine of 24 moisture analyses had a problem with fit.

Because of substantial variability in results among our analyses of soil moisture, we conducted a *post hoc* meta-analysis to generate an average effect size. We included the effects from reliable models (n = 15) of shade treatment on soil moisture, estimated as Hedge’s D. We conducted a random-effects meta-analysis with R package Metafor (R version 4.1.1, Metafor version 3.8-1) and included season and depth as additional random effects.

For both our seed count data and our temperature and moisture data, we calculated multiple p-values and thus no single p-value should be interpreted in isolation. We did not correct for multiple comparisons because we did not consider individual p-values as valid tests of our overall hypotheses and we did not use our p-values for dichotomous null hypothesis testing. Instead, we used p-values here as continuously varying evidence regarding clarity of effects. Further, we looked for consistency among p-values as further evidence of clarity of effect (Amrhein *et al.*, 2017).

Finally, we conducted a series of post hoc analyses that incorporated the values from our seeded experiments into previously constructed demographic models of bluebunch wheatgrass at our study site (Shriver *et al.*, 2021). These earlier demographic models used size-structured demographic models to compare vital rates (Easterling et al. 2000) between unmanipulated populations on north and south-facing slopes across four different annual transitions and then vital rates were incorporated into an integral projection model to explore how these rates influenced growth of our study populations. The estimates of vital rates were generated using Bayesian generalized linear mixed models with Stan and the 'rstan' package (Stan Development Team 2020). For details of the original demographic models, consult Shriver et al. (2021). When constructing these original models, there was insufficient data on seed-to-seedling transitions, and so Shriver et al. modeled a range of plausible seed-to-seedling transition values and, in so doing, generated a range of model estimates of annual population growth (λ) (Figure 5 in Shriver *et al.*, 2021). For this current paper, we refined the parameterization of these demographic models using data from our shade experiments. To accomplish this, we adjusted the integral projection models to incorporate the seed-to-seedling transition as detected in the first spring of a plant's life, and the survival of seedlings from that first spring to the second spring, which we assume is primarily influenced by the drought of the first summer. To accomplish this, we added a discrete class, first year plants, to our integral projection model. Plants entering the first-year class were composed of the total seed production of all plant in the population multiplied by the recruitment rate. The recruitment rate was calculated as the fraction of seeds sown in the experimental plots that germinated and survived to the first census. Plants in the first-year class then entered the size-based portion of our structured population model based on the survival rates observed from year 1 to 2 in experimental plots, and assuming the growth rates of first year plants is analogous to the smallest plants in the size based model. In doing this, we assume that a seedling in its first year is qualitatively different from a seedling in the following year in its ability to survive summer drought because seedlings in the first year will have smaller root systems on average, even if matched for stem number, the measure of plant size in the demographic models. We parameterized each of our eight demographic models (4 annual transitions X 2 aspects) multiple times, (a) all models with estimates from the shaded plots from the first experiment, (b) all models with estimates from the open plots from the first experiment, (c) the south-facing population with estimates from open plots and the north-facing population with estimates from shaded plots, all from the first experiment, and (d) the south-facing population with estimates from open plots and the north-facing population with estimates from shaded plots, all from the second seeded experiment. With these different model parameterizations, we generated estimates of population growth (λ) ranging from the most favorable seedling environment we observed (highest survival in shaded plots) to the least favorable (lowest survival in unshaded plots). Population growth was calculated as the dominant eigenvalues of the structured population model.

Data and code from our analyses are available at https://doi.org/10.17605/OSF.IO/CE7NS.

Results:

Shading on south-facing slopes dramatically increased seedling success relative to unshaded control plots. In the two experimentally-seeded scenarios, the probability of a seed having germinated and survived into a second growing season were between 5 and 21 times higher in shaded plots compared to unshaded plots (Tables 1, S1, Fig 2 - 4). A modest portion of this difference could be attributable to seed germination or early seedling success; the probability of a seed having germinated and the seedling having emerged and survived until June of the first year was between 1.3 and 2.1 times higher in shaded than in open plots (Table 1, odds ratios). In contrast, survival from late in the first spring to the following late spring was between 7 and 106 times higher in shaded than in open plots (Table 1, odds ratios), indicating an overwhelmingly large effect of solar radiation on seedling survival over the first summer. In the unseeded plots, results were more variable year to year, though most shaded plots contained new seedlings in most years, and most unshaded plots did not contain new seedlings in most years. By the end of the fifth growing season in the unseeded plots, the differences between treatments were striking; the mean number of surviving bluebunch plants in shaded plots was >13 (range = 5 to 30) and the mean number in unshaded plots was <1 (range = 0 to 3) (Tables 1, S2, Fig 5).

Soil in shaded plots was consistently and substantially cooler than soil in open plots (by between, on average, 2.5° and 7.5° C) when measured between late May and July (Tables 2, S3). However, soil moisture differences between shaded and open plots were small and inconsistent (Tables 3, S4), and therefore we cannot draw clear conclusions about the effect of our experimental shading on soil moisture. When we included the 15 separate moisture measurement effects in a single random-effects meta-analysis, the estimated average Hedge's D was 0.2957 (95% CI: -0.1051 to 0.6965). Thus, our results are consistent with shaded plots having contained more soil moisture on average, but the point estimate for the effect size is only moderate and the variability around this average effect is substantial enough that we must consider the possibilities that moisture did not differ between treatments or was higher in open plots.

When we incorporated seed and seedling success data from our seeded shade experiments in previously constructed demographic models from our study site, we found that in nearly all scenarios, the estimated rate of population growth was higher for north-facing populations than for south-facing populations, and in multiple plausible scenarios, populations on south-facing slopes appeared to be shrinking (Fig. 6). The only scenario that kept nearly all estimates of population growth (λ) from both slopes above 1 was universally applying seed and seedling survival data from only the shaded plots (Fig. 6a). When we used seed and seedling data from only unshaded plots from the first experiment (Fig. 6b), the south-facing population showed declining populations in two years, and the north-facing population showed a decline in one year. When we assigned the north-facing population seed and seedling success data from shade plots, and the south-facing population seed and seedling success data from unshaded plots, we found substantially higher estimates of lambda in the north-facing population than in south-facing the south-facing population in all years, and values consistently >1 for the north-facing population, and often <1 for the south-facing population (Fig. 6c, d).

Discussion:

Responses of bluebunch wheatgrass seedlings to our shade treatments were dramatic and differences in sunlight and temperature between these treatments appeared sufficient to explain the much lower success of bluebunch wheatgrass seedlings in open plots relative to shaded plots. The higher success of seeds or seedlings in the shade was consistent across three separate experiments conducted across multiple years. The largest differences in success between open and shaded plots was in survival of seedlings from the first to the second spring of life, suggesting that seedling survival over the first summer, rather than seed germination or seedling emergence, was the life stage most strongly impacted by our experimental treatment. Also, soils in shaded plots were consistently cooler across five different years, though soil moisture did not differ consistently between shaded and open plots. These results, taken together with demographic modelling that combine these seed and seedling success data with observation demographic data from adult plants, suggest that the lower density of bluebunch wheatgrass on south-facing slopes relative to north-facings slopes at our study site may be driven substantially by lower first-summer survival of seedlings caused by higher solar radiation and temperatures on south-facing slopes. This case study is consistent with growing evidence that, in environments with water limitation during the growing season, climate warming may especially threaten seedling establishment.

Our most unexpected observation was a clear difference in seedling success despite no clear difference in soil moisture between shaded and open plots. We had hypothesized that difference in soil moisture was the driver of difference in seedling survival. This hypothesis is supported by correlative work elsewhere with bluebunch wheatgrass which found that moisture deficits were at least weakly associated with reduced seedling survival (James *et al.*, 2019), and especially by previous measurements from north and south-facing slopes at our site using identical methods to those we report here, which found a clear pattern of higher soil moisture on north-facing slopes from March through September (Shriver *et al.*, 2021). That difference in soil moisture between north and south-facing slopes may well contribute to the differences in bluebunch wheatgrass demography between those slopes, and in our experimental plots, moisture differences between treatments may have existed at some sampling times, and these differences may also have contributed to differences in seedling success. However, the relatively consistent difference in seedling success between open and shaded plots despite highly variable soil moisture trends suggests that a difference in soil moisture was not the primary causal factor behind the differences we observed in seedling success. Further, the results from our shade plots suggest that differences in solar radiation, or differences in temperature, which were clear and consistent, are sufficient to drive differences in bluebunch wheatgrass seedling survival.

The lack of consistent soil moisture differences between shade and open plots is, itself, puzzling, and we are unsure of the explanation. However, one possibility is that, because the shaded areas were relatively small (2 m x 2 m), soil moisture either diffused out the sides of the shaded plots into the surrounding hotter, drier soils or evaporated into the approximately uniform low humidity on south-facing slopes. That possibility assumes that the differences in soil moisture we observed between north and south-facing slopes in the one summer we measured it are typical, but that may not be the case. Another possibility is that the differences between north and south-facing slopes typically disappear as universally dry conditions develop in summer, as has been found in some other arid and semi-arid systems with winter precipitation and summer drought (Western *et al.*, 1999). A possible mechanism driving such homogenization of soil moisture in the dry season could be higher plant density in wetter areas (like north-facing slopes and shaded plots) leading to more transpiration of water from these areas, thus matching the greater evaporation on south-facing slopes (Fatichi *et al.*, 2015).

Our shade treatment was designed to mimic the difference in solar radiation, and thus differences in temperature and moisture, between north and south-facing slopes, and we succeeded in influencing soil temperatures as expected. The average temperature differences we observed between shaded and open plots (between 2.5° and 7.5° C from late May into July) were similar to those we previously observed between north and south-facing slopes (from > 3°C in April and May to >5° C in July and >10° C in September (Shriver *et al.*, 2021)). Since the temperature patterns associated with dramatic differences in seedling survival in our experimental plots were comparable to those we observed between unmanipulated north and south-facing slopes, this raises the possibility that temperature differences between the two slopes may directly drive demographic differences in bluebunch wheatgrass between these slopes. Correlative analysis of data from controlled seeding of bluebunch wheatgrass at other sites found that warmer temperatures were associated with both lower seed germination and lower rates of seedling emergence, although not with seedling survival over the first year (James *et al.*, 2019), the time when we observed our strongest effects. Interestingly, in contrast to these findings, some prior laboratory work found that warmer temperatures increased the success of bluebunch wheatgrass seedlings, although plants in that study were watered to field capacity every other day (Aguirre & Johnson, 1991), which could have mitigated the effects of high temperatures, as we explain in the next paragraph. Clearly further work is needed to resolve the roles of temperature and moisture in the early life stages of this species, both at our study site and more generally.

