



## RESEARCH ARTICLE

# Native lagomorphs prolong legacy effects limiting restoration of imperiled shrub-steppe communities

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Over the last +150 years, increases in woody vegetation in drylands and associated declines in herbaceous vegetation have led to widespread interest in reversing this trend. However, the effects of native, noncharismatic herbivores, such as lagomorphs, on these efforts are largely unknown. For 11 years post-treatment, we quantified the effects of native lagomorphs on restoration efforts in sagebrush (*Artemisia* L.) communities exhibiting legacy effects of past management, including depleted understories and overabundant sagebrush. Reducing sagebrush and seeding perennial grasses was necessary to attain substantial increases in large perennial grass cover and density, but this outcome was realized only with lagomorph exclusion. A small native bunchgrass and perennial forb cover and density increased in all treatments with lagomorph exclusion. This suggests that lagomorphs contribute to the persistence of a depleted understory in areas with increased woody vegetation. In areas where sagebrush was reduced, the cover and density of sagebrush was greater with lagomorph exclusion. This suggests that lagomorphs could hinder sagebrush recovery after disturbances that reduce or eliminate sagebrush. Lagomorph herbivory had a substantial effect on vegetation dynamics and affected the outcome of restoration efforts in these dryland systems. This could reduce livestock forage and alter habitat of wildlife species, potentially affecting their conservation. Lagomorphs and other noncharismatic, native herbivores may facilitate the persistence of depleted understories in areas where woody plants have increased. Results of this study suggests that the potential effects of lagomorph and other native herbivores should be considered and addressed in management, restoration, and conservation plans.

**Key words:** brush management, jackrabbits, native herbivores, restoration, seeding success, seedling defoliation

## Implications for Practice

- Native lagomorphs contribute to the persistence of shrub dominance and depleted understories prolonging the effects of prior mismanagement.
- Native lagomorphs can hinder passive and active restoration efforts, and subsequently, their effects may need to be mediated to increase restoration success.
- Potential effects of lagomorphs and other native herbivores need to be considered in management, restoration, and conservation plans.

## Introduction

Ecological legacy effects in arid-land systems from prior mismanagement are often a restoration challenge (Monger et al. 2015). Simply removing or limiting the effects of the original source of degradation (passive restoration) may not be sufficient to facilitate recovery. Though active restoration is likely needed, it may fail as other barriers to recovery may limit success and prolong legacy effects. This may be a particular issue where woody plants have increased and legacy effects are long-lived even after woody vegetation control (McClaran et al. 2008; Throop & Archer 2008), especially if other barriers, such as herbivores, prolong the effects of prior mismanagement.

Woody plants have proliferated at the expense of perennial herbaceous vegetation over the past +150 years in many drylands (Van Auken 2009; Archer et al. 2011; Sala & Maestre 2014).

Woody plant proliferation with associated declines in herbaceous vegetation can increase soil erosion risk (Schlesinger et al. 1999; Ritchie et al. 2005; Pierson et al. 2007), decrease ecosystem services (Ding et al. 2020), and reduce the economic value of the land for livestock production (Scholes & Archer 1997; Archer et al. 2011). The adverse effects of increases in woody vegetation and affiliated decreases in herbaceous vegetation have resulted in widespread interest in converting recently developed woodlands and shrublands back to savannahs, grassland, and shrub-steppe communities. Efforts to increase herbaceous vegetation and reduce woody vegetation are often accomplished with mechanical treatments, prescribed fire, herbicide applications, or combinations thereof (Archer et al. 2011). However, control of woody plants alone does not necessarily lead to autogenic recovery of

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herbaceous vegetation (Archer et al. 2011; Archer & Predick 2014). When desired plant species or functional groups are no longer abundant or the woody vegetation treatment reduces these desired plants, undesirable herbaceous vegetation may increase (Johnson & Fulbright 2008; Davies et al. 2012). Seeding perennial herbaceous vegetation after woody plant reduction may be necessary to achieve desired outcomes, though successful outcomes are far from certain. Failure of restoration projects is all too common in drylands as multiple potential barriers to success must be overcome (United States Government Accountability Office 2006; Svejcar et al. 2017). Abiotic barriers, such as low soil moisture, are often attributed to seedling mortality, but biotic barriers, such as herbivory, may play an outsized role in herbaceous plant establishment in woody plant-encroached ecosystems.

Herbivores can alter restoration trajectories by grazing and browsing residual and new vegetation (Ruzicka et al. 2010; Gornish & Santos 2016). Grazing and browsing may have direct (e.g. mortality of seedlings) and indirect (e.g. altering competition, impacts of soil moisture) effects on desirable plant recovery. Because of the potential for herbivory to limit recovery, non-native herbivores (horses, cattle, sheep) are often excluded after restoration actions. Native ungulates may also be excluded from restoration projects at times (e.g. Averett et al. 2017), but small native herbivores often have unrestricted access. Native herbivores may limit restoration success by preventing desired vegetation establishment (Augustine & Frelich 1998; Abercrombie et al. 2019; Guzmán et al. 2021). However, effects of some other native herbivores, especially noncharismatic species such as lagomorphs, are lesser known and often overlooked in many dryland plant communities (Gibbens et al. 1993). Lagomorphs are well-known regulators of both productivity and plant community composition in temperate grasslands (e.g. Crawley 1990; Edwards & Crawley 1999). The effects of lagomorphs may be particularly important in arid and semi-arid rangelands that have low populations of ungulates because they may be the primary native herbivore (Abercrombie et al. 2019). Thus, these unobtrusive but ubiquitous herbivores may play an outsized role in determining directionality and persistence of plant community composition. Understanding the effects of lagomorphs on the persistence of woody plant encroachment and on efforts to reverse the increase in woody plants and to promote perennial herbaceous vegetation is needed to guide and improve conservation and restoration.

