



Plant-Soil Feedbacks and Facilitation Influence the Demography of Herbaceous Alpine Species in Response to Woody Plant Range Expansion

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Plant species migrations, or range shifts, in response to changing climate are one of many interacting factors influencing plant population and community dynamics in an era of global change. Range shifts may cause novel assemblages of competing species because species may respond to changing climate at different rates. Range-expanding species may directly influence resident species through resource competition or indirectly by modifying the local environment both aboveground and belowground. Further, range-expanding plant species can create novel plant-soil feedbacks (PSFs) by altering soil microbial community structure and function and the interactions of resident plant species with microbial symbionts. These changes can have important implications for resident plant population dynamics and their ability to coexist with novel competitors. Here we test the impacts of competitive interactions and plant-soil feedbacks (PSFs) of a range-expanding sagebrush species (*Artemisia rothrockii*) on the demography and population growth rates of two resident alpine plant species (*Koeleria macrantha* and *Eriogonum ovalifolium*). We use an experimental, multi-year field approach combined with integral projection modeling to determine how PSFs and competition influence species coexistence in both the historic and range expansion zone of *A. rothrockii*. We find that sagebrush has an overall net negative effect on herbaceous plant demography, primarily due to negative PSFs for plants growing in sagebrush-conditioned soil. However, these negative soil effects are partially buffered via facilitation effects for herbs growing under or nearby sagebrush canopies. In general, population growth rates were more sensitive to survival than other demographic rates, furthermore this sensitivity to survival was higher for herbaceous species in sagebrush soils. Identifying the major drivers of plant population dynamics and species interactions remains an important and unresolved question in ecology. PSFs are a central mechanism influencing plant species interactions, yet the majority of PSF research has made little direct connection between plant population dynamics and PSFs *in situ*. We believe that utilizing a field-based approach, focusing on multiple components of plant demography, is an important next step in understanding the role of PSFs and species interactions in a changing world.

Keywords: plant-soil (belowground) feedbacks, range expansion, alpine, global change, demography, population dynamics, woody plant encroachment, integral projection model (IPM)

INTRODUCTION

Changes in climate and land use are creating novel communities of organisms around the globe (Tylianakis et al., 2008; Lurgi et al., 2012). In terrestrial ecosystems, species migrations or range shifts, often upwards in latitude or elevation, are an important mechanism driving these changes (Parmesan et al., 2003; Valéry et al., 2008). Species ranges may become larger (expansion), smaller (contraction), or simply shift in their distribution along a climate or land use gradient (Sexton et al., 2009; Chen et al., 2011). Range shifts are limited by both environmental and biotic filters as well as species dispersal abilities (HilleRisLambers et al., 2012) and many species are unable to migrate (Zhu et al., 2012). Together, these changes in species distributions are “reshuffling” the composition of plant communities, and often have significant community and ecosystem consequences, such as altered nutrient cycling and net primary production (Wardle et al., 2011; Alexander et al., 2016; Manrubia et al., 2019).

Competitive interactions between local and range-expanding plant species will influence both the ability of the range-expanding species to successfully establish and the capacity of resident plant species to persist within their historic distribution (Körner et al., 2008; Alexander et al., 2016; Fadrique and Feeley, 2016). Successful range shifts may require strong competitive abilities, while lack thereof may limit a species' ability to colonize a new area (Krapek and Buma, 2018; Neuschulz et al., 2018). In fact, novel plant competitors were equally or more influential than warming on plant performance in plant community transplants across an alpine elevation gradient (Alexander et al., 2015). The outcomes of species interactions are determined by coexistence mechanisms including the balance between inter- and intraspecific competition and negative density dependence (Callaway et al., 1997; Chesson, 2000; Mangan et al., 2010; Piao et al., 2014). Assessing the influence of range-expanding competitors on the demography and population dynamics of resident plant species will be critical to predicting whether resident and range-expanding species will successfully coexist.

In addition to altered competitive interactions, species range shifts may have indirect effects on resident plants through altering the local environment or trophic interactions. For example, range-expanding plant species can modify local resource pools, microclimate conditions, densities of species-specific herbivores or pollinators and interactions with soil organisms (Tylianakis et al., 2008; Metcalfe et al., 2011). Plant-soil-feedbacks (PSFs) are plant-induced changes to the soil which feedback to affect plant performance (Van der Putten et al., 2013). PSFs can play an important role in shaping plant species interactions and promoting species coexistence (Bever et al., 1997, 2012; Bever, 2003). For example, PSFs can help maintain species diversity by enhancing negative soil feedbacks on conspecific individuals via the accumulation species-specific soil pathogens (Bever, 2003). On the other hand, positive PSFs can lead to competitive exclusion and species dominance, thereby reducing overall diversity (Bever, 2003). Non-native invasive species often create PSFs which further promote their invasion, including reducing the diversity of mycorrhizal fungi or soil mutualists of resident species (Hawkes

et al., 2006), enhancing native soil pathogens (Eppinga et al., 2006), or selecting for microbes which preferentially degrade their own litter (Austin et al., 2014). Range-shifting plant species can also influence resident plant species via PSFs (Dostálek et al., 2016) and changes in mycorrhizal dominance (Williams et al., 2013), however further information is necessary to determine under which range-expansion scenarios this will occur (Tomliolo and Ward, 2018).

Range-expanding species that are functionally dissimilar to the native plant community may create strong PSFs, as plant origin alone (native vs. range expanding) does not necessarily predict impacts on soil microbial communities (Manrubia et al., 2019; Ramirez et al., 2019). These PSFs may arise through multiple mechanisms, including changes in the quantity or chemistry of leaf and root litter entering soil organic matter pools, changes to soil hydrology via rooting depth and structure, or association with novel microbial mutualists or pathogens (Klironomos, 2002; Wardle et al., 2004). For example, Mesquite trees expanding into desert grasslands associate with N-fixing bacteria and have deep taproots, thus altering soil nutrient pools, microbial communities and water availability for resident grasses (Wilson et al., 2001). Novel secondary compounds in litter of range-expanding species can also alter interactions of other plants with mycorrhizal fungi and free-living soil microbes (Weaver and Klarich, 1977; Nilsson et al., 1993; Wardle et al., 1998), creating potentially positive or negative PSFs.

Finally, PSFs can alter many components of the plant life cycle, including growth, survival, and reproduction, however the majority of PSF research has only considered effects on plant growth or biomass (Hovatter et al., 2013; Dudenhöffer et al., 2017). For example, seed germination may be limited by species-specific pathogens, particularly in close proximity to conspecific individuals (Mangan et al., 2010) and flower production can be enhanced by spatial heterogeneity of PSFs (Burns et al., 2017). Additionally, PSFs may cause contrasting responses across distinct phases of the plant life cycle, such as increased growth or vegetative biomass but decreased seed germination or flowering (Mehrabi et al., 2015; Dudenhöffer et al., 2017) creating an overall neutral effect on plant fitness. Therefore, all demographic life stages need to be simultaneously considered for a complete picture of how PSFs influence plant population dynamics (Dudenhöffer et al., 2017).