Although differences in solar radiation or temperature rather than differences in soil moisture seem to have driven differences in seedling success between shaded and open plots, moisture probably still played a role in the different seedling success between these treatments. Plants in open plots, because they were hotter, likely experienced a greater vapor pressure deficit due to higher rates of transpiration (McDowell *et al.*, 2016). This water pressure deficit might have been further exacerbated if the plants exposed to more light and higher temperatures in the open on south-facing slopes had higher rates of photosynthesis, and thus higher moisture demands (Chaves *et al.*, 2016). The plants in the open may also have been at risk of heat damage to their metabolic machinery, including denaturing of enzymes (Chaves *et al.*, 2016). To mitigate this heat damage, some plants, including those in arid and semi-arid areas, open stomata to transpire water and thus reduce their temperature through evaporative cooling (Chaves *et al.*, 2016; Urban *et al.*, 2017). Therefore, plants in open plots may have had higher moisture demands than the plants in the shaded, cooler plots, and limited access to moisture could have therefore been more costly to plants in the open than to plants in the shade.

Our study system is characterized by cool season precipitation and warm season drought, and thus perennial plants here presumably experience water limitation every summer (Kulmatiski *et al.*, 2006). Established perennials appear less strongly affected by summer drought than young perennials, most likely because the deep roots of established plants give them access to more soil moisture. We see evidence of the success of established individuals in bluebunch wheatgrass at our study site, where established plants usually remain green into summer, well after the rains typically cease and most annuals die. Further, large bluebunch wheatgrass plants survive to the following year at very high rates. In fact, in ten year of monitoring established individuals, we have never seen a plant with >70 stems in one year die before the subsequent year, regardless of the severity of drought. In contrast, as we and others (James *et al.*, 2019) have observed, bluebunch wheatgrass seedlings often die before their second growing season, presumably due in some large degree to their shallow roots and relatively poor access to moisture in the face of temperature stress.

Although our experiments did not directly address the role of competition from annuals in limiting the success of seedling perennials, our results provide insight into this hypothesis. Some prior work has identified competition from the invasive annual cheatgrass as a factor limiting success of bluebunch wheatgrass seedlings (Harris, 1967; Aguirre & Johnson, 1991), but results from a network of sites with large samples suggest that temperature and moisture may be more important than the presence of cheatgrass to predicting bluebunch wheatgrass seedling success (James *et al.*, 2019). In all our experiments, annuals were abundant in both treatments, although annuals were probably somewhat less abundant in the first year of the seeded experiments since we raked those plots at planting, killing some annuals that had established with the start of the rains in the autumn. Despite the abundance of annuals, perennials established themselves in shaded plots at many times the rate that they established in open plots. Therefore, we feel confident in ruling out the hypothesis that the primary factor limiting perennial establishment on south-facing slopes is the high abundance of annuals. Of course, there may be some role of annuals in limiting perennial establishment, and this role could interact with temperature to be more severe on south-facing slopes. However, solar radiation or temperature are almost certainly of major importance. All this said, if annual plants do play some special role in limiting the success of perennial grasses through competition with seedlings, this could mean that the seedlings in our shaded plots faced more obstacles to success than seedlings growing naturally on north-facing slopes. This in turn could mean that our estimates of seedling success from shaded plots are underestimates of seedling success from north-facing slopes, and that our demographic models therefore underestimate the potential differences between north and south-facing slopes.

Although competition from neighboring annuals may not strongly influence seedling bluebunch wheatgrass survival, our results are consistent with the possibility that neighboring plants may instead sometimes facilitate the success of seedlings by shading them. In particular, shade from woody shrubs may help herbaceous perennial seedlings survive in some contexts (Huber-Sannwald & Pyke, 2005; Boyd & Davies, 2012; Poulos *et al.*, 2014). However, at our site, shrub cover has a limited distribution, with sagebrush rare on both slopes, and rabbitbrush rare on south-facing slopes and only moderately common on north-facing slopes. Therefore, most grass seedlings at our site receive only the more limited shade provided by adjacent herbaceous annuals or perennials. On south-facing slopes, where we conducted our experiments, overall herbaceous cover is lower than on north-facing slopes, due both to the lower productivity and the much lower density of large perennial grasses. Thus, we expect weak, if any, facilitation effects from shading by herbaceous plants on south-facing slopes. This expectation is supported by observations from our naturally-seeded open plots where seedling recruitment was extremely low over multiple years despite being surrounded by tall bunchgrass. Further, unlike our experimentally-seeded plots, we did not rake the naturally-seeded plots, so all residual litter and annual plants that could have provided some shade persisted within the plot. Although limited opportunities for facilitation by shading exist on south-facing slopes, north-facing slopes may have more such opportunities. North-facing slopes presumably have more shade at the soil surface due to higher perennial density, and this could mean that the contrast between the solar environments experienced by seedlings on north-facing and south-facing slopes is even greater than the differences we created between our shade and open plots. However, whether this additional shade on north-facing slopes would facilitate seedling success or would limit seedlings via competition is unclear. The stress-gradient hypothesis (Goldberg & Novoplansky, 1997) predicts a shift from facilitation to competition as conditions become more favorable to growth, as they do as we move from south-facing to north-facing slopes, but we do not know whether conditions are sufficiently favorable on north-facing slopes for competition to have become important.

If the differences in seedling success between our experimental treatments is similar to differences between bluebunch wheatgrass seedlings on north and south-facing slopes, seedling success is likely to be a major demographic driver of the differences in abundance of bluebunch wheatgrass between north and south-facing plots. We saw this especially clearly when we applied the rates of seed and seedling survival from our experiments to existing demographic models from our population. The rates of seed and seedling survival in the open plots of our experiments were often insufficient to create a stable or growing population in our models of south-facing populations. However, the rates from our shaded plots were sufficient to create a growing population in models of the population on north-facing slopes in every one of the four years modeled. Further, demographic models from the south-facing population indicated this population would grow if its seedling success rate could match that from shaded plots, which indicates that low levels of ambient seedling success are alone sufficient to cause this population to shrink. Conversely, demographic models from the north-facing population indicated this population could shrink, at least in some years, if its seedling success rate matched that from open plots. Thus, it seems that differences in seedling success may be sufficient to explain the observed differences in bluebunch wheatgrass populations between north and south-facing slopes.

Implications:

Climate warming may already be triggering demographic collapse in some populations of bluebunch wheatgrass due to dramatically reduced seedling success, and we hypothesize that many other plant species are likely to be similarly threatened by climate change. Evidence of this particular demographic threat is growing, especially in environments where seedlings often face water limitation. For instance, warmer and drier conditions are associated with reduced tree seedling density in regenerating forests in the Rocky Mountains (Stevens-Rumann *et al.*, 2018), and the dry conditions increasing with climate warming in South Western Australia are associated with reduced seedling number in regenerating shrublands (Enright *et al.*, 2014). Further, across a large sample of dryland plant community restoration efforts, aridity, which is increased by higher temperatures driving higher evapotranspiration, appears correlated with lower seedling recruitment (Shackelford *et al.*, 2021).

From the standpoint of conserving bluebunch wheatgrass populations, our work provides a mix of good and bad news. The good news is that, if plants can be helped through the seedling stage and allowed time to develop deep roots, they may be likely to survive well in the types of environments we studied. This may be possible at large spatial scales if shrubs, such as sagebrush, that provide shade to grass seedlings, can be preserved or revegetated (Huber-Sannwald & Pyke, 2005). However, the bad news is that these environments are getting hotter and drier (Bradford *et al.*, 2020), and so seedling establishment may become even less likely on south-facing slopes, and with shaded micro-sites becoming rare due to fire (Davies *et al.*, 2011), bluebunch wheatgrass plants may disappear from these slopes. Further, if north-facing slopes warm sufficiently, even the current strongholds of bluebunch wheatgrass in this landscape may also face demographic collapse. Of course, conserving bluebunch wheatgrass is a narrow objective, and a broader objective of conserving the semi-arid rangeland ecosystems in which bluebunch wheatgrass grows may also face major challenges if other species in these systems are also facing reduced seedling survival or other demographic challenges in a warmer, drier world.

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Contributors table

A.G.: Formal analysis, and Investigation, and Writing - original draft. E.C.: Formal analysis, Investigation, and Writing - original draft. L.P.: Formal analysis, Methodology, Software, and Visualization. M.S.: Formal analysis, Investigation, and Writing - original draft. R.K.S.: Data curation, Formal analysis, Methodology, Software, Visualization, Writing - original draft, and Writing - review & editing. T.H.P.: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing - original draft, and Writing - review & editing.

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Figure headings

Figure 1. Solar radiation at Spring Gulch, Wallula Gap Biological Station, WA, USA as a proportion of the average solar radiation received on south-facing slopes for the entire year, and separately for December, March, and June. This figure demonstrates that most areas on north-facing slopes receive substantially less solar radiation than south-facing slopes throughout the year (north facing slopes mostly receive 20%-40% of the radiation on the south-facing sites in December, 30%-60% in March, and 50%-80% in June, with north-facing slopes receiving an average of 40%-70% of the radiation reaching south-facing values annually). The demography transects are black polygons on the yearly-sum map. The location of each pair of shaded-unshaded plots are white symbols (triangles: seeded experiment 1; circles: seeded experiment 2; squares: unseeded experiment) on the December map. To generate the percentages shown on the maps using ArcGIS Desktop (10.8.2 Build 283888), we divided the monthly average solar radiation for each pixel on the map by the average solar radiation from slopes within 22.5° of south-facing for that month. This denominator excludes solar radiation data from slopes shallower than 10° because our monitoring and experimental sites are steeper than 10° and most of the area on the map below this threshold are currently or formerly under cultivation, and thus do not contain our studied plant community. For more details about the solar radiation models, see Figure S1.