In western North America, Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* [Beetle & A. Young] S.L. Welsh) communities with a depleted understory and overabundant sagebrush overstory are a particularly challenging management dilemma because of the legacy effects of prior mismanagement. These communities developed because of historic heavy, repeated grazing by livestock during the growing season depleted the understory; however, cessation of livestock grazing does not restore the understory as recovery is likely limited by high abundance of sagebrush (Davies et al. 2016, 2021b). Overabundant sagebrush can be reduced with mechanical, herbicide, or prescribed fire treatments, but increases in perennial herbaceous vegetation are often not achieved as a matter of course (Davies et al. 2011; Beck et al. 2012). Instead, highly flammable, exotic annual

grasses may increase substantially with sagebrush reduction, putting the plant community at risk of frequent fires and further degradation (Davies et al. 2012).

Seeding after sagebrush reduction can increase perennial grasses, but increases may be limited, and exotic annual grasses may still increase substantially (Davies & Bates 2014; Davies et al. 2021b). Lagomorphs have limited woody plant restoration efforts (Holl & Quiros-Nietzen 1999; McAdoo et al. 2013; Forsyth et al. 2015); thus, they could also be limiting herbaceous vegetation recovery. In Arizona, lagomorphs were significant consumers of herbaceous vegetation in shrub-encroached arid grasslands, potentially acting as a biofeedback contributing to the persistence of shrubs (Abercrombie et al. 2019). Similarly, prairie dogs shaped vegetation structure in sagebrush grasslands in Wyoming (Connell et al. 2018). Thus, lagomorphs likely impact efforts to restore perennial understories in degraded sagebrush communities.

The purpose of this study was to investigate the effects of lagomorphs on management legacies and restoration efforts. Specifically, we evaluated the effects of lagomorph herbivory on natural (passive) recovery and on active restoration efforts to increase perennial herbaceous vegetation in Wyoming big sagebrush communities with depleted understories and overabundant sagebrush. To accomplish this task, we investigated the effects of lagomorph herbivory on sagebrush communities with depleted understories that received passive restoration and active restoration treatments (mechanical reduction of sagebrush with and without seeding of perennial grasses). We hypothesized that (1) lagomorphs maintain shrub dominance and limit understory vegetation through herbivory and (2) though reducing sagebrush and seeding perennial bunchgrasses would be necessary to increase bunchgrass cover and density, exclusion of lagomorphs is also necessary to realize the benefits of these treatments.

## Methods

### Study Area

The study was conducted in Wyoming big sagebrush communities with depleted understories in southeast Oregon 40–50 km southwest of Burns, Oregon, U.S.A. Common perennial grasses at the study sites included bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve), Thurber's needlegrass (*Achnatherum thurberianum* [Piper] Barkworth), squirreltail (*Elymus elymoides* [Raf.] Swezey), and Sandberg bluegrass (*Poa secunda* J. Presl). Dominant perennial bunchgrasses would have been bluebunch wheatgrass and Thurber's needlegrass if these communities were intact (NRCS 2013). Exotic annual grasses were present across the study area, but their cover was low prior to treatment. The understory was considered depleted because perennial herbaceous cover and density were low. Prior to treatment, Sandberg bluegrass, large perennial bunchgrass and perennial forb foliar cover were <2, <2, and <1%, respectively. These cover values are substantially less than those found in relatively intact Wyoming big sagebrush communities (Davies et al. 2006; Davies & Bates 2010; Bates & Davies 2019). Sagebrush cover was 15% prior to treatment, which is 20–50% greater than the average cover in intact Wyoming big sagebrush communities

(Davies et al. 2006; Davies & Bates 2010), suggesting that sagebrush may be limiting herbaceous vegetation. Study sites were on locations classified as a Loamy 10-12PZ (R023XY212OR) ecological site (NRCS 2013) and separated by approximately 15 km. Elevations ranged from 1,263 to 1,350 m and slopes were generally flat across the study sites. Soils had a physical crust at the surface and were loamy, well-drained, and moderately deep. The local climate consists of cool, wet winters and hot, dry summers. Average annual (1981–2010) precipitation was 244 mm (PRISM 2020). Study sites were grazed by livestock prior to study initiation, but livestock (cattle and feral horses) were excluded for the duration of the experiment.