Woody plant range shifts are occurring in mountainous regions globally due to a variety of global change drivers including warming temperatures, increased CO₂, altered precipitation, and changes in fire and grazing regimes (Myers-Smith et al., 2011). In the White Mountains of California, climate and land use change has led to an upward range expansion of a dominant subalpine shrub species, *Artemisia rothrockii* A. Gray (Rothrock sagebrush) into alpine grasslands over the last 60 years (Kopp and Cleland, 2014). This range expansion has coincided with decreased abundance of a native bunchgrass [*Koeleria macrantha* (Ledeb.) Schult] and cushion plant (*Eriogonum ovalifolium* Nutt.), however the mechanism(s) of these species' declines are unknown (Kopp and Cleland, 2014). We sought to determine the relative importance of direct competition with sagebrush vs. indirect soil effects, a form of

apparent competition, for driving the decline in abundance of *K. macrantha* and *E. ovalifolium* in the White Mountains.

Specifically, we asked: Does sagebrush range expansion influence the demography of native alpine plant species in the White Mountains? Are sagebrush influences on demography and population growth rates (λ s) via direct competition and/or apparent competition via PSFs, and what are the relative strengths of these mechanisms? We hypothesized that sagebrush creates negative PSFs for *K. macrantha* and *E. ovalifolium*, which manifest in lower demographic and population growth rates for plants growing in sagebrush soil. Inducing negative PSFs is a common mechanism by which non-native invasive plants gain a competitive advantage over resident species (Suding et al., 2013), and we extend this line of reasoning to a native range-expanding species. We predicted that the negative effects of PSFs will be stronger than the effects of direct competition with sagebrush because competitive interactions can be weak or shift to facilitation in stressful abiotic conditions, such as alpine environments (Callaway et al., 2002; Maestre et al., 2009).

MATERIALS AND METHODS

Location

This study takes place in the subalpine to alpine zones of the White Mountains of California, which lie on the western edge of the Great Basin in the rain shadow of the Sierra Nevada range. The climate is cold and dry, receiving between 327 and 456 mm of precipitation annually and mean annual temperatures span from 0.9 to -1.7°C (Hall, 1991). These mountains have extremely diverse soil histories (Mooney and Zavaleta, 2016) but this study was confined only to granitic soils (Colluvium derived from granite) and east-/south-east-facing slopes to control for edaphic and topographic variation. Abiotic soil characteristics across the elevation gradient and plant communities of this area are summarized in Collins et al. (2016), but in general, soils have low levels of organic matter ($\sim 1.7\text{--}2.6$ mg/L TOC, $0.8\text{--}0.34$ mg/L TON) and low soil moisture ($\sim 1.9\text{--}10.3\%$ VWC), which both increase with elevation. Soil pH is slightly acidic (~ 6) across the study area.

Study Species

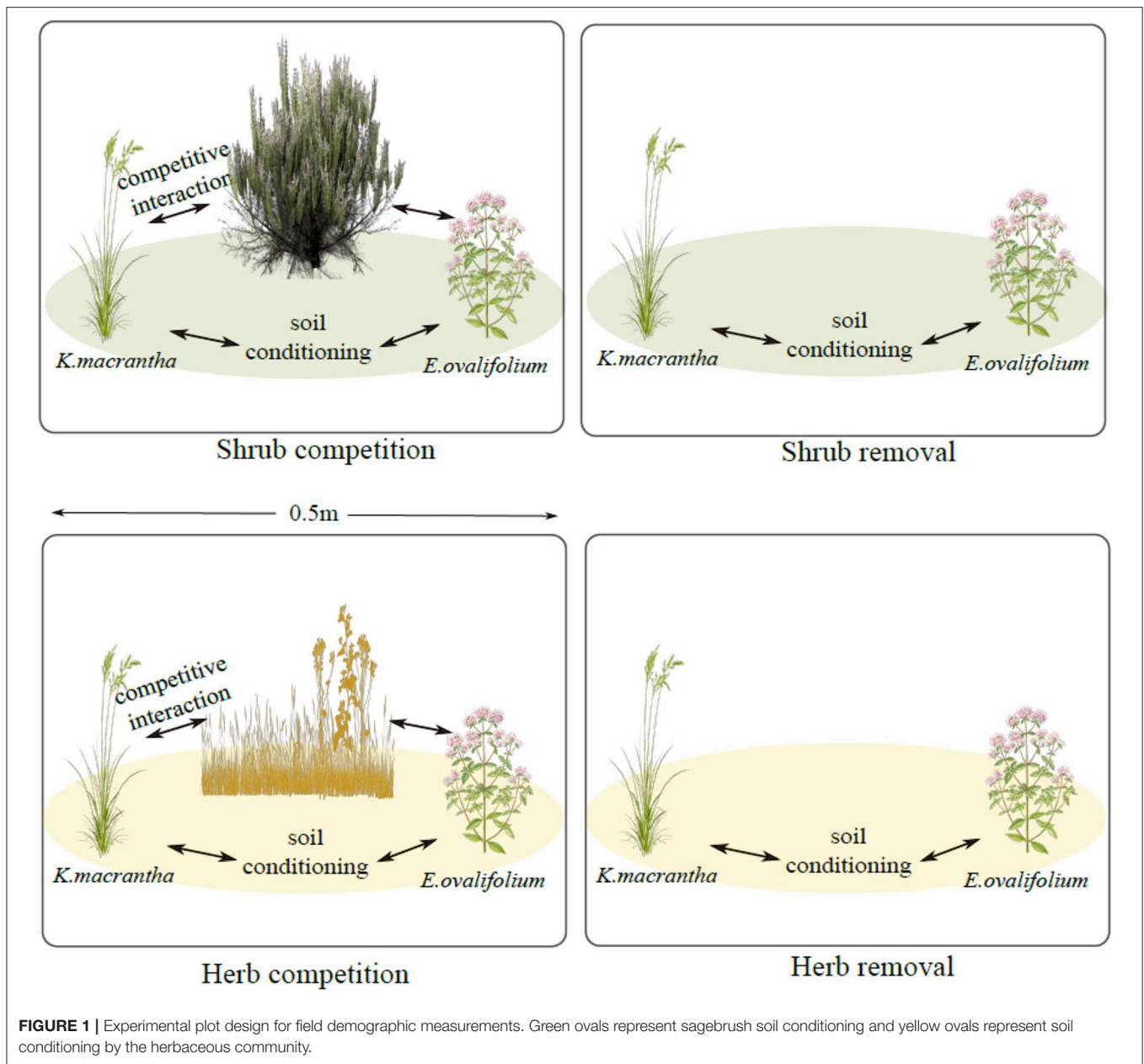
We conducted this study across a gradient of *A. rothrockii* range expansion from subalpine ($<3,500$ m) to alpine ($>3,500$ m) zones that has been documented in the White Mountains over the last 50 years (Kopp and Cleland, 2014). In 1961, *A. rothrockii* was not present at the 3,800 m site, was found in moderate to low densities at the 3,500 m site, and high densities at the 3,200 m site (Mooney et al., 1962; Kopp and Cleland, 2014). Currently, it is found at high densities, but with more spacing between individuals ($\sim 1\text{--}2$ m) at the low and middle elevation sites, and in isolated circular patches ~ 10 m wide but with shrubs more closely clustered at high elevation sites (Kopp and Cleland, 2018, personal observation). Therefore, this gradient spans from the “historic range” of *A. rothrockii* at low elevations to the leading edge of the “expansion range” at high elevations where *A. rothrockii* transitions from an almost continuous population to isolated patches.