Figure 2. Violin plots depicting the proportion of bluebunch wheatgrass seeds germinated and surviving to a given sampling time (a, b) or seedlings surviving to a later sampling time (c) in experimentally-seeded unshaded (open) and shaded plots established in the winter of 2011-2012.

Figure 3. Violin plots depicting the proportion of bluebunch wheatgrass seeds germinated and surviving to a given sampling time (a, b, c) or seedlings surviving to a later sampling time (d, e) in experimentally-seeded unshaded (open) and shaded plots established in the winter of 2018-2019.

Figure 4. A shaded (left) and open (unshaded, right) plot from the second experimental seeding experiment. These photos were taken June 8th of the second spring (2020) after experimental initiation. Note the abundance of green grass, mostly bluebunch wheatgrass, in the shade plot and the presence of only one evident bluebunch wheatgrass plant in the open plot.

Figure 5. Violin plot depicting the number of bluebunch wheatgrass seedlings alive in June of 2022, the fifth growing season after unseeded unshaded (open) and shaded plots were established in the winter of 2017-2018.

Figure 6. Posterior distributions for estimated population growth rate (λ) on north and south-facing slopes for bluebunch wheatgrass at the Wallula Gap Biological Station, Washington, USA incorporating seed and seedling success data derived from our seeded shade experiments. Each panel corresponds to a single annual transition. The variability in estimates within a year and aspect derives from carrying through all uncertainty in parameter estimates from vital rate models based on observational data presented in a prior paper (Shriver *et al.*, 2021). The observational demographic data are identical in each set of four annual panels, but in the first set, (a) all seed and seedling data come from shaded plots in the first shade experiment, in (b) all seed and seedling data come from unshaded plots in the first shade experiment, in (c) the seed and seedling data for south-facing populations come from unshaded plots and the seed and seedling data for north-facing populations come from shaded plots from the first shade experiment, and in (d) the seed and seedling data for south-facing populations come from unshaded plots and the seed and seedling data for north-facing populations come from shaded plots from the second shade experiment.

Table 1. Estimates from generalized linear (mixed) model comparisons of seed and seedling success between shaded and open plots. Binomial estimates presented both untransformed and as odds ratios.

Analysis and error type Fixed effects	Estimate	SE	Estimate as odds ratio	Z	p
2011-seeded					
Binomial error					
2012 counts/seed count					
Intercept	-4.70772	0.13873		-33.94	$<2 \times 10^{-16}$
Treatment (shade – open)	0.75687	0.05258	2.13	14.39	$<2 \times 10^{-16}$
2013 counts/seed count					
Intercept	-6.6168	0.2401		-27.56	$<2 \times 10^{-16}$
Treatment (shade – open)	1.7027	0.1153	5.48	14.77	$<2 \times 10^{-16}$
2013 counts/2012 counts					
Intercept	-2.2245	0.3365		-6.612	3.80×10^{-11}
Treatment (shade – open)	1.9594	0.1575	7.10	12.439	$<2 \times 10^{-16}$
2018-seeded					
Binomial error					
2019 counts/seed count					
Intercept	-4.79749	0.09372		-51.19	$<2 \times 10^{-16}$
Treatment (shade – open)	0.24329	0.04628	1.28	5.257	0.000000146
2020 counts/seed count					
Intercept	-7.7955	0.1883		-41.4	$<2 \times 10^{-16}$
Treatment (shade – open)	3.0629	0.1559	21.4	19.65	$<2 \times 10^{-16}$
2021 counts/seed count					
Intercept	-9.0529	0.3513		-25.77	$<2 \times 10^{-16}$
Treatment (shade – open)	3.5919	0.2701	36.3	13.3	$<2 \times 10^{-16}$
2020 counts/2019 counts					
Intercept	-3.1582	0.3303		-9.562	$<2 \times 10^{-16}$
Treatment (shade – open)	4.6605	0.205	105.7	22.737	$<2 \times 10^{-16}$
2021 counts/2020 counts					
Intercept	-1.5051	0.4759		-3.162	0.00156
Treatment (shade – open)	1.644	0.3693	5.18	4.452	0.00000851
2018- unseeded					
2018 new seedling counts					
Poisson error					
Intercept	-0.1823	0.4472		-0.408	0.684
Treatment (shade – open)	1.9741	0.4773		4.136	0.0000353
2019 new seedling counts					
negative binomial error					
Intercept	-1.792	1.048		-1.71	0.087342
Treatment (shade – open)	3.689	1.105		3.337	0.000846
2020 new seedling counts					
negative binomial error					
Intercept	-0.6931	0.6459		-1.073	0.283
Treatment (shade – open)	3.6288	0.7141		5.081	0.00000375
2021 new seedling counts					

negative binomial error					
Intercept	-1.792	1.077		-1.664	0.0961
Treatment (shade – open)	1.386	1.252		1.107	0.2684
2022 new seedling counts					
Poisson error					
Intercept	-18.3	2334.17		-0.008	0.994
Treatment (shade – open)	18.91	2334.17		0.008	0.994
2022 – all surviving seedlings germinated 2018-2021					
negative binomial error					
Intercept	-0.4055	0.5599		-0.724	0.469
Treatment (shade – open)	3.0082	0.6239		4.822	0.00000142

Table 2. Estimates from general linear mixed model comparisons of soil temperatures between shaded and open plots.

Fixed effects	estimate	SE	Df	t	p
2016: May - early June					
Intercept	22.315	1.258	8.278	17.738	7.06 x 10^{-8}
Treatment (shade – open)	-5.185	1.312	5	-3.952	0.0108
2016: mid-late June					
Intercept	25.000	0.9803	7.6344	25.501	1.15 x 10^{-8}
Treatment (shade – open)	-3.2407	0.9231	5	-3.511	0.0171
2016: July					
Intercept	29.9074	1.1057	7.1604	27.048	1.79 x 10^{-8}
Treatment (shade – open)	-3.8889	0.9515	5	-4.087	0.00947
2017: May - early June					
Intercept	20.6667	0.9324	9.5987	22.164	1.45 x 10^{-9}
Treatment (shade – open)	-2.5	1.1762	5	-2.126	0.0869
2017: mid-late June					
boundary (singular) fit					
2017: July					
Intercept	27.6667	0.4595	7.4896	60.215	2.47 x 10^{-11}
Treatment (shade – open)	-3.3333	0.4216	5	-7.906	0.000521
2018: mid-late June					
Intercept	31.3333	3.1831	5.1678	9.844	0.000153
Treatment (shade – open)	-4.2167	0.8179	5	-5.156	0.003598
2020: mid-late June					
Intercept	38.425	1.104	10.838	34.815	1.79 x 10^{-12}
Treatment (shade – open)	-7.563	1.058	7	-7.145	0.000186
2021: mid-late June					
Intercept	43.975	3.743	7.725	11.747	3.36 x 10^{-6}
Treatment (shade – open)	-6.875	1.663	7	-4.134	0.00438

Table 3. Estimates from general linear mixed model comparisons of soil moisture (proportion by mass) between shaded and open plots.

Fixed effects	estimate	SE	Df	t	P
2016: May - early June 0-10 cm					
Intercept	0.08123	0.008122	8.545688	10.002	5.25×10^{-6}
Treatment (shade – open)	0.003131	0.008902	4.602111	0.352	0.741
2016: May - early June 10-20 cm					
Intercept	0.078175	0.009138	8.219896	8.555	2.28×10^{-5}
Treatment (shade – open)	0.000878	0.00945	5	0.093	0.930
2016: May - early June 20-30 cm					
Intercept	0.063105	0.006799	9.454386	9.282	4.69×10^{-6}
Treatment (shade – open)	-0.00481	0.008381	5	-0.574	0.591
2016: mid-late June 0-10 cm					
Intercept	0.045788	0.003651	9.998452	12.541	1.93×10^{-7}
Treatment (shade – open)	-0.0023	0.005131	5.000201	-0.448	0.673
2016: mid-late June 10-20 cm					
Intercept	0.042736	0.003117	9.743637	13.709	1.09×10^{-7}
Treatment (shade – open)	-0.00136	0.004035	4.999984	-0.337	0.750
2016: mid-late June 20-30 cm					
Intercept	0.063105	0.006799	9.454386	9.282	4.69×10^{-6}
Treatment (shade – open)	-0.00481	0.008381	5	-0.574	0.591
2016: July 0-10 cm					
boundary (singular) fit					
2016: July 10-20 cm					
boundary (singular) fit					
2016: July 20-30 cm					
Intercept	0.027191	0.002954	9.654589	9.205	4.34×10^{-6}
Treatment (shade – open)	0.005081	0.003762	4.99999	1.351	0.235
2017: May - early June 0-10 cm					
boundary (singular) fit					
2017: May - early June 10-20 cm					
boundary (singular) fit					
2017: May - early June 20-30 cm					
boundary (singular) fit					
2017: mid-late June 0-10 cm					
Intercept	0.022488	0.003853	8.867905	5.836	0.000263
Treatment (shade – open)	0.005886	0.004369	5	1.347	0.235685
2017: mid-late June 10-20 cm					
Intercept	0.040694	0.003466	8.69024	11.742	1.26×10^{-6}
Treatment (shade – open)	0.003423	0.003834	5	0.893	0.413
2017: mid-late June 20-30 cm					

boundary (singular) fit					
2017: July 0-10 cm					
Intercept	0.015414	0.002513	7.960469	6.134	0.000285
Treatment (shade – open)	0.006005	0.002498	5	2.404	0.06129
2017: July 10-20 cm					
Intercept	0.035697	0.003397	7.013316	10.507	1.52 x 10^{-5}
Treatment (shade – open)	-0.00065	0.002832	5	-0.228	0.828
2017: July 20-30 cm					
Intercept	0.042952	0.004576	9.935375	9.386	2.97 x 10^{-6}
Treatment (shade – open)	0.005674	0.006205	5	0.914	0.402
2018: mid-late June 0- 10cm					
boundary (singular) fit					
2018: mid-late June 0- 10cm					
Intercept	0.02602	0.01258	9.98837	2.069	0.0655
Treatment (shade – open)	0.02144	0.01748	4.99997	1.226	0.2746
2018: mid-late June 0- 10cm					
boundary (singular) fit					
2019: July 0-10 cm					
boundary (singular) fit					
2019: July 10-20 cm					
Intercept	0.028745	0.001908	12.12368	15.067	3.24 x 10^{-9}
Treatment (shade – open)	0.006897	0.002358	6.95422	2.925	0.0224
2019: July 20-30 cm					
Intercept	0.036697	0.001852	9.724229	19.815	3.47 x 10^{-9}
Treatment (shade – open)	0.00397	0.00152	7	2.611	0.0349

Figure 1.