### Experimental Design and Measurements

A randomized complete block design with study site ( $n = 2$ ) as the blocking variable was utilized in this study. Each block consisted of six  $30 \times 50$ -m plots with a 2-m buffer between plots. Vegetation treatments were replicated in two  $30 \times 50$ -m plots in each block (3 treatments  $\times$  2 plot replicates = 6 plots per block) and were: (1) untreated control, (2) sagebrush reduced (unseeded sagebrush reduction), and (3) sagebrush reduced with perennial grasses seeded (seeded sagebrush reduction). In each block, one vegetation treatment replicate had lagomorphs excluded and the other did not. Thus, each factorial combination of lagomorph herbivory and vegetation treatment occurred once at each block. Black-tailed jackrabbits (*Lepus californicus*), a native species, were the only lagomorph observed at the study sites. Mountain cottontails (*Sylvilagus nuttallii*), a native species, also occupy the study area, but were not observed at the study sites. Sagebrush was reduced by mowing at a 20 cm height in September of 2008 with a Schulte XH 1500 rotary cutter (Schulte Equipment Co., Englefield, Saskatchewan, Canada). In seeded sagebrush reduction plots, seeding was applied after mowing with a Laird Rangeland Drill (Laird Welding & Manufacturing Works, Merced, CA). The grass seed mix consisted of crested wheatgrass (*Agropyron desertorum* [Fisch.] Schult.) and Siberian wheatgrass (*Agropyron fragile* ssp. *sibericum* [Roth] P. Candargy) with each seeded at 5.6 kg pure live seed (PLS)/ha. These non-native bunchgrasses were selected for seeding instead of native bunchgrasses to test if lagomorphs affected restoration actions because native bunchgrass species are less likely to establish (Robertson et al. 1966; Hull 1974; Wood et al. 1982). Thus, seeding these non-native bunchgrasses increase the likelihood that we could investigate if lagomorphs affect seeded bunchgrass establishment. These species can also be used in efforts to restore ecosystem function, though not native composition. Lagomorphs were excluded using 61 cm tall chicken wire fence with 2.54 cm mesh size erected around exclusion plots. No lagomorphs were observed in the lagomorph exclusion treatment areas for the duration of the study, while lagomorphs were commonly observed in the other treatment areas. Other wildlife species (mule deer, pronghorn, elk), though not abundant, were not excluded from study plots.

Vegetation cover and density were measured in June for 11 years (2009–2019). Herbaceous canopy cover by species

was visually estimated in  $40 \times 50$ -cm quadrats located at 3-m intervals (3 through 45 m) along four parallel 50-m transects spaced 5 m apart in each treatment plot (15 quadrats per transect, 60 quadrats per plot). Quadrats had markings dividing them into 5, 10, 25, and 50% segments to improve visual estimates of cover. Herbaceous density was measured by species by counting all perennial plants rooted inside the  $40 \times 50$ -cm quadrats and all annual plants rooted in a permanently marked 10% segment of the  $40 \times 50$ -cm quadrats. Sagebrush cover was measured using the line intercept method on each of the 50-m transects. Sagebrush density was measured by counting all individual sagebrush plants rooted in  $2 \times 50$ -m belt transects positioned over each of the 50-m transects.

### Statistical Analyses

We used repeated measures analysis of variance using the mixed model procedure (Proc Mixed) with year as the repeated variable in SAS version 9.4 (SAS Institute Inc., Cary, NC, U.S.A.) to evaluate vegetation treatment and lagomorph herbivory effects. Vegetation treatment and lagomorph herbivory were considered fixed effects in analyses. Block and block-by-vegetation treatment interactions were treated as random variables in models. The vegetation treatment-lagomorph herbivory interaction was included in all models, but only reported when significant. Other two-way and three-way interactions were included in the error term to improve sensitivity of analyses. The appropriate covariance structure was determined for each model using the Akaike's information criterion (Littell et al. 1996). Herbaceous vegetation was grouped into five categories for analyses: perennial bunchgrasses (excluding Sandberg bluegrass), Sandberg bluegrass, annual grasses, perennial forbs, and annual forbs. Sandberg bluegrass was analyzed independent of the other bunchgrasses because it is smaller statured, develops earlier, and often responds differently to grazing and fire (McLean & Tisdale 1972; Yensen et al. 1992; Davies et al. 2021a). The annual grass group was solely comprised of non-native species, primarily cheatgrass (*Bromus tectorum* L.). The perennial forb group was solely composed of native species. The annual forb group was largely consisted of non-native species (>80% of total cover and density). In unseeded treatments, the perennial bunchgrass group was solely composed of native species. Statistical significance was set at  $p \leq 0.05$  and means were reported with standard errors (mean  $\pm$  SE).