Artemisia rothrockii is a California endemic shrub, while *K. macrantha* and *E. ovalifolium* are more widespread throughout the western United States and span a wide habitat range from pinyon juniper woodlands to subalpine forests, and alpine fellfield (Calflora, 2019). Sagebrush, primarily *A. tridentata*, is known to strongly compete with herbaceous plant species for water and nutrients, particularly phosphorus, across the intermountain west (Robertson, 1947; Caldwell et al., 1985; Fowler, 1986; Ryel et al., 2004). Sagebrush also directly alters the abiotic soil environment including enhancing water and nutrients below its canopies as compared to herbaceous soils (Collins et al., 2016). Additionally, sagebrush alters the soil microbial community structure and function, including the diversity and community composition of soil bacteria and fungi, substrate induced respiration (CO_2 flux) and extracellular enzyme activity (Collins et al., 2016, 2018, and unpublished data).

These changes are likely to have important feedbacks on herbaceous plant species by altering the relative abundances of microbial taxa, such as species-specific soil mutualists and pathogens. In addition, secondary compounds in sagebrush litter may alter how herbaceous plants (grasses, forbs etc.) interact with mycorrhizal fungi and free-living soil microbes (Weaver and Klarich, 1977; Nilsson et al., 1993; Wardle et al., 1998). Aboveground sagebrush removal led to the re-establishment of herbaceous cover (including *K. macrantha* and *E. ovalifolium*) after 4 years in the White Mountains suggesting potentially high levels of interspecific competition (Kopp and Cleland, 2018). However, indirect soil effects of sagebrush on alpine plant growth, a form of apparent competition, may be as strong or stronger than the direct effects of competition with sagebrush (Allen et al., 2018).

Experimental Design

We monitored populations of *K. macrantha* and *E. ovalifolium* at three elevations described previously: 3,200, 3,500, and 3,800 m (3,200 m site: UTM: 396148 E; 4151156 N; 3,500 m site: UTM: 390629 E124157248 N; 3,800 m site: UTM: 390445 E; 4159559 N-UTM Zone 11). In July 2015, we established 30 experimental blocks, each with four 0.5×0.5 m plots (treatments) and each block was repeated 5 times for each species at each elevation (site). Each plot has one of the following 4 treatments: shrub competition, shrub removal, herbaceous competition and herbaceous removal (Figure 1). Shrub plots (competition and removal) were selected where individuals of *K. macrantha* and/or *E. ovalifolium* were growing directly under or very nearby (<0.25 m) a sagebrush canopy. Herbaceous plots (competition and removal) were selected in the interspaces of sagebrush between 1 and 5 m away from the nearest shrub canopy, based on the sagebrush density at each site. For competition plots, the entire plant community was left intact. For shrub removal plots, aboveground sagebrush biomass was removed by cutting down stems at the base. For herb removal plots, aboveground biomass of all non-target herbaceous plant species was removed by manually clipping with scissors. For both removal plots, only aboveground biomass was removed to prevent significant disturbance to soil structure. All treatments were maintained annually, and any regrowth trimmed back.



Our experiment was designed to disentangle above- and belowground influences of sagebrush on herbaceous plant demography under natural field conditions. Plants growing in removal plots are experiencing soil legacies (both biotic and abiotic) of either the shrub or the herbaceous community, but without aboveground competition from the removed species. In the non-removal plots (competition), plants are experiencing both the soil conditioning and competition from shrubs and/or herbs. By comparing performance of the focal species in the shrub plots and the shrub removal plots, we can therefore isolate the effect of shrub competition (Figure 1). Similarly, by comparing the herbaceous plots to the herb-removal plots, we estimated the effects

of shrub PSFs, in the absence of shrub competition, we compared the shrub removal plots to the herbaceous removal plots, because the primary difference between those plots was the identity of plants conditioning the soil. Sagebrush, soil conditioning overwhelms that of herbaceous plants in its litter chemistry and biomass, and creates a distinct soil environment underneath its crown (Welch, 2005; Collins et al., 2016) and therefore we attribute soil effects to sagebrush directly. However, we do not estimate PSFs of the herbaceous community, as the species composition was more variable across sites, and soil conditioning is much less concentrated than under shrub canopies.

Field-based approaches for measuring plant-soil feedbacks have been used successfully in other studies (Kulmatiski, 2006;

Mccarthy-Neumann and Ibáñez, 2012). Nonetheless, there are trade-offs to this approach relative to more traditional controlled experiments in a greenhouse or common garden. A strength of this approach is that soils are conditioned in the field, under natural climate conditions and over longer time periods, creating a more realistic soil environment (Kulmatiski and Kardol, 2008; Pernilla Brinkman et al., 2010). Additionally, this approach does not risk spurious effects that can occur with soil sterilization (Bonanomi et al., 2005). A limitation of a field-based approach, however, is that it is not possible to disentangle the influences of soil microbial communities and the physical soil environment in the field (Kulmatiski and Kardol, 2008; Pernilla Brinkman et al., 2010). Thus, our estimated PSFs include all physio-chemical and microbial changes caused by sagebrush soil conditioning to be plant-soil feedbacks potentially influencing plant demography.

Demographic Measurements

Within each of the four plots (treatments) in all blocks, we tagged up to five adult individuals, depending on species density at the site, of either *K. macrantha* or *E. ovalifolium* and took initial demographic measurements in July 2015. For *K. macrantha*, plant area was calculated by multiplying height of the tallest leaf (cm) by width of the tussock (cm). For *E. ovalifolium*, plant area was calculated through digital image analysis. Photos of each individual plant were taken with a ruler for scale in the field and were then analyzed in ImageJ (Version 1.51 J8) based on the methodology of Jarou (2009). For both species, we measured flowering status (Y/N), and number of inflorescences of each flowering individual. Seed production per inflorescence was calculated as a single value for each species on 100 additional inflorescences which were counted in the laboratory using a dissecting microscope to ensure seed maturity/viability. Beginning in 2016, mortality was also recorded as alive (Y/N) for each individual. Plots were re-sampled yearly in mid-July to early August (depending on snow melt) and all measurements taken for three subsequent years, for a total of four years of measurements (2015, 2016, 2017, 2018).

Recruitment probabilities were estimated using seed germination trials for each species. In September 2017, mature seeds from both species were collected from 10 individuals at each elevation. Seeds were placed in 12×12 cm mesh bags and then deployed in the field by fixing them to the upper soil surface using metal stakes. Each bag contained 10 seeds and for each species, 12 bags were deployed at each elevation site, six under sagebrush canopies and six in shrub interspace. Bags were collected in mid-July 2018, and total number of germinated seeds in each bag were recorded. Probabilities were calculated as the total of germinated seeds/sum seeds deployed. Due to low overall germination, single probabilities were calculated for each species and were not elevation- or treatment-specific. In addition, due to low germination percentages and slow growth of alpine plants, we were unable to measure recruit sizes in the field. For *K. macrantha*, we estimated recruit size distribution from the seedling dataset of Chu and Adler (2014). For *E. ovalifolium*, due to the lack of available information on this species, we simulated seedling size data based on the smallest 2.5% of adults in the dataset, which produced a size distribution of 0.001–2.5 cm² and

a mean of 0.6 cm². While this modeling choice could affect the magnitude of estimated population growth rates, it should not bias the analysis of treatment effects.