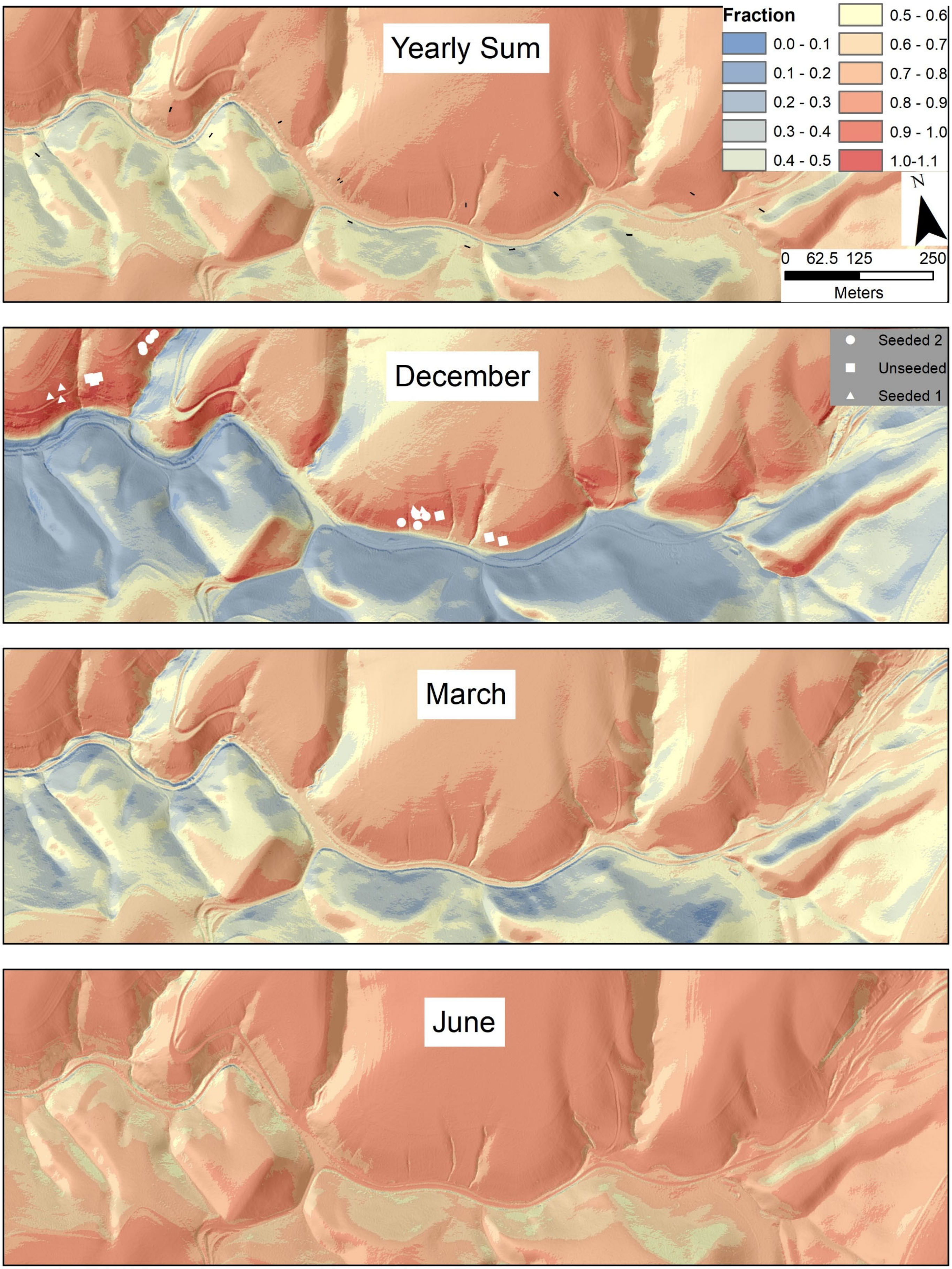

Yearly Sum
Fraction
0.0 - 0.1
0.1 - 0.2
0.2 - 0.3
0.3 - 0.4
0.4 - 0.5
0.5 - 0.6
0.6 - 0.7
0.7 - 0.8
0.8 - 0.9
0.9 - 1.0
1.0-1.1
N
0
62.5
125
250
Meters
December
Seeded 2
Unseeded
Seeded 1
March
June

Figure 2.

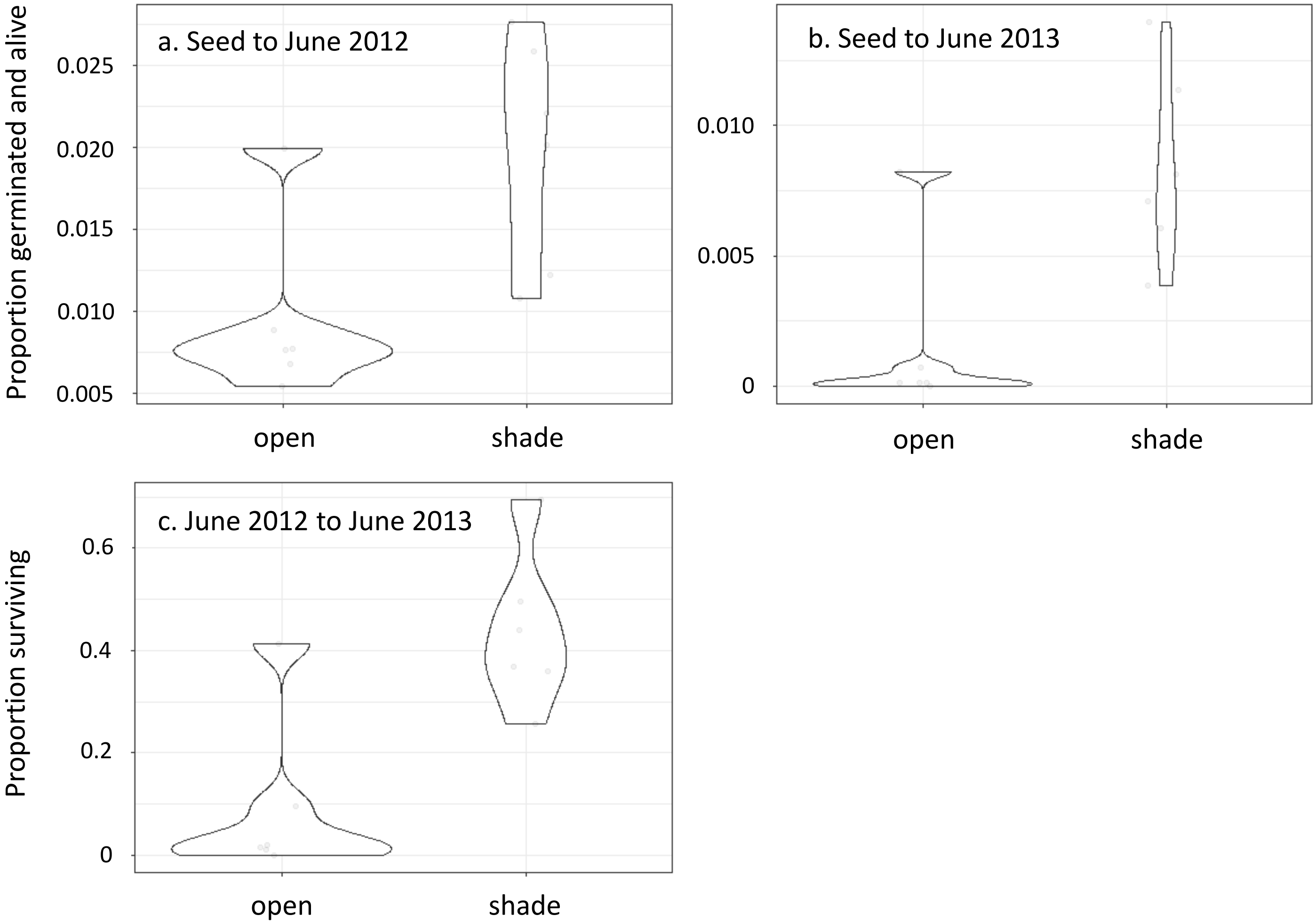

a. Seed to June 2012
Proportion germinated and alive
0.025
0.020
0.015
0.010
0.005
open
shade
b. Seed to June 2013
0.010
0.005
0
open
shade
c. June 2012 to June 2013
Proportion surviving
0.6
0.4
0.2
0
open
shade

Figure 3.