## Results

### Cover

The response of perennial bunchgrass cover to vegetation treatment was influenced by lagomorph herbivory (Table S1; Fig. 1A;  $p < 0.001$ ). At the conclusion of the study in seeded and unseeded sagebrush reduction treatments, perennial bunchgrass cover was 15- and 2-fold greater in areas where lagomorphs were excluded, respectively. Seeding perennial bunchgrasses after sagebrush reduction substantially increased

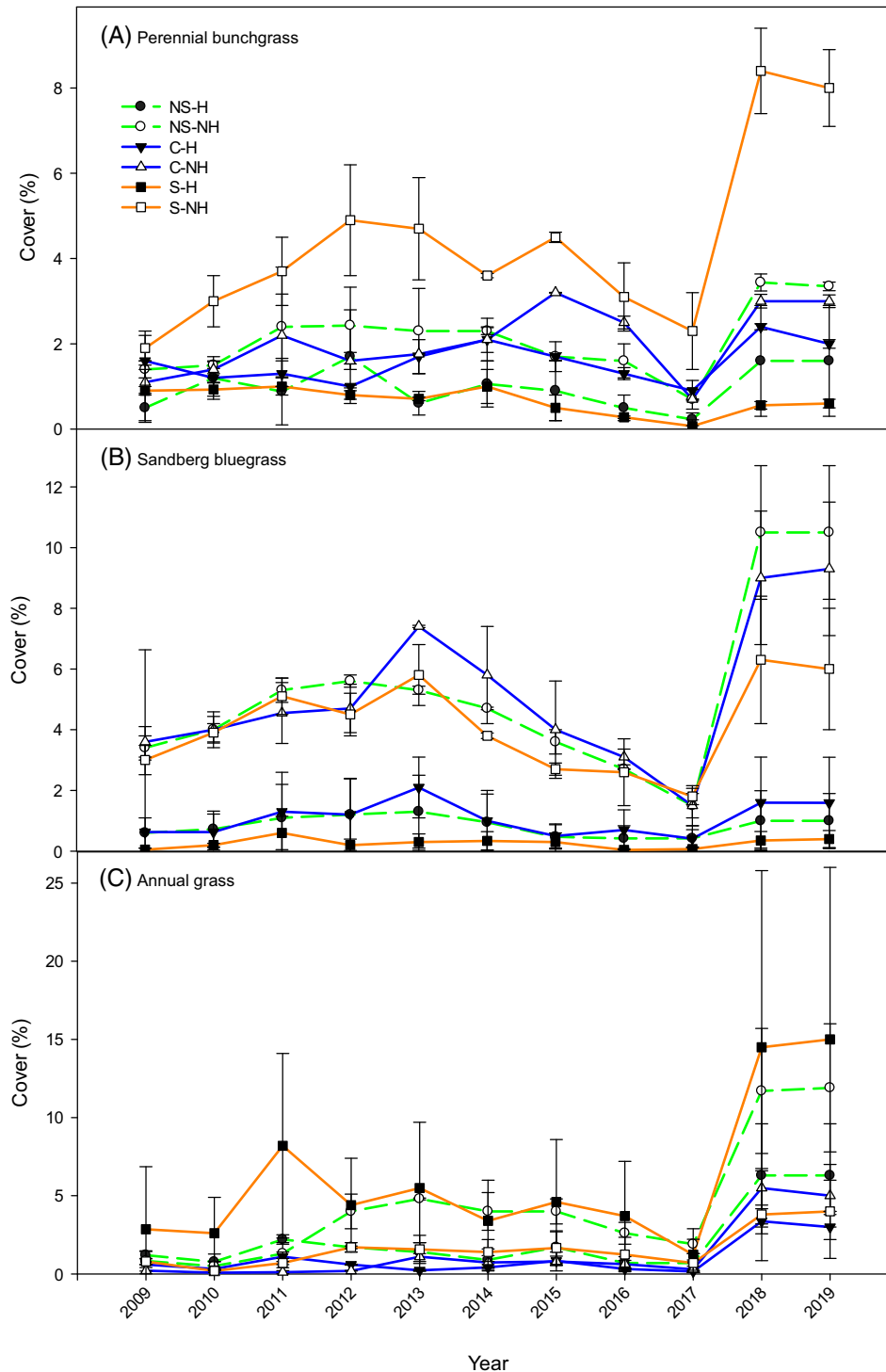


Figure 1. (A) Perennial bunchgrass (excluding Sandberg bluegrass), (B) Sandberg bluegrass, and (C) exotic annual grass cover (mean  $\pm$  SE) in sagebrush reduction treatments with (NS-H) and without (NS-NH) lagomorph herbivory, untreated control with (C-H) and without (C-NH) lagomorph herbivory, and sagebrush reduction treatments followed with perennial bunchgrass seeding with (S-H) and without (S-NH) lagomorph herbivory from 2009 to 2019. Sagebrush reduction and seeding were implemented in the fall of 2008.

perennial bunchgrass cover when lagomorphs were excluded. Perennial bunchgrass cover generally increased with time ( $p < 0.001$ ). Sandberg bluegrass cover did not vary among vegetation treatments (Fig. 1B;  $p = 0.181$ ). Sandberg

bluegrass cover was less with lagomorph herbivory ( $p < 0.001$ ) and generally increased with time ( $p < 0.001$ ), especially in areas where lagomorphs were excluded. The response of annual grass cover to treatment varied by