Population Modeling

We calculated size-dependent demographic rates (growth, survival probability, flowering probability, and seed production) using 229 and 224 individuals of *K. macrantha* and *E. ovalifolium*, respectively. Plant size was logged in all models for normality and seed number was logged to transform from count data to continuous. Germination probability was estimated as a single value for each species based on seed germination trials, and recruit size was estimated using an intercept only linear model using the dataset from Chu and Adler (2014) for *K. macrantha* and a simulated dataset of realistic recruit sizes for *E. ovalifolium* as described above.

We used mixed effects models for each demographic rate, including fixed effects of size, treatment and elevation, and a random effect of year. We fit these as Bayesian models using the brms package (Bürkner, 2018) in R (R Core Team, 2015), and using the default non-informative, improper priors for all models. We used a “nested” model structure with elevation effects nested within treatments. Importantly, we fit this model with elevation nested within treatments in order to allow for “partial pooling” of information across elevations within each treatment. Partial pooling allowed separate estimates of demographic rates at each treatment \times elevation combination, but the data from different elevations, within a treatment, informed each other. This approach is therefore a compromise between complete pooling of data across elevations and independent estimates for each elevation \times treatment. This was a conservative modeling decision based on the observation that mortality events in particular were sparse in the dataset; the partial pooling prevents biases from sparse data, such as the chance event that an elevation has no mortality (see **Figure S3** for comparison of the “partial pooling” model with a “no pooling” model). We tested for the treatment and elevation effects on each demographic rate by calculating pairwise contrasts using the posterior distributions and computing the probabilities that the difference between each pair was different from zero.

Using the posterior distributions from the demographic rate models, we constructed integral projection models (IPMs) to calculate population growth rates (lambdas) for each species within each treatment \times elevation combination. These population models and estimated lambdas were used as a way to integrate the effects of sagebrush across multiple phases of the plant life cycle, rather than accurate projections of population growth rates. Thus, we consider lambda to be an estimate of the relative fitness of each species among the different plot treatments, and do not suggest they will accurately predict changes in population sizes over time. The effects of shrub and herbaceous competition, as well as shrub PSFs, on lambdas were calculated using a-priori contrasts between the lambdas estimated in the different treatments: Shrub Competition = (Shrub competition) – (Shrub removal); Herb Competition = (Herb competition) – (Herb removal); Shrub PSF = (Shrub removal) – (Herb removal) (**Figure 1**). These contrasts were

TABLE 1 | Contrasts among vital rates for *Koeleria macrantha* (KOMA) and *Eriogonum ovalifolium* (EROV). Pr(negative) represents the probability that the effect of Treatment 1 < Treatment 2, whereas Pr(positive) is the probability that the effect of Treatment 1 > Treatment 2 [and is equal to 1 – Pr(negative)]. Only contrasts with probabilities >0.75 are displayed.

Vital rate	Elevation	Spp.	Treatment 1	Treatment 2	Pr(negative)	Pr(positive)	
Growth	3,200	KOMA	Herb	Shrub	0.16	0.84	
		KOMA	Herb	Shrub removal	0.08	0.92	
		KOMA	Herb removal	Shrub	0.13	0.87	
		KOMA	Herb removal	Shrub removal	0.07	0.94	
		KOMA	Herb removal	Shrub removal	0.14	0.86	
	3,800	KOMA	Herb	Shrub	0.17	0.83	
		KOMA	Herb	Shrub removal	0.10	0.90	
		KOMA	Herb removal	Shrub	0.11	0.89	
		KOMA	Herb removal	Shrub removal	0.06	0.94	
Survival	3,200	KOMA	Herb	Herb removal	0.04	0.96	
		KOMA	Herb	Shrub	0.22	0.78	
		KOMA	Herb	Shrub removal	0.17	0.83	
		KOMA	Herb removal	Shrub	0.81	0.19	
		KOMA	Herb removal	Shrub removal	0.80	0.20	
	3,500	KOMA	Herb	Herb removal	0.77	0.23	
		3,800	KOMA	Herb	Herb removal	0.05	0.95
	KOMA		Herb	Shrub	0.23	0.77	
	KOMA		Herb	Shrub removal	0.11	0.89	
	Flowering	3,200	KOMA	Herb removal	Shrub	0.84	0.16
KOMA			Herb	Herb removal	0.85	0.15	
KOMA			Herb removal	Shrub	0.24	0.76	
KOMA			Herb removal	Shrub removal	0.12	0.88	
3,500			KOMA	Herb	Herb removal	0.84	0.16
		KOMA	Herb	Shrub	0.81	0.20	
		KOMA	Herb	Shrub removal	0.80	0.20	
3,800		KOMA	Herb	Herb removal	0.13	0.87	
		KOMA	Herb	Shrub	0.01	0.99	
		KOMA	Herb	Shrub removal	0.05	0.95	
	KOMA	Herb removal	Shrub	0.06	0.94		
Seeds	3,200	KOMA	Shrub	Shrub removal	0.82	0.18	
		KOMA	Herb	Shrub	0.08	0.92	
		KOMA	Herb removal	Shrub	0.02	0.98	
		KOMA	Shrub	Shrub removal	0.98	0.02	
		3,500	KOMA	Herb removal	Shrub	0.80	0.20
	3,800		KOMA	Herb	Herb removal	0.23	0.77
		KOMA	Herb	Shrub	0.00	1.00	
		KOMA	Herb	Shrub removal	0.01	0.99	
		KOMA	Herb removal	Shrub	0.00	1.00	
		KOMA	Herb removal	Shrub removal	0.03	0.97	
Growth	3,500	EROV	Herb	Herb removal	0.15	0.85	
		EROV	Herb	Shrub	0.13	0.87	
		EROV	Herb	Shrub removal	0.12	0.88	
		3,800	EROV	Herb	Herb removal	0.05	0.95
			EROV	Herb	Shrub	0.00	1.00
	EROV		Herb	Shrub removal	0.00	1.00	
	EROV		Herb removal	Shrub	0.00	1.00	
	EROV		Herb removal	Shrub removal	0.00	1.00	
			EROV	Shrub	Shrub removal	0.23	0.77

(Continued)