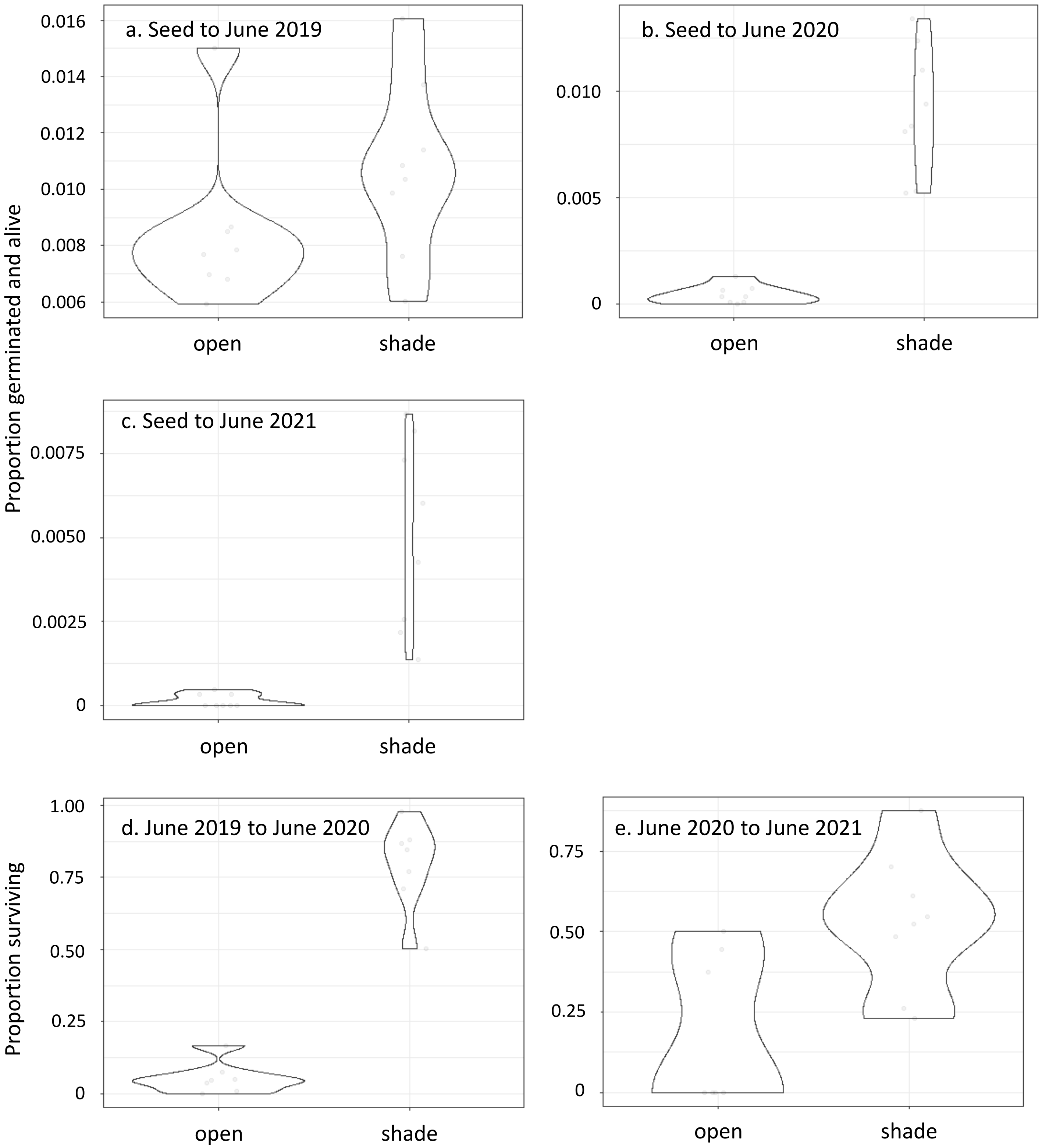

Proportion germinated and alive
a. Seed to June 2019
0.016
0.014
0.012
0.010
0.008
0.006
open
shade
b. Seed to June 2020
0.010
0.005
0
open
shade
c. Seed to June 2021
0.0075
0.0050
0.0025
0
open
shade
Proportion surviving
d. June 2019 to June 2020
1.00
0.75
0.50
0.25
0
open
shade
e. June 2020 to June 2021
0.75
0.50
0.25
0
open
shade

Figure 4.

Figure 5.

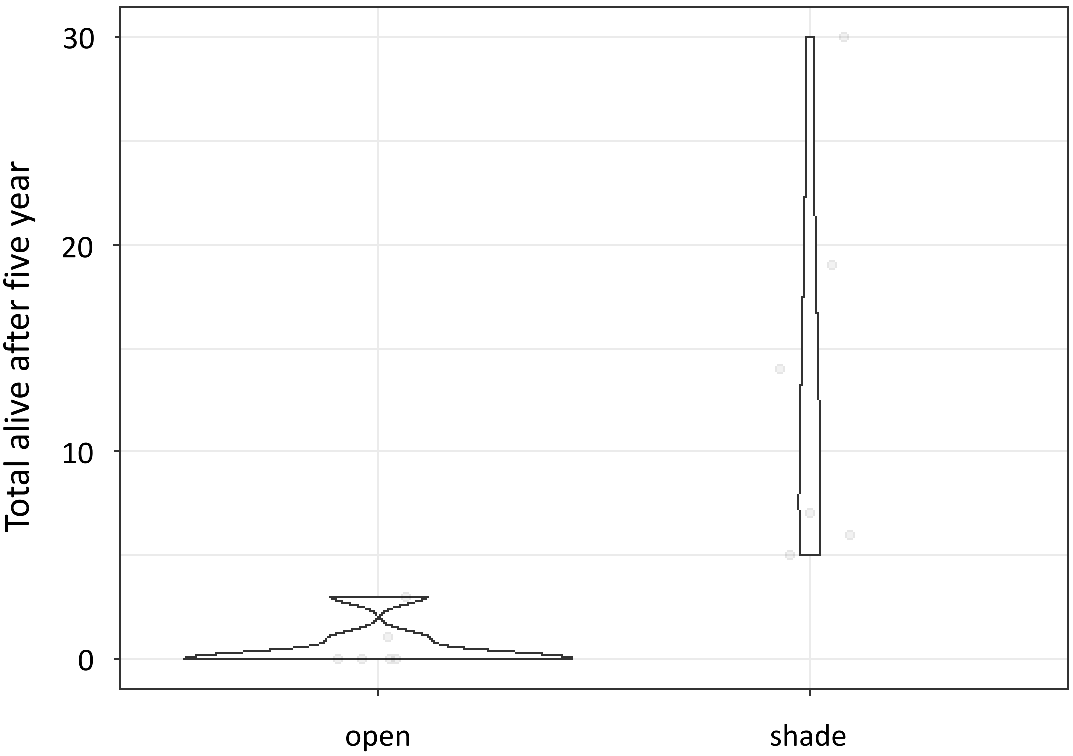


Figure 6a.

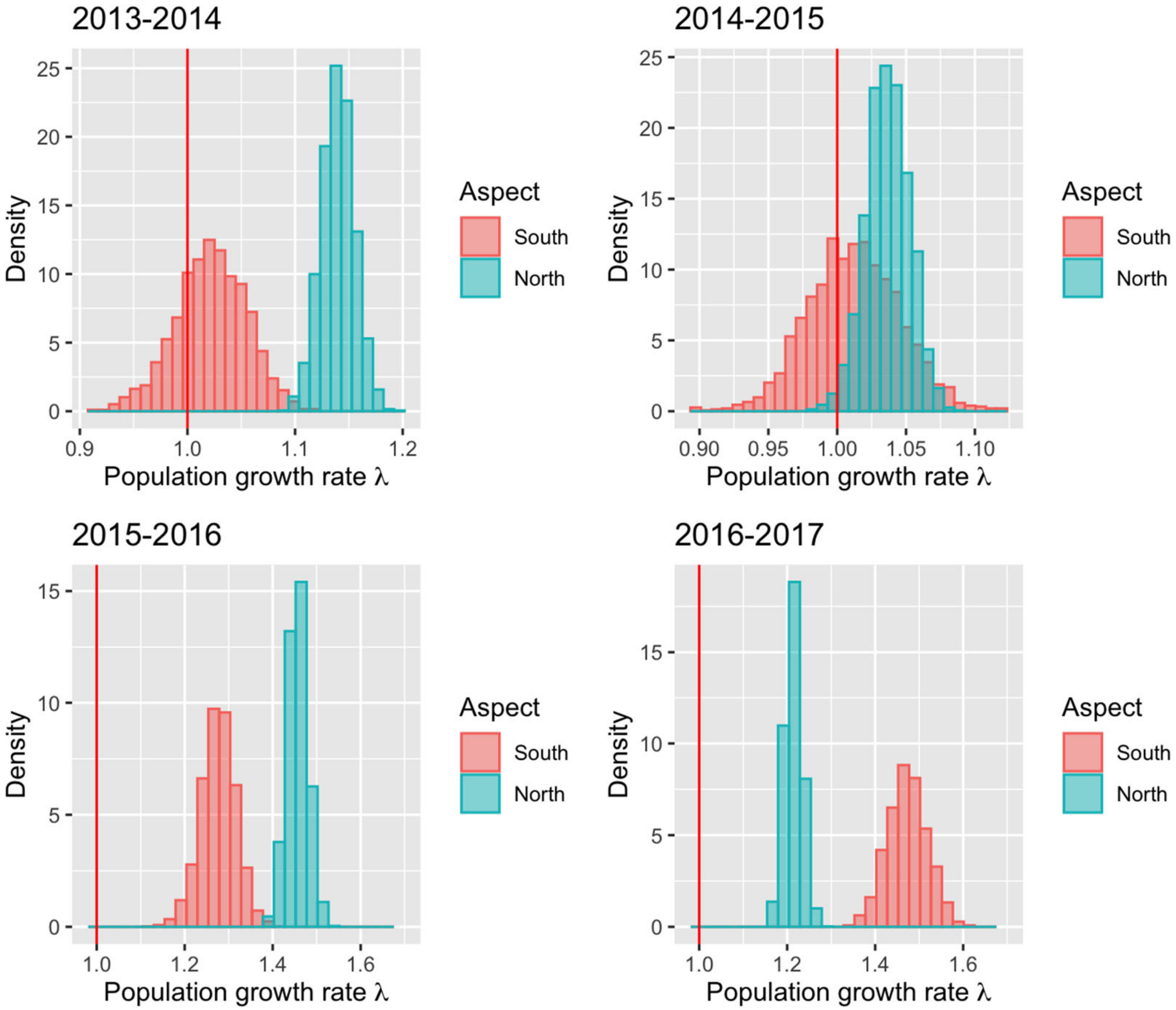

2013-2014
2014-2015
2015-2016
2016-2017
Density
Population growth rate λ
Aspect
South
North
0
5
10
15
20
25
0.9
1.0
1.1
1.2
0.90
0.95
1.00
1.05
1.10
1.2
1.4
1.6

Figure 6b.