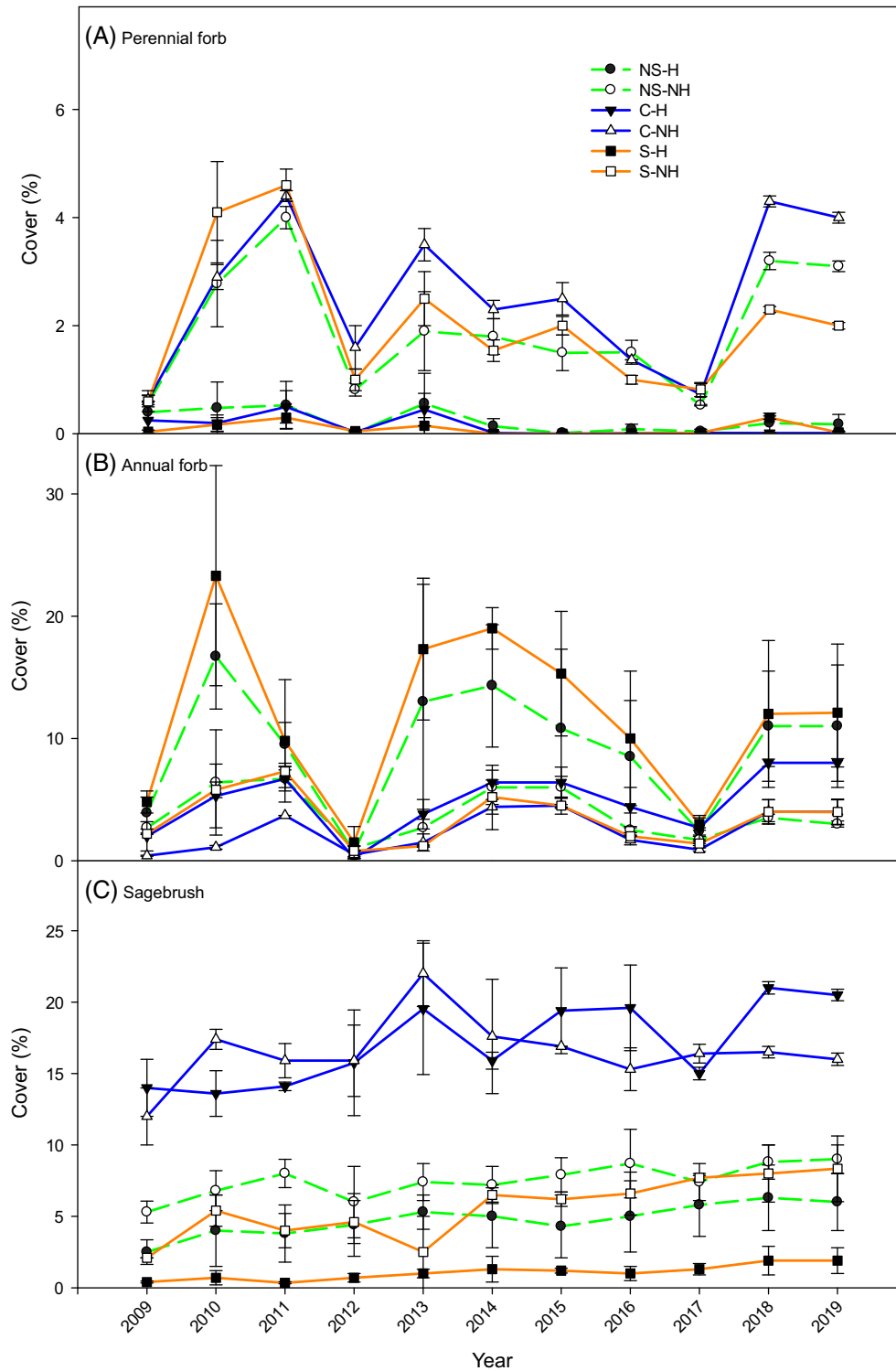


Figure 2. (A) Perennial forb, (B) annual forb, and (C) sagebrush cover (mean  $\pm$  SE) in sagebrush reduction treatments with (NS-H) and without (NS-NH) lagomorph herbivory, untreated control (C-H) with and without (C-NH) lagomorph herbivory, and sagebrush reduction treatments followed with perennial bunchgrass seeding with (S-H) and without (S-NH) lagomorph herbivory from 2009 to 2019. Sagebrush reduction and seeding were implemented in the fall of 2008.

lagomorph herbivory (Fig. 1C;  $p < 0.001$ ). Annual grass cover was greater without herbivory in the untreated control and the unseeded sagebrush reduction treatment, but was

greater with herbivory in the seeded sagebrush reduction treatment. Annual grass cover varied among years ( $p < 0.001$ ). Perennial forb cover did not vary among vegetation treatments