TABLE 1 | Continued

Vital rate	Elevation	Spp.	Treatment 1	Treatment 2	Pr(negative)	Pr(positive)	
Survival	3,200	EROV	Herb	Herb removal	0.80	0.20	
		EROV	Herb	Shrub	0.96	0.04	
		EROV	Herb	Shrub removal	0.91	0.09	
		EROV	Herb removal	Shrub	0.88	0.12	
	3,500	EROV	Herb	Shrub	0.91	0.09	
		EROV	Herb removal	Shrub	0.86	0.14	
		EROV	Shrub	Shrub removal	0.16	0.84	
		EROV	Herb	Herb removal	0.22	0.78	
	3,800	EROV	Herb	Shrub	0.16	0.84	
		EROV	Herb	Shrub removal	0.09	0.91	
		EROV	Herb removal	Shrub removal	0.21	0.79	
		EROV	Herb removal	Shrub removal	0.04	0.96	
Flowering	3,500	EROV	Herb	Herb removal	0.04	0.96	
		EROV	Herb	Shrub	0.00	1.00	
		EROV	Herb	Shrub removal	0.01	0.99	
		EROV	Herb removal	Shrub	0.12	0.88	
	3,800	EROV	Herb	Herb removal	0.15	0.85	
		EROV	Herb	Shrub	0.00	1.00	
		EROV	Herb	Shrub removal	0.00	1.00	
		EROV	Herb removal	Shrub	0.00	1.00	
	Seeds	3,200	EROV	Herb	Shrub	0.03	0.97
			EROV	Herb removal	Shrub	0.04	0.96
			EROV	Shrub	Shrub removal	0.95	0.05
			EROV	Herb	Herb removal	0.83	0.17
3,500		EROV	Herb	Shrub	0.06	0.94	
		EROV	Herb removal	Shrub	0.01	0.99	
		EROV	Herb removal	Shrub removal	0.24	0.76	
		EROV	Shrub	Shrub removal	0.93	0.07	
3,800		EROV	Herb	Herb removal	0.92	0.08	
		EROV	Herb	Shrub	0.04	0.96	
		EROV	Herb removal	Shrub	0.00	1.00	
		EROV	Herb removal	Shrub removal	0.20	0.80	
		EROV	Shrub	Shrub removal	0.96	0.04	

calculated from the posterior distributions of estimated lambdas within each treatment \times elevation.

Finally, we conducted elasticity analyses to assess the contributions of different demographic rates to lambdas, and the effects of treatments on demographic rate sensitivities. The elasticity analyses on growth, survival, and probability of reproduction determine the sensitivity of lambda to changes in specific demographic rates. For all IPM analyses, we used modified R code from Ellner et al. (2016).

RESULTS

Demographic Rate Models

All demographic rates varied by treatment and elevation for both species. Pairwise contrasts for all demographic rates among plot treatments within each elevation and the probabilities that each treatment is greater (or less) than another treatment are listed in

Tables S1 and S2. Here we report contrasts where the probability was >0.75 (Table 1).

We find in general that demographic rates tended to be highest in herbaceous and herbaceous removal plots for both species, and this pattern was strongest at the high and low elevation sites. For *K. macrantha*, growth was highest in herbaceous plots at the low elevation site and in herbaceous removal plots at the middle and high elevation sites. Growth in herbaceous and herbaceous removal plots was higher in than in shrub and shrub removal plots which suggests that sagebrush has a negative effect on *Koeleria* growth (Table 1, Figure S1). Survival varied greatly by treatment and elevation and overall was highest herbaceous removal plots at the middle elevation site and herbaceous plots at the low and high elevation sites (Table 1, Figure 2, Figure S1). Probability of flowering was greatest in herbaceous and herbaceous removal plots particularly at high elevation, however was higher in shrub plots at the middle elevation site (Table 1, Figure S1). Similarly seed production was higher in

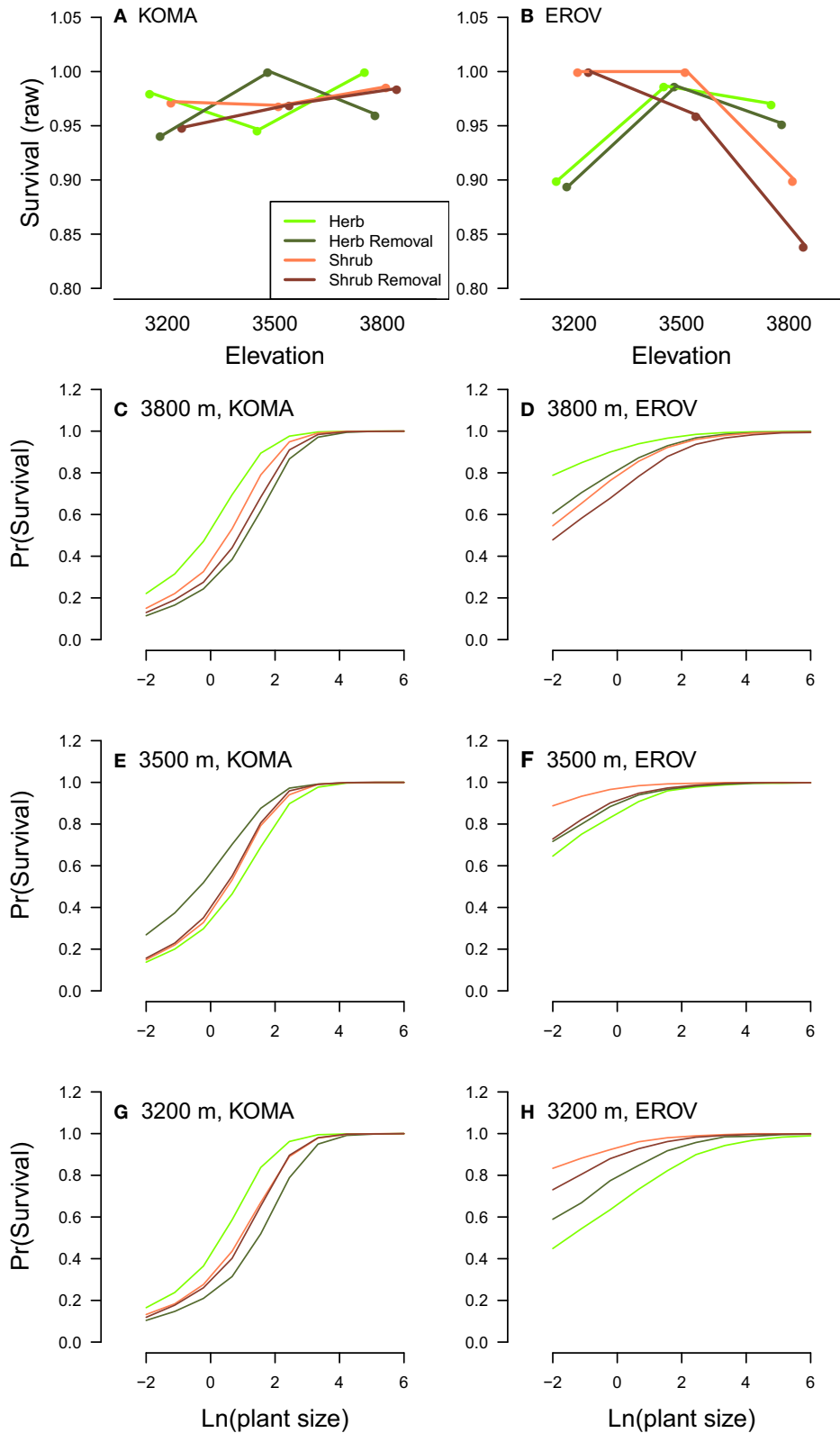
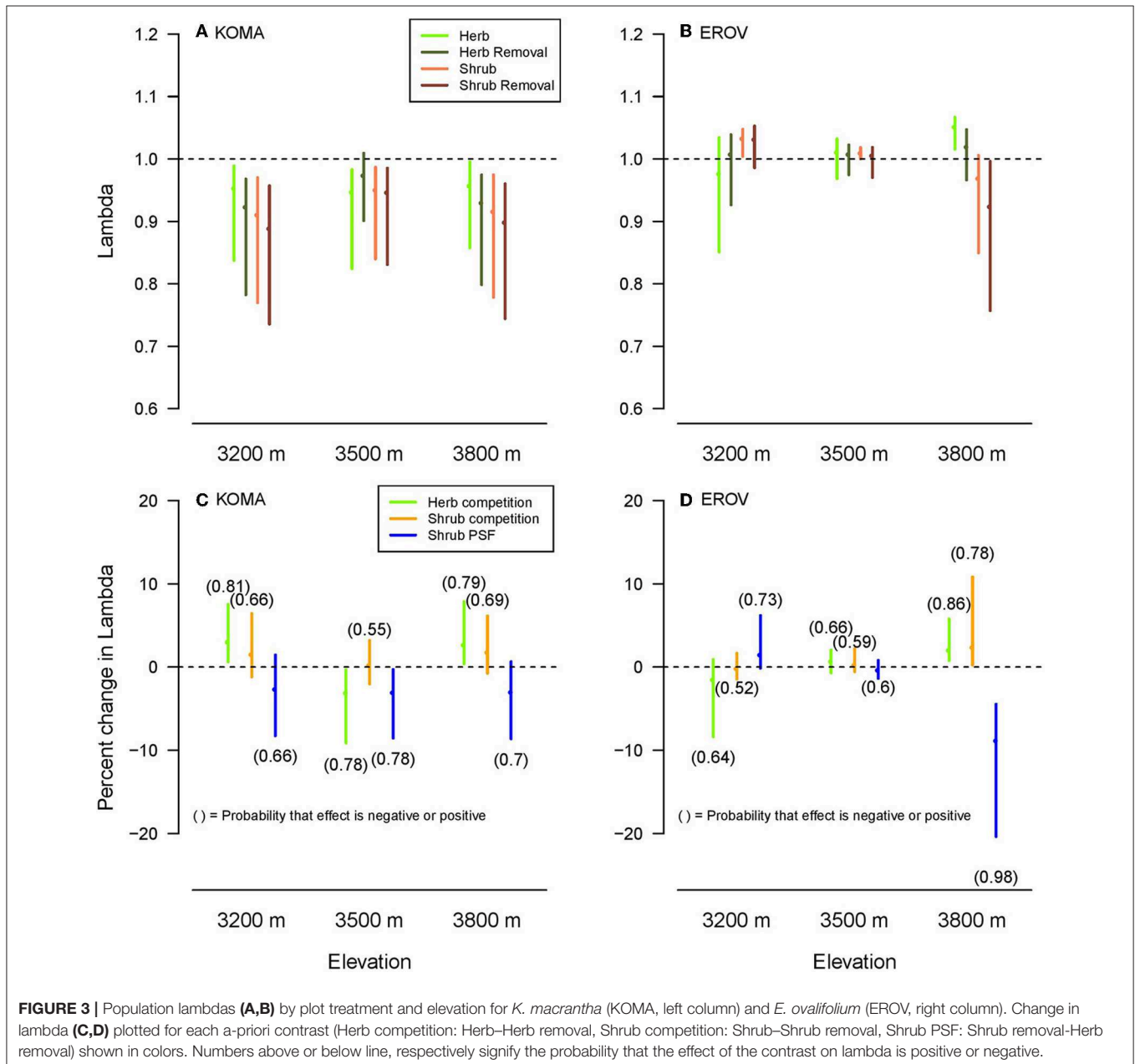