2013-2014
2014-2015
2015-2016
2016-2017
Density
Population growth rate λ
Aspect
South
North
0
10
20
30
40
0.80
0.85
0.90
0.95
1.00
1.05
1.0
1.1
1.2
1.10
1.15
1.20

Figure 6c.

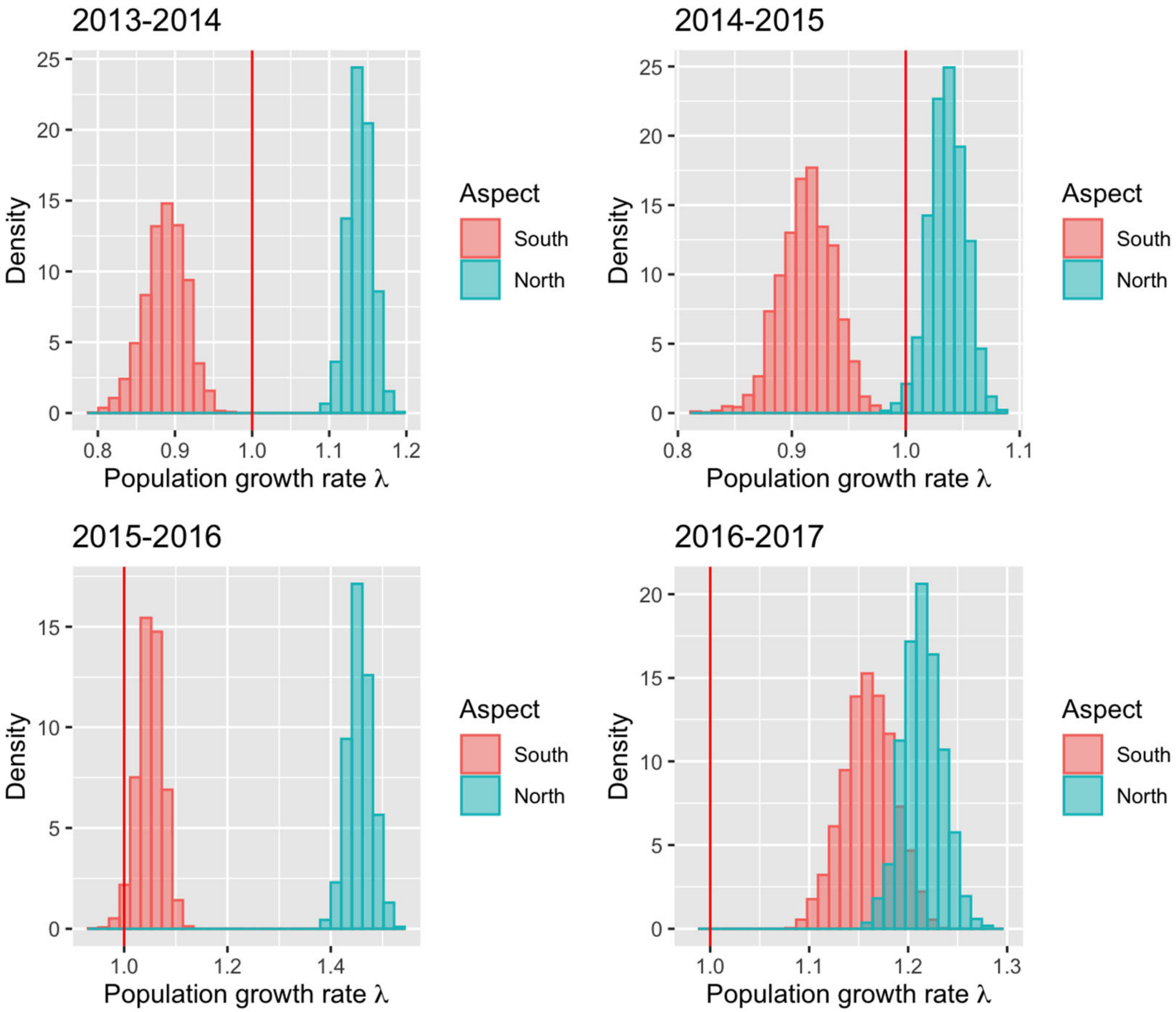
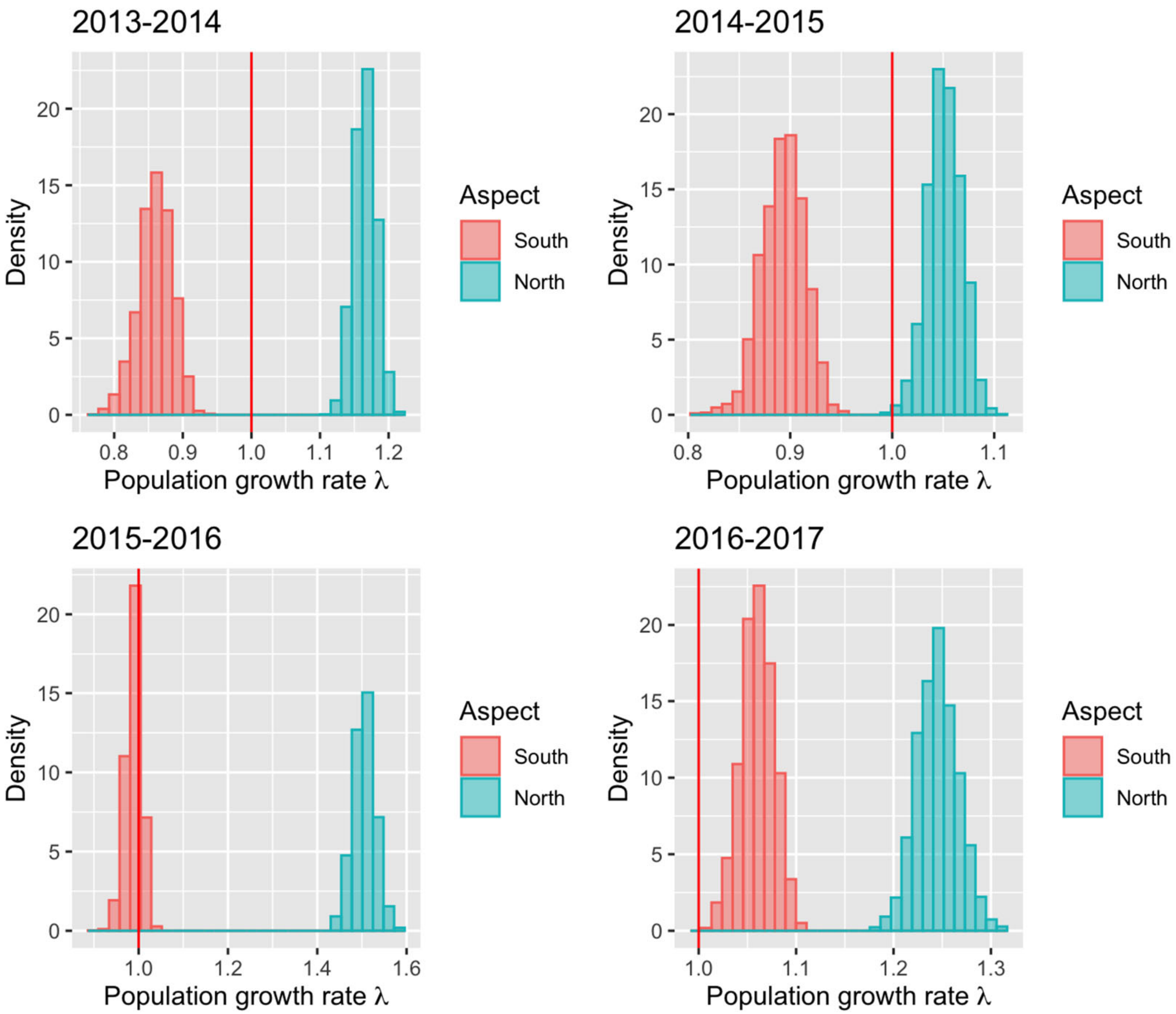

2013-2014
2014-2015
2015-2016
2016-2017
Density
Population growth rate λ
Aspect
South
North
0
5
10
15
20
25
0.8
0.9
1.0
1.1
1.2
1.4
1.3

Figure 6d.


2013-2014
Density
0
5
10
15
20
0.8
0.9
1.0
1.1
1.2
Population growth rate λ
Aspect
South
North
2014-2015
Density
0
5
10
15
20
0.8
0.9
1.0
1.1
Population growth rate λ
Aspect
South
North
2015-2016
Density
0
5
10
15
20
1.0
1.2
1.4
1.6
Population growth rate λ
Aspect
South
North
2016-2017
Density
0
5
10
15
20
1.0
1.1
1.2
1.3
Population growth rate λ
Aspect
South
North

Supplement to:

Potential demographic collapse in a common perennial bunchgrass on south-facing slopes in a semi-arid grassland via dramatically reduced seedling establishment

Timothy H. Parker[a,d]
Alex Gerber[a]
Erin Campbell[a]
Molly Simonson[a]
Robert K. Shriver[b]
Lyman Persico[c]

[a] Biology Department, Whitman College, Walla Walla, WA 99362 USA
[b] Department of Natural Resources and Environmental Sciences, University of Nevada, Reno, Nevada 89557 USA
[c] Geology Department, Whitman College, Walla Walla, WA 99362 USA
[d] Corresponding author: parkerth@whitman.edu