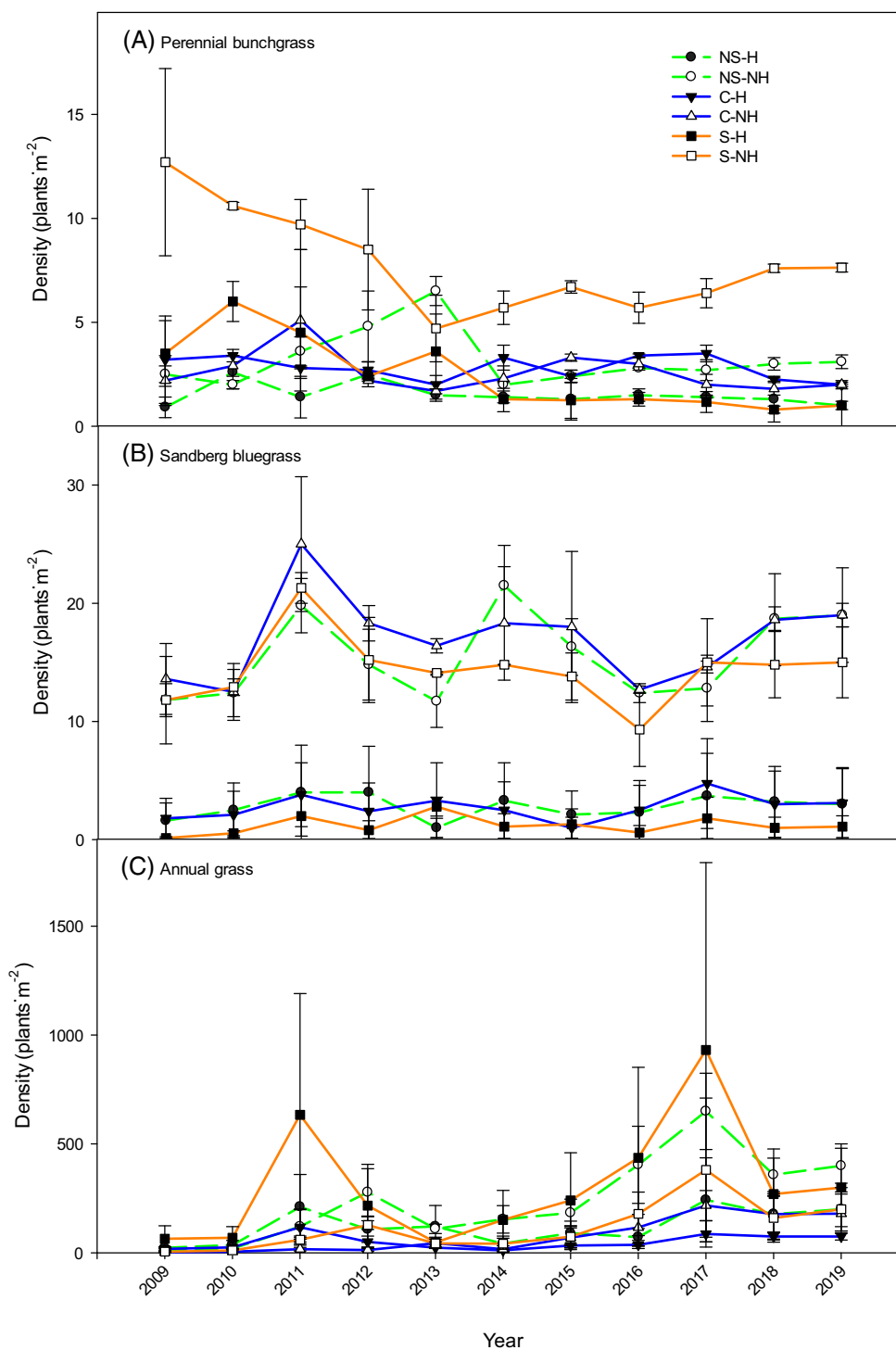


Figure 3. (A) Perennial bunchgrass (excluding Sandberg bluegrass), (B) Sandberg bluegrass, and (C) exotic annual grass density (mean  $\pm$  SE) in sagebrush reduction treatments with (NS-H) and without (NS-NH) lagomorph herbivory, untreated control (C-H) with and without (C-NH) lagomorph herbivory, and sagebrush reduction treatments followed with perennial bunchgrass seeding with (S-H) and without (S-NH) lagomorph herbivory from 2009 to 2019. Sagebrush reduction and seeding were implemented in the fall of 2008.

(Fig. 2A;  $p = 0.523$ ), but decreased with lagomorph herbivory ( $p < 0.001$ ) and varied among years ( $p < 0.001$ ). The response of annual forb cover to vegetation treatment was influenced by lagomorph herbivory (Fig. 2B;  $p = 0.003$ ).

Annual forb cover was greater with herbivory in all vegetation treatments, but the difference between herbivory and herbivory excluded was most pronounced in the seeded sagebrush removal treatment and least in the untreated