FIGURE 2 | Plot treatment effects on survival for *K. macrantha* (KOMA, left column) and *E. ovalifolium* (EROV, right column). Raw survival data is shown in the top row (A,B) plotted by elevation (m) on the x-axis and by plot treatments in different colors. Modeled probability of survival is shown in the bottom figures (C–H) and plotted separately for each elevation by species combination, with individual plant size on the x-axis and colored lines signifying different plot treatments.

shrub plots at the middle elevation site which suggests that sagebrush may have a positive effect on reproduction at this site which counters the negative effects on growth and survival (Table 1, Figure S1). At low and high elevations flowering and seed production were greater in herbaceous and herbaceous removal plots than in shrub and shrub removal plots, which follows the general pattern we observe for the other demographic rates (Table 1, Figure S1).

Many patterns observed in *K. macrantha* demographic rates were similar for *E. ovalifolium*. Growth was highest in herbaceous and herbaceous removal plots at the middle and high elevation sites and no treatments were different at the low elevation site. Growth in herbaceous and herbaceous removal plots was

higher in than in shrub and shrub removal plots which suggests that sagebrush also has a negative effect on *Eriogonum* growth (Table 1, Figure S2). Survival also varied by treatment and elevation and overall was highest shrub and shrub removal plots at the low and middle elevation site, but then dropped significantly at the high elevation site, and fell below both herbaceous and herbaceous removal plots (Table 1, Figure 2, Figure S2). Probability of flowering was greatest in herbaceous and herbaceous removal plots, particularly at high elevation, and was higher than shrub and shrub removal plots except at low elevation where no treatments differed (Table 1, Figure S2). Seed production was highest in herbaceous and herbaceous removal plots across all elevations but especially at the high elevation site.



This suggests that sagebrush has a more negative influence on *Eriogonum* than *Koeleria* reproduction, particularly in the range expansion zone (Table 1, Figure S2).

Population Growth Rates (Lambdas)

Lambda values were higher overall for *E. ovalifolium* than *K. macrantha*, while the differences among lambdas across treatments and elevations were distinct for each species. Herb and herb removal plots had higher median lambda values than shrub and shrub removal plots for *K. macrantha* at low and high elevations and for *E. ovalifolium* at high elevation (Figures 3A,B). This reflects the general pattern observed in the demographic rate models where negative effects of sagebrush were strongest at the two ends of the elevation gradient. At 3,500 m elevation, lambdas did not differ among the plot treatments except for a slight increase in herbaceous removal plots for *K. macrantha* (Figure 3A). Lambdas in shrub and shrub removal plots were higher than in herb and herb removal plots for *E. ovalifolium* at 3,200 m elevation (Figure 3B). This is likely due to the fact that survival was higher in shrub and shrub removal plots at this site, as survival has a very large contribution to lambda in this system (see elasticity analyses).

For the a-priori contrasts, Herb competition (herb competition-herb removal) had a positive effect (probability >0.75) on lambda for *K. macrantha* at 3,200 and 3,800 m elevations and *E. ovalifolium* at 3,800 m elevation, and a negative effect on lambda for *K. macrantha* at 3,500 m elevation (Figures 3C,D). Shrub competition (shrub competition – shrub removal) had a positive effect on lambda for *E. ovalifolium* at 3,800 m elevation, and slightly positive to neutral effect at other elevations (Figures 3C,D). Shrub PSFs (shrub removal – herb removal) had a negative effect on lambda for *E. ovalifolium* at 3,800 m elevation and *K. macrantha* at 3,500 m elevation and slightly negative to neutral effect on lambda at other elevations except for *E. ovalifolium* at 3,200 m where the effect was slightly positive (Figures 3C,D).