Supplement

Figure S1

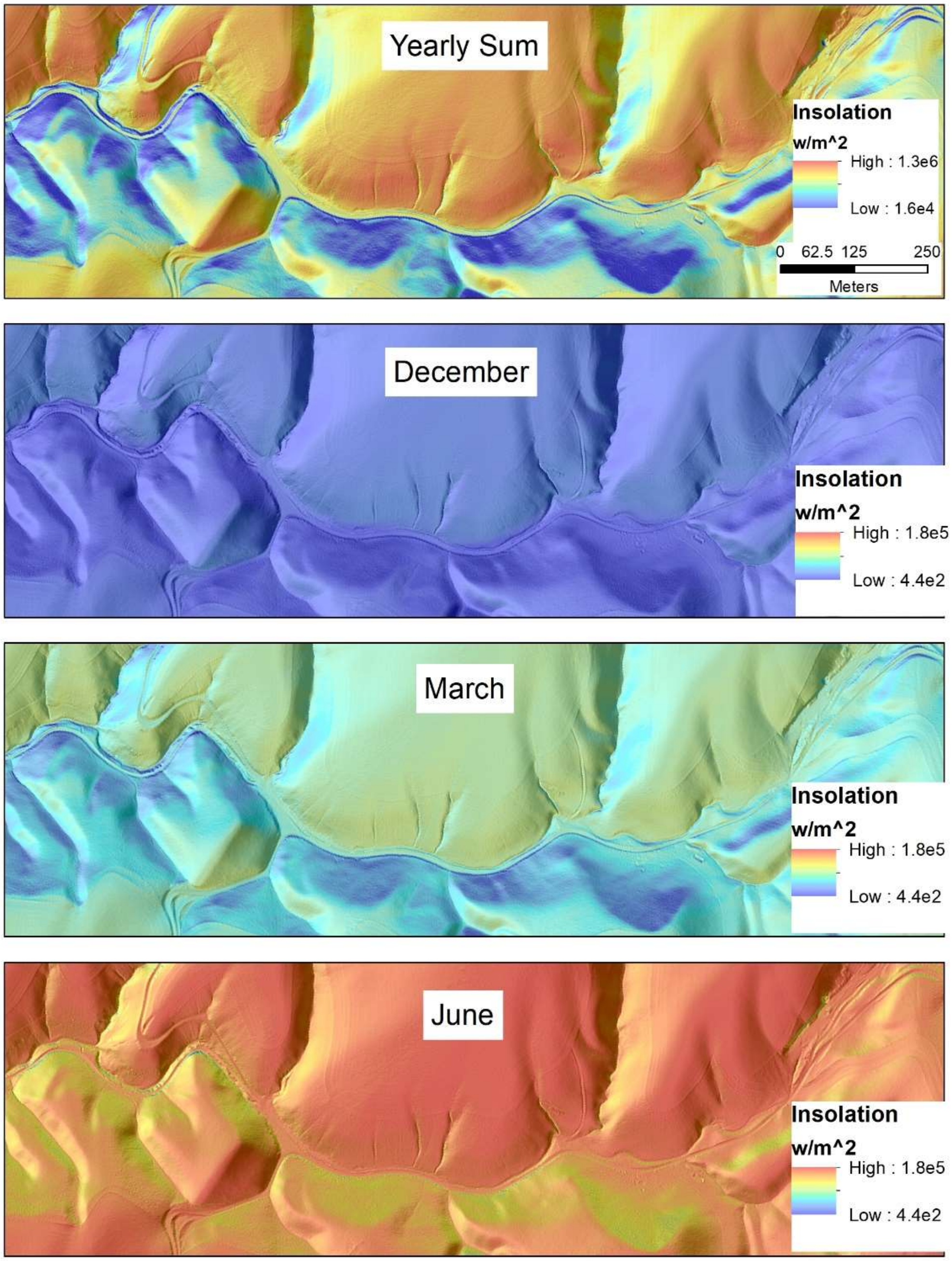


Figure S1. Total solar radiation (insolation: direct and diffuse) at Spring Gulch derived from a 1 m resolution digital elevation model. The digital elevation model was derived from a fall/winter 2017 Lidar scan of Columbia, Garfield, and Walla Walla counties, WA, USA (Quantum_Spatial, 2018). We modeled solar radiation for the year with monthly intervals for 2022 using ArcGIS Desktop (10.8.2 Build 283888). In Spring Gulch, total yearly insolation ranges from 1.6×10^4 – 1.3×10^6 watts per square meter and is strongly controlled by aspect. The shading scale is identical across the December, March, and June maps to show low insolation solar radiation in winter relative to spring and summer.

Figure S2

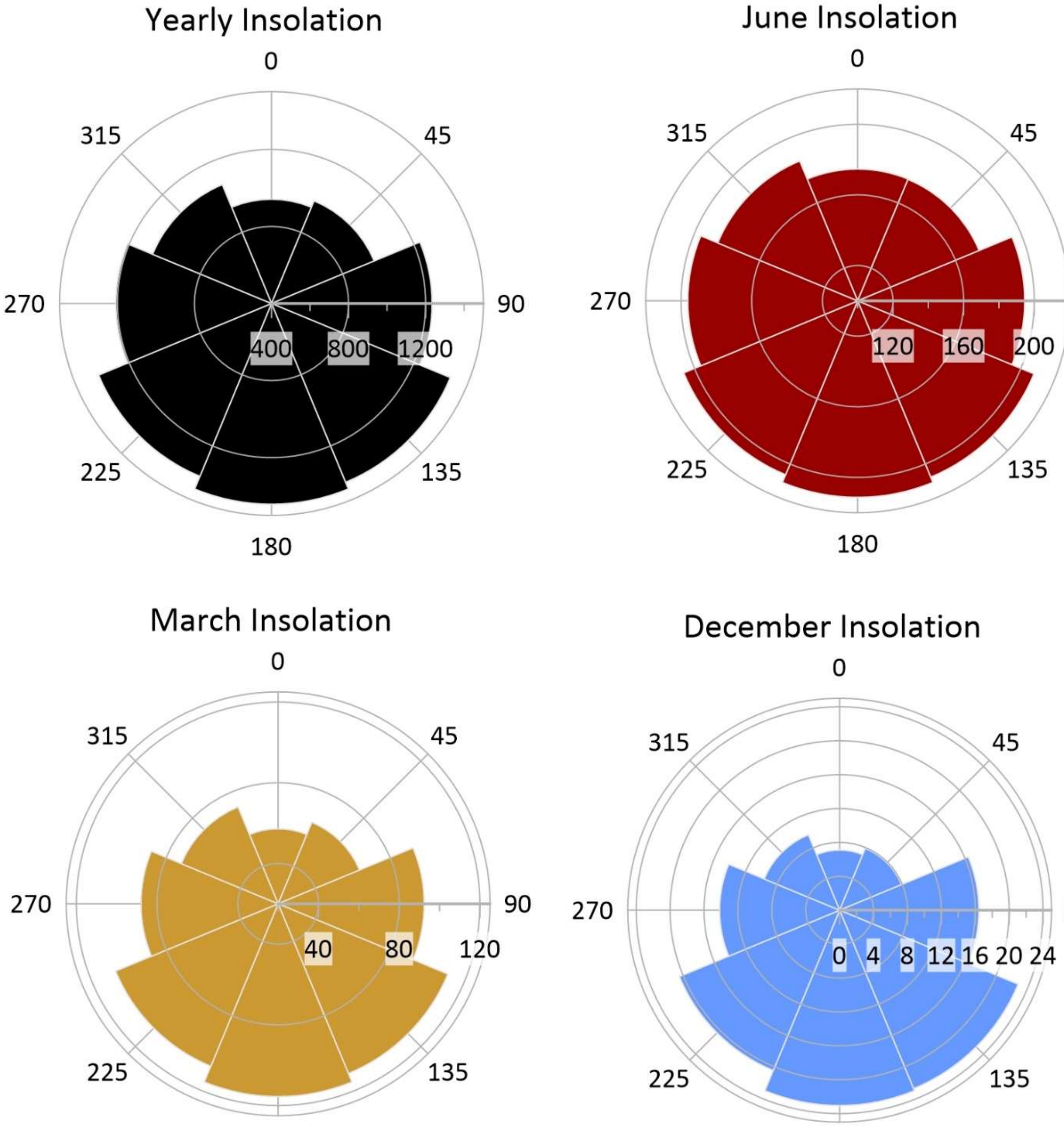


Figure S2. Solar radiation (insolation; 10^3 watts/square meter) on slopes throughout the study area estimated for slope angles greater than 8°. We used eight aspect bins (each 45°) in which to calculate the average solar radiation in the study area (extent of Figures 1 and S1). In each aspect class we summed the solar radiation values for each pixel and divided by the total number of pixels (area) in that aspect class. Southerly aspects receive the most solar radiation and the difference between north and south-facing slopes is greatest in December and least in June.