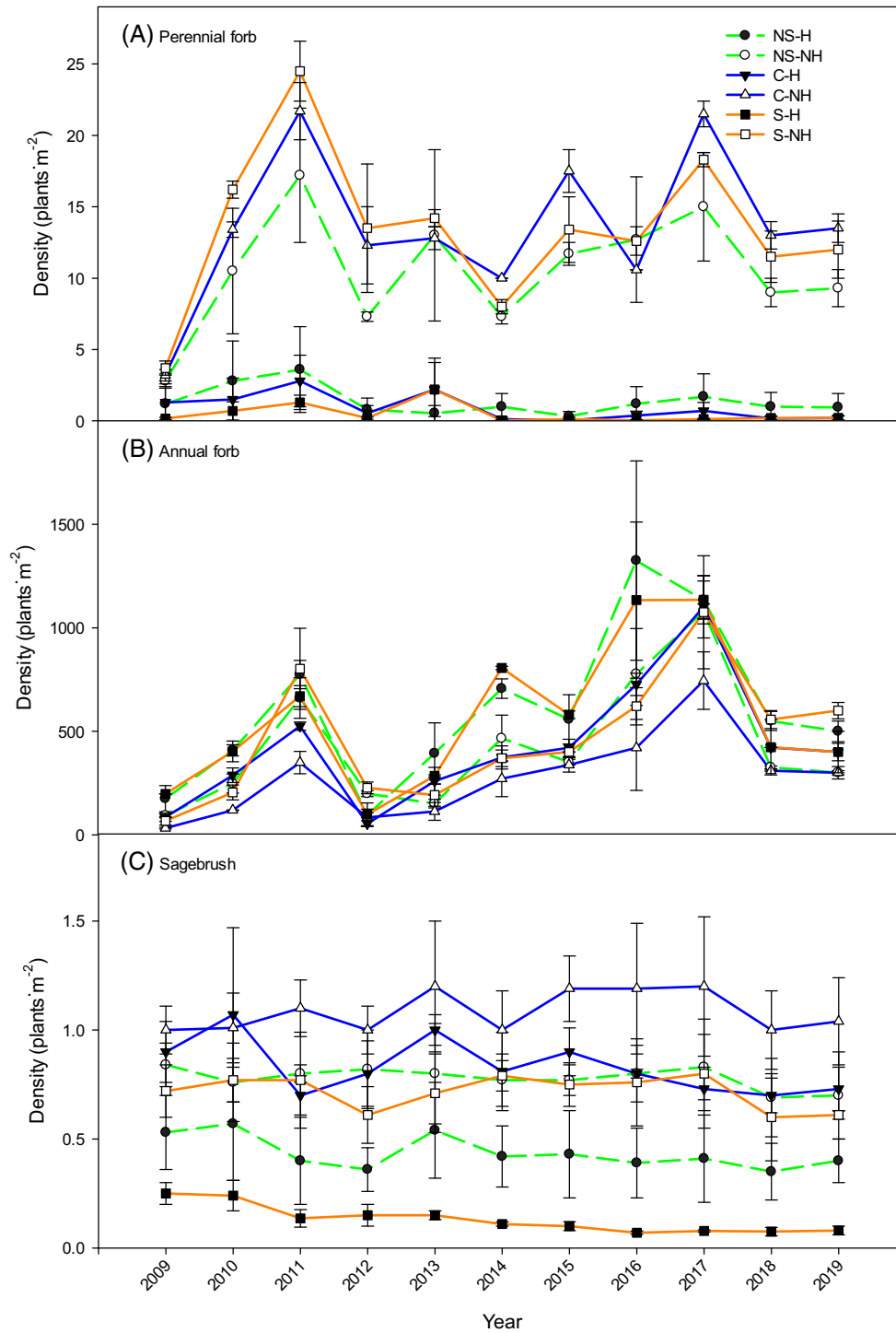


Figure 4. (A) Perennial forb, (B) annual forb, and (C) sagebrush density (mean  $\pm$  SE) in sagebrush reduction treatments with (NS-H) and without (NS-NH) lagomorph herbivory, untreated control (C-H) with and without (C-NH) lagomorph herbivory, and sagebrush reduction treatments followed with perennial bunchgrass seeding with (S-H) and without (S-NH) lagomorph herbivory from 2009 to 2019. Sagebrush reduction and seeding were implemented in the fall of 2008.

control. Annual forb cover varied among years, but no clear pattern emerged ( $p < 0.001$ ). The response of sagebrush cover to treatment varied by lagomorph herbivory (Fig. 2C;  $p < 0.001$ ). Sagebrush cover was generally in

the untreated control with and without herbivory, but was less with herbivory in seeded and unseeded sagebrush reduction treatments. Sagebrush cover generally increased with time ( $p = 0.004$ ).

## Density

The response of perennial bunchgrass density to vegetation treatment was influenced by lagomorph herbivory (Table S2; Fig. 3A;  $p < 0.001$ ) and year ( $p = 0.002$ ). Perennial bunchgrass density was generally not influenced by herbivory in the untreated control. In seeded and unseeded sagebrush reduction treatments, herbivory decreased perennial bunchgrass density. Perennial bunchgrass density was greatest in the seeded sagebrush reduction treatment when lagomorphs were excluded. Perennial bunchgrass density initially decreased and then, after 2013, generally increased with time in the seeded sagebrush reduction treatment with lagomorph exclusion. In contrast, perennial bunchgrass density was similar across time in the other vegetation treatments. Sandberg bluegrass density did not vary among vegetation treatments (Fig. 3B;  $p = 0.288$ ), was less with herbivory ( $p < 0.001$ ) and varied among years ( $p = 0.002$ ). The response of annual grass density to vegetation treatment was influenced by lagomorph herbivory (Fig. 3C;  $p < 0.001$ ). In untreated control and unseeded sagebrush reduction treatments, annual grass density was initially greater with herbivory, but became greater without herbivory from 2014 to the end of the study. In the seeded sagebrush reduction treatment, lagomorph herbivory increased annual grass density. Annual grass density varied among years ( $p < 0.001$ ). The response of perennial forb density to vegetation treatment was influenced by lagomorph herbivory (Fig. 4A;  $p = 0.013$ ). Herbivory decreased perennial forb density across all three vegetation treatments; however, the difference appeared less pronounced in the unseeded sagebrush reduction treatment compared to the other treatments. Perennial forb density varied among years ( $p < 0.001$ ). Annual forb density did not vary among vegetation treatments (Fig. 4B;  $p = 0.083$ ). Annual forb density was generally greater with lagomorph herbivory ( $p < 0.001$ ) and varied among years ( $p < 0.001$ ). The response of sagebrush density to vegetation treatment was influenced by lagomorph herbivory (Fig. 4C;  $p < 0.001$ ). Herbivory generally reduced sagebrush density, but the effect appears more pronounced where seeding occurred after sagebrush was reduced.