Elasticity Analyses

Survival had the highest impact on population lambdas of all demographic rates (max elasticity values ~0.35–0.45) for both species however *E. ovalifolium* had slightly higher elasticity than *K. macrantha*, particularly at the high elevation site in shrub and shrub removal plots (Figure S4). Growth had the next highest impact on lambda (max elasticity values ~0.16–0.25) for both species however *K. macrantha*, had higher elasticities than *E. ovalifolium*, which signifies that growth contributed more to population lambdas in the grass species. Additionally, the influence of plant growth on lambdas was more important at larger size class transitions [moving from size class $\sim z(\log) 4$ to $\sim z(\log) 5$] for *Koeleria* vs. smaller size class transitions [$\sim z(\log) 2$ to $\sim z(\log) 3$] for *Eriogonum* (Figure S5). This shows that changes in the growth rate of larger, smaller individuals are more important for population lambdas in the grass, cushion plant, respectively. Growth elasticities did not vary noticeably by elevation or treatment. Probability of reproduction contributed the least to population lambdas, however had a much more

significant contribution for *Eriogonum* (max elasticities ~0.005–0.016) than *Koeleria* (max elasticities ~0–0.0025) (Figure S4).

DISCUSSION

Understanding the broader implications of species range shifts will be crucial as climate change continues to promote differential species migration and novel species interactions (Midgley et al., 2007; Tomiolo and Ward, 2018). In this study, we sought to tease apart the potential above- and belowground mechanisms by which a range-expanding sagebrush species, *Artemisia rothrockii*, affected the demography of two herbaceous alpine plant species. We found that sagebrush most often had a net negative effect on the demographic rates and population lambdas of herbaceous species. Our results suggest that these effects were driven by negative PSFs for plants growing in sagebrush conditioned soil, counteracting facilitative effects of sagebrush aboveground. However, we found variation among species and across elevations suggesting that the effects of sagebrush PSFs vary based on abiotic conditions of the site and for herbaceous species identity. Overall these results show for the first time, using a manipulative field experiment and demographic modeling, that shrubs may have both positive and negative impacts on herbaceous plant demography due to distinct aboveground and belowground mechanisms.

Demographic Rates and Lambdas

Sagebrush affected the demography and population lambdas of both *E. ovalifolium* and *K. macrantha* across an elevation gradient in the White Mountains. Specifically, plants growing with sagebrush, or in its conditioned soils, tended to have slower growth, reduced probability of flowering and lower seed production than those growing in herbaceous dominated soils. Thus, population lambdas that were highest in herbaceous and herbaceous removal plots and lowest in shrub and shrub removal plots, respectively (Figure 3). This supports the hypothesis that sagebrush would have a negative effect on the demography of native alpine plants. These differences were particularly pronounced at the high elevation site and were consistent for both species of interest, suggesting the strong influence of sagebrush on herbaceous plant population dynamics in the range expansion zone.

Similar to our findings, an herbaceous forb species growing in association with four Mediterranean montane shrubs had reduced reproductive output including lower number of seeds and reproductive stems, and lower infructescence volume compared to individuals growing in open areas (Macek et al., 2016). In our study system, however, previous work showed that *A. rothrockii* slowed the phenology and reduced the flower production of a *Trifolium* cushion plant via shading, thus decreasing the benefits of climate warming on reproduction (Kopp and Cleland, 2015). This contrasts somewhat with our finding of reduced reproductive output (flowering and seeds) in both shrub and shrub removal plots, suggesting that the relative importance of shading vs. belowground effects may vary among herbaceous species.

Survival of *E. ovalifolium* was a notable exception to this overall pattern, being significantly higher in shrub and shrub removal plots at low and middle elevations. However, survival sharply declined in shrub and shrub removal plots at the high elevation site for *E. ovalifolium* (Figure 3B). For *K. macrantha*, survival was intermediate in shrub and shrub removal plots depending on elevation. These treatment effects on survival were critical because overall mortality was low across the observation period (~2% *Koeleria*, ~2.5% *Eriogonum*). Low mortality rates are common for slow-growing alpine species that are well-adapted to stressful abiotic conditions (Körner, 2003). Therefore, when mortality events do occur, they can strongly impact population growth rates (see Elasticity analyses).

The differences in how *E. ovalifolium* and *K. macrantha* responded to the experimental treatments reflect the large differences in their life history characteristics. *E. ovalifolium* is a slow growing, long lived, cushion plant while, *K. macrantha* is a/perennial bunchgrass with an average lifespan between 7 and 10 years (Dixon, 2000; Rundel et al., 2005; Anderson, 2006). *Koeleria* is solely wind pollinated, while *Eriogonum* is wind pollinated, but also largely insect and bird pollinated, and produces many fewer seeds per inflorescence. Finally, *Koeleria* senesces most of its aboveground biomass annually, while *Eriogonum* retains green leaves throughout the winter. Despite these strong differences, overall patterns in lambda were relatively similar, particularly at high elevation sites, where sagebrush establishment is most recent and therefore demographic rates will potentially be most responsive.

Elasticity Analyses

We used elasticity analyses to understand which demographic rates contributed most to the observed patterns in population lambdas and how robust lambda values were to changes in demographic rates. Survival had the largest contribution to population lambdas, followed by growth and then probability of reproduction. Elasticities also varied among the two species, treatments and by elevation. *Eriogonum* had higher elasticities in response to changes in survival, particularly at high elevation in shrub and shrub removal plots. This suggest that in areas of recent sagebrush establishment, population growth may be particularly affected by mortality events for this species, and more so than when growing in the herbaceous plant community.

Although survival was the most important demographic rate for both species, changes in growth were more important for *Koeleria* than *Eriogonum*, likely due to faster growth and a shorter lifespan of this grass species. Finally, the probability of reproduction had a very minor influence on lambda but was significantly more important for *E. ovalifolium* than *K. macrantha*. Again, this likely reflects differences in the life history characteristics of these species in that *Eriogonum* produces fewer seeds per inflorescence and has a more complex pollinator strategy, making reproduction a more important component of its overall population growth. Overall, lower lambda values suggest that *K. macrantha* is more likely than *E. ovalifolium* to decline in the future (Figures 3A,B), however, more years of data are needed to confirm this trend.

Above and Belowground Effects on Lambdas

We found support for the hypothesis that the effects of sagebrush PSFs on lambda would be more negative than the effects of sagebrush competition. The effects of sagebrush presence on lambda were neutral to slightly positive suggesting weak competition to facilitation, with the strongest positive effect for *E. ovalifolium* at the high elevation site. This supports the well-known hypothesis that species interactions will become more positive (facilitative) as abiotic stress increases (Callaway et al., 2002; Maestre et al., 2009).

Nurse plant facilitation of herbs commonly occurs through enhanced resources, such as water and nutrients and by buffering effects of extreme temperatures, wind or snow in the understory (Körner, 2003). Indeed, *A. rothrockii* has increased soil moisture and higher soil organic matter content below its canopies as compared to shrub interspace areas in the White Mountains (Collins et al., 2016); however, the effect of sagebrush facilitation on herbaceous demography was not consistent across elevations and herbaceous species. Facilitation intensity can increase with functional dissimilarity among species at the cold and wet end of a stress gradient (Gallien et al., 2018) suggesting that shrubs may most strongly facilitate herbs at high elevations. Despite this, overall lambda values for shrub plots tended to be lower than herbaceous plots regardless of treatment, suggesting that the benefits do not outweigh the costs of growing in association with this shrub species.