Figure S3

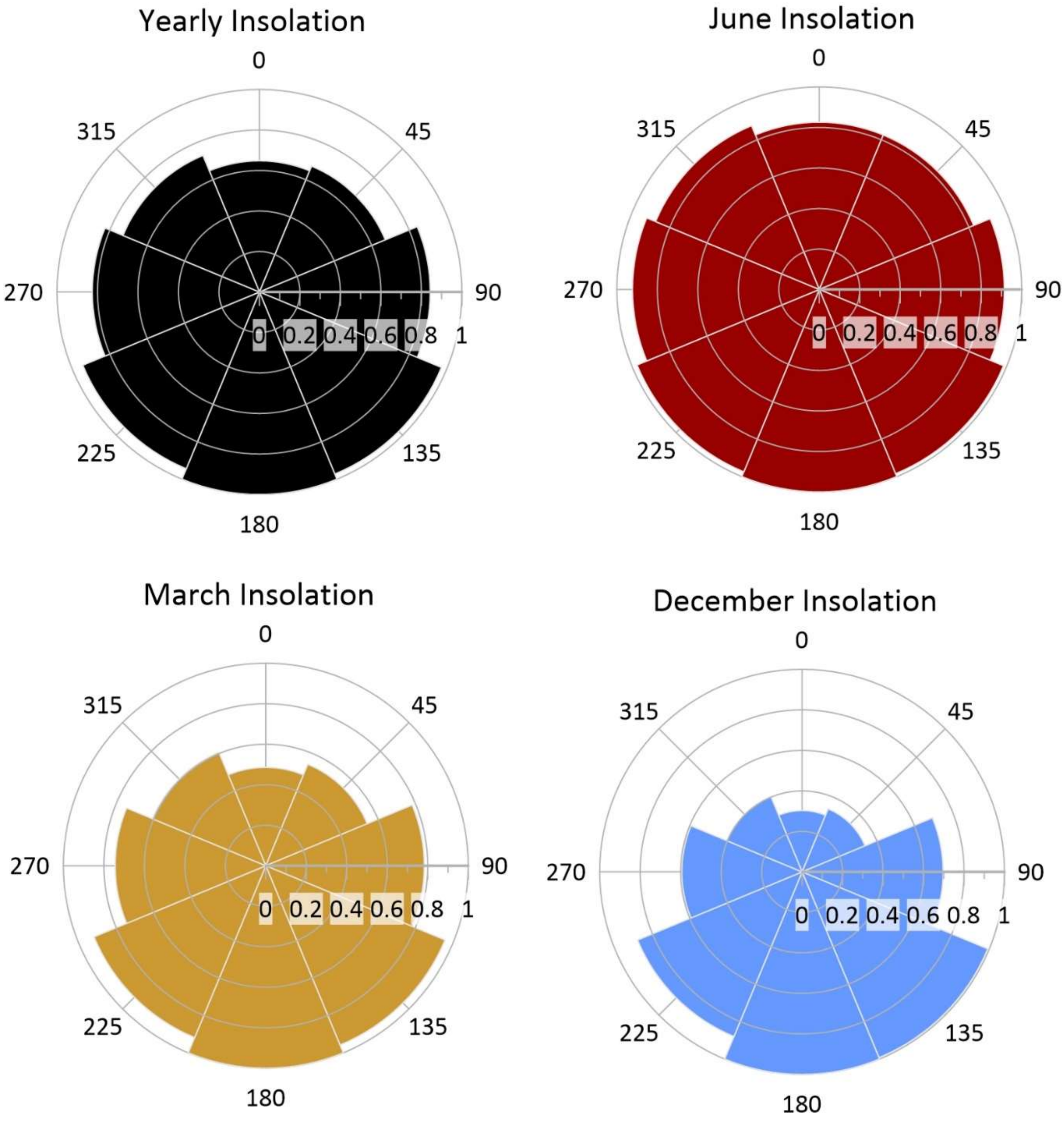


Figure S3. Solar radiation (insolation) on slopes greater than 10° estimated as a proportion of the average on slopes within 22.5° of south-facing (similar to Figure 1 in the main text). North aspect slopes receive ~65% the solar radiation of the average received on south aspect slopes for the entire year and approximately 30% in December, 50% in March, and just over 80% in June.

Table S1. Mean proportion of bluebunch wheatgrass seeds germinated and surviving to a given sampling time or seedlings surviving to a later sampling time in experimentally-seeded open and shaded plots derived from generalized linear mixed models via the emmeans package.

treatment	emmean	SE	df	lower.CL	upper.CL
Seed to June 2012					
Open	0.00894	0.00123	Inf	0.00683	0.0117
Shade	0.01888	0.0025	Inf	0.01455	0.0245
Seed to June 2013					
Open	0.00134	0.00032	Inf	0.000835	0.00214
Shade	0.00729	0.00159	Inf	0.004746	0.01118
Seedlings in June 2012 to June 2013					
Open	0.0976	0.0296	Inf	0.053	0.173
Shade	0.4341	0.0768	Inf	0.294	0.586
Seed to June 2019					
Open	0.00818	0.000761	Inf	0.00682	0.00982
Shade	0.01041	0.000952	Inf	0.0087	0.01245
Seed to June 2020					
Open	0.000411	7.74E-05	Inf	0.000284	0.000595
Shade	0.008726	1.00E-03	Inf	0.006969	0.010922
Seed to June 2021					
Open	0.000117	4.11E-05	Inf	5.88E-05	0.000233
Shade	0.004231	9.83E-04	Inf	2.68E-03	0.006667
Seedling in June 2019 to 2020					
Open	0.0408	0.0129	Inf	0.0218	0.0751
Shade	0.8179	0.044	Inf	0.7157	0.8891
Seedling in June 2020 to 2021					
Open	0.182	0.0708	Inf	0.0803	0.361
Shade	0.535	0.0797	Inf	0.3802	0.683

Table S2. Mean number of bluebunch wheatgrass seedlings detected at a given sampling time in unseeded open and shaded plots derived from generalized linear mixed models via the emmeans package.

treatment	emmean	SE	df	lower.CL	upper.CL
New seedlings 2018					
Open	0.833	0.373	Inf	0.347	2.0
Shade	6.0	1.0	Inf	4.328	8.32
New seedlings 2019					
Open	0.167	0.175	Inf	0.0214	1.3
Shade	6.667	2.342	Inf	3.3485	13.3
New seedlings 2020					
Open	0.5	0.323	Inf	0.141	1.77
Shade	18.8	5.736	Inf	10.368	34.21
New seedlings 2021					
Open	0.167	0.179	Inf	0.0202	1.38
Shade	0.667	0.427	Inf	0.1903	2.34
New seedlings 2022					
Open	0	2.63E-05	Inf	0	Inf
Shade	1.83	5.53E-01	Inf	1.02	3.0
Total surviving seedlings 2022					
Open	0.667	0.373	Inf	0.223	2.0
Shade	13.5	3.717	Inf	7.87	23.2

Table S3. Mean soil temperatures (°C) in open and shaded plots derived from general linear mixed models via the emmeans package.

treatment	emmean	SE	df	lower.CL	upper.CL
2016: May - early June					
Open	22.3	1.26	8.28	19.4	25.2
Shade	17.1	1.26	8.28	14.2	20
2016: mid-late June					
Open	25	0.98	7.63	22.7	27.3
Shade	21.8	0.98	7.63	19.5	24
2016: July					
Open	29.9	1.11	7.16	27.3	32.5
Shade	26	1.11	7.16	23.4	28.6
2017: May - early June					
Open	20.7	0.932	9.6	18.6	22.8
Shade	18.2	0.932	9.6	16.1	20.3
2017: mid-late June					
boundary (singular) fit					
2017: July					
Open	27.7	0.459	7.49	26.6	28.7
Shade	24.3	0.459	7.49	23.3	25.4
2018: mid-late June					
Open	31.3	3.18	5.17	23.2	39.4
Shade	27.1	3.18	5.17	19	35.2
2020: mid-late June					
Open	38.4	1.1	10.8	36	40.9
Shade	30.9	1.1	10.8	28.4	33.3
2021: mid-late June					
Open	44	3.74	7.72	35.3	52.7
Shade	37.1	3.74	7.72	28.4	45.8

Table S4. Mean soil moisture (proportion by mass) in open and shaded plots derived from general linear mixed models via the emmeans package.

treatment	emmean	SE	df	lower.CL	upper.CL
2016: May - early June 0-10 cm					
Open	0.0812	0.00837	8.51	0.0621	0.1
Shade	0.0844	0.00751	7.98	0.0670	0.102
2016: May - early June 10-20 cm					
Open	0.0782	0.00914	8.22	0.0572	0.0991
Shade	0.0791	0.00914	8.22	0.0581	0.1
2016: May - early June 20-30 cm					
Open	0.0631	0.0068	9.45	0.0478	0.0784
Shade	0.0583	0.0068	9.45	0.0430	0.0736
2016: mid-late June 0-10 cm					
Open	0.0458	0.00365	10.0	0.0377	0.0539
Shade	0.0435	0.00365	10.0	0.0354	0.0516
2016: mid-late June 10-20 cm					
Open	0.0427	0.00312	9.74	0.0358	0.0497
Shade	0.0414	0.00312	9.74	0.0344	0.0483
2016: mid-late June 20-30 cm					
Open	0.0631	0.0068	9.45	0.0478	0.0784
Shade	0.0583	0.0068	9.45	0.0430	0.0736
2016: July 0-10 cm					
boundary (singular) fit					
2016: July 10-20 cm					
boundary (singular) fit					
2016: July 20-30 cm					
Open	0.0272	0.00295	9.65	0.0206	0.0338
Shade	0.0323	0.00295	9.65	0.0257	0.0389
2017: May - early June 0-10 cm					
boundary (singular) fit					
2017: May - early June 10-20 cm					
boundary (singular) fit					
2017: May - early June 20-30 cm					
boundary (singular) fit					
2017: mid-late June 0-10 cm					
Open	0.0225	0.00385	8.87	0.0138	0.0312
Shade	0.0284	0.00385	8.87	0.0196	0.0371
2017: mid-late June 10-20 cm					
Open	0.0407	0.00347	8.69	0.0328	0.0486
Shade	0.0441	0.00347	8.69	0.0362	0.052
2017: mid-late June 20-30 cm					
boundary (singular) fit					

2017: July 0-10 cm					
Open	0.0154	0.00251	7.96	0.00961	0.0212
Shade	0.0214	0.00251	7.96	0.01562	0.0272
2017: July 10-20 cm					
Open	0.0357	0.0034	7.01	0.0277	0.0437
Shade	0.0350	0.0034	7.01	0.0270	0.0431
2017: July 20-30 cm					
Open	0.0430	0.00458	9.94	0.0327	0.0532
Shade	0.0486	0.00458	9.94	0.0384	0.0588
2018: mid-late June 0-10 cm					
boundary (singular) fit					
2018: mid-late June 10-20 cm					
Open	0.0260	0.0126	9.99	-0.00201	0.0541
Shade	0.0475	0.0126	9.99	0.01943	0.0755
2018: mid-late June 20-30 cm					
boundary (singular) fit					
2019: July 0-10 cm					
boundary (singular) fit					
2019: July 10-20 cm					
Open	0.0287	0.00191	12.0	0.0246	0.0329
Shade	0.0356	0.00206	12.4	0.0312	0.0401
2019: July 20-30 cm					
Open	0.0367	0.00185	9.72	0.0326	0.0408
Shade	0.0407	0.00185	9.72	0.0365	0.0448

Literature cited:

Quantum_Spatial 2018. Washignton 3 Counties LiDAR Techical Data Report, Contrct No. G16PC00016, Task Order No. G17PD01222**:** 36.