As predicted, the effects of shrub PSFs on lambda were generally negative, implying that in the absence of competition, plants growing in shrub-conditioned soils had lower growth, survival and reproduction than those growing in herbaceous-conditioned soils. The one exception to this pattern was a slightly positive effect on lambda for *E. ovalifolium* at the low elevation. PSFs are therefore a potentially strong form of apparent competition by which sagebrush negatively impacts resident plant species. Many factors can determine the strength of PSFs of range expanding species on native communities and whether they are positive or negative. For example a range-expanding forb species had positive PSFs that enhanced the growth of a co-occurring native grass species, but only in the expansion zone (Dostálek et al., 2016). Here we find accordingly that sagebrush PSFs were stronger in the range expansion zone than in the native range (high vs. low elevation), but unlike the previous study, effects on resident plants were negative rather than positive. This may be due to differences in the time of soil conditioning between the historic and range expansion zones, as sagebrush is more recently established at high elevation sites. Range expanding species may also impose different PSFs depending on their relatedness to the resident community. Koorem et al. (2018) found that range expanders that were unrelated to resident plant species reduced the biomass production of the resident plant community, whereas related range expanding species did not. In our study, PSFs may be enhanced because sagebrush is not closely related (congeneric) with either herbaceous species.

Due to our experimental design however, we can only speculate whether the PSFs of sagebrush on resident plant species are due to changes in soil microbial communities, abiotic soil conditions, or both. One potential PSF mechanism is through secondary compounds (e.g., terpenes, jasmonic acid) in aromatic shrubs, such as *Artemisia* that can enter the soil through leaf litter and root exudates and have strong negative effects on plant growth, metabolism, and seed germination (Weaver and Klarich, 1977; Kelsey et al., 1978; Karban, 2007). These classes of chemicals can also strongly influence soil microbial community structure and function including microbial biomass C and N, respiration, nitrogen fixation, soil faunal substrate choice, and mycorrhizal networks of co-occurring plant species (Weston and Putnam, 1985; Wardle et al., 1998; Asensio et al., 2012; Austin et al., 2014). For example, organic compounds in the dwarf shrub *Empetrum hermaphroditum* greatly reduced ectomycorrhizal infection of root tips and mycorrhizal uptake of soil nitrogen for pine seedlings (Nilsson et al., 1993). Labile C in these compounds may also stimulate free-living (saprotrophic) microbial growth and nutrient immobilization, thus increasing resident plant-microbial competition for limiting soil nutrients. This was proposed as a mechanism by which *Betula*, *Empetrum*, and *Cassiope* shrub species inhibited the growth of nearby graminoid species in arctic soils (Michelsen et al., 1995). Therefore, via secondary chemicals, sagebrush may similarly alter plant-microbe competition in ways that enhance their own growth and nutrient acquisition to the detriment of co-occurring herbaceous plant species.

In previous work, we found that soils under sagebrush had higher bacterial diversity but lower fungal diversity than soils under herbaceous plants, and this corresponded with a decrease in both pathogenic and mutualistic fungi (Collins et al., 2016, 2018, and unpublished data). A change in soil mutualist to pathogen ratios has been shown to facilitate both inter- and intracontinental range expansions, as plants may benefit from decreased species-specific pathogens, while utilizing more generalist soil mutualists (van der Putten et al., 2016). However, the patterns we observe in this study suggest the opposite may be true for herbaceous plants growing in association with the range expander (sagebrush), which may still be experiencing negative effects of their own soil pathogens, but also a decreased abundance of soil mutualists. These effects may strengthen over time in the range expansion zone with more sagebrush soil conditioning, or they may attenuate as herbaceous plants become adapted to the sagebrush soil community (Rout and Callaway, 2012).

We acknowledge that the experimental plot treatments do not completely isolate the effects of sagebrush soil conditioning, and there may be other factors contributing to the changes in lambdas in the shrub PSF contrasts. It is possible, for example, that removal of shrub facilitation could negatively impact lambdas in shrub removal plots. However, we find that shrubs are weaker facilitators than the herbaceous community, and yet the difference between shrub removal and herbaceous removal plots is mostly negative, suggesting that lack of shrub facilitation is not driving the negative PSFs. It is also possible that some belowground competition may still occur

between herbaceous and shrub roots after aboveground shrub removal, however we expect these interactions to be minor and short term, while soil legacy effects left by sagebrush can last many years after shrub removal or death (Collins et al., 2016, 2018). Therefore, the demographic patterns observed in shrub removal plots are very likely attributable to sagebrush soil conditioning, although we cannot rule out some remnant belowground competition. Additionally, our experiment lacks distinct “conditioning” and “feedbacks” phases, but instead measures feedbacks over a longer, continuous time frame. While this has the strength of being more relevant to population dynamics, which unfold over longer time periods than most discrete PSF experiments, it also may dampen the ability to disentangle PSFs during the transition period after aboveground biomass removal.

Overall the patterns we observed were variable and sometimes weak, however this is to be expected due to the slow growth, low mortality and high stress tolerance of plants in alpine environments, and the relatively short observation period (4 years) given these species’ lifespans. Nonetheless, the data show that the effects of sagebrush on lambdas were more negative than the effects of the herbaceous community, particularly in the absence of aboveground competition and at middle and high elevation sites, providing a potential PSF mechanism for the observed declines in cover of *K. macrantha* and *E. ovalifolium* in areas of sagebrush expansion. While stronger effect sizes may have been observed in a more controlled greenhouse setting, estimating longer-term population dynamics in a field setting is more indicative of likely consequences for the species in nature.

CONCLUSIONS

Alpine landscapes are characterized by heterogeneous microclimates, resource availability and species interactions which can have large impacts on plant fitness (Körner, 2003). The movement of woody shrubs upwards in elevation, occurring in alpine ecosystems across the globe due to climate and land use change, may therefore alter these landscapes and affect the persistence of rare and endemic plant species. Here we find that shrubs can have both positive and negative impacts on herbaceous alpine plants simultaneously, and through both above and belowground mechanisms. Shrubs may facilitate herbs growing under or nearby their canopies particularly at high elevations, likely by shielding the effects of extreme temperatures, wind or snow. At the same time, shrubs may cause negative effects on herbaceous plants through PSFs predictably from changes in litter chemistry and their influences on plant growth and soil microbial community structure and function. These changes created by shrubs may impact multiple components of the plant life cycle, including growth, survival, and reproduction, and these components can have divergent responses which together determine the net outcomes for population growth.

The majority of PSF research has been carried out in controlled environments, particularly greenhouse experiments,

while little direct connection has been made between plant population dynamics and PSFs *in situ* (Kulmatiski and Kardol, 2008; Kulmatiski et al., 2008; Heinze et al., 2016). In addition, while conceptually well-developed, attempts to disentangle the effects of direct competition and PSFs on population dynamics and species coexistence have been rare (Bever et al., 1997; Revilla et al., 2013). The experimental field approach used here can help isolate direct competitive interactions vs. influences of soil conditioning on plant demography. By coupling these experiments to demographic modeling, it is possible to scale the aboveground and belowground effects of a range-expanding species to the effects on population dynamics and species coexistence over time. We believe this approach of combining estimates of PSFs in the field with species-specific population modeling is an important next step in understanding plant community dynamics in a changing world.

DATA AVAILABILITY STATEMENT

The datasets generated by this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

CC developed the research questions, designed and set up the experimental plots, collected the field data, and wrote the first draft of the manuscript. JD and TB analyzed the data and ran the statistical models. All authors created the graphics, wrote

the sections of the manuscript, contributed to the manuscript revision, read and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2019.00417/full#supplementary-material>

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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