## Discussion

Native herbivores, such as lagomorphs, can be important drivers of vegetation dynamics in drylands. In our study, lagomorph herbivory substantially influenced the outcome of restoration actions as well as vegetation cover and density in untreated controls. Though others have recognized that lagomorphs can influence plant communities (e.g. Gibbens et al. 1993; McAdoo et al. 2004; Abercrombie et al. 2019) and woody plant restoration efforts (e.g. Holl & Quiros-Nietzen 1999; McAdoo et al. 2013; Forsyth et al. 2015), their impacts on legacy effects and efforts to reverse long-term effects of mismanagement have been largely overlooked. Our results suggest that the effects of lagomorphs can be substantial and, therefore, merit further investigation. Additional information on lagomorph, and likely other native herbivores, effects are needed to improve management, conservation, and restoration plans.

Our results suggest that lagomorphs can adversely affect efforts to increase herbaceous vegetation in plant communities with overabundant woody vegetation. Though perennial bunchgrasses seeding after sagebrush reduction was necessary for substantially increases in bunchgrass cover and density, exclusion of lagomorphs was also necessary to realize the full benefits of seeding efforts. We suspect that lagomorphs caused high mortality of perennial bunchgrass seedlings through heavy defoliation. In Nevada, lagomorphs consumed up to 200 kg/ha of crested wheatgrass (one of the two species we seeded) seedlings when other forage was limited (McAdoo et al. 2004). Our finding that herbivory limited seedling survival is counter to reports that defoliation benefited crested wheatgrass seedling survival (Denton et al. 2021), though this study used clipping to simulate herbivory as opposed to measuring native mammal herbivory. Also in disagreement with our results, lagomorph herbivory did not influence seeded bunchgrass establishment in Nevada (Roundy et al. 1985). It may be that lagomorph herbivory pressure was relatively greater in our study than Roundy et al. (1985). In addition, site, weather, other forage availability differences may have contributed to dissimilar responses. Our results suggest the potential for lagomorph herbivory may need to be considered when weighing the challenges to and potential risk of failure with restoration efforts, particularly those involving seeding. Quantitative assessments of how lagomorph population densities and selectivity for seeded species influences outcomes would be valuable.

Herbivory by lagomorphs may act as a biotic feedback maintaining depleted understories in degraded shrub communities. In our study, Sandberg bluegrass, a native bunchgrass, and perennial forb cover and abundance increased with lagomorph exclusion in the untreated controls. This implies that lagomorphs contribute to and likely maintain the depleted understories in these overly shrub-dominated communities. In shrub-encroached grasslands in Arizona, desert cottontails (*Sylvilagus audubonii*) were speculated to contribute to the competitive advantage and persistence of shrubs (Abercrombie et al. 2019). In plant communities where woody vegetation has increased substantially, lagomorphs and likely other native herbivores may contribute to the perpetuation of high shrub dominance and depleted understories.

Lagomorph effects on sagebrush varied by treatment and suggest that they can limit sagebrush recovery after disturbance. Lagomorphs do not appear to influence sagebrush cover in untreated control areas, but limited its recovery where sagebrush was reduced. This is likely because lagomorphs have limited ability to affect mature sagebrush plants because of their size. In contrast, lagomorphs can cause mortality of sagebrush seedlings by cutting them off near the ground surface. Pygmy rabbits (*Brachylagus idahoensis*), a smaller lagomorph, decreased sagebrush seedling density and cover near their mounds (Parson et al. 2016). Similarly, in a sagebrush transplant study in Nevada, lagomorphs caused mortality of sagebrush seedlings by cutting them off just above the ground (McAdoo et al. 2013). Results from the untreated control also support our conclusion that lagomorphs can cause mortality of sagebrush seedlings, as sagebrush cover was not influenced by lagomorph herbivory, but sagebrush



density was less with lagomorph herbivory. Lagomorphs likely reduce sagebrush density by causing mortality of sagebrush seedlings in the untreated control, but not likely to influence sagebrush cover because mature plants constituted the majority of it. The effects of lagomorphs on sagebrush suggest that they may pose a substantial barrier to sagebrush and other shrub restoration in some locations. This is similar to other work showing that lagomorphs can limit the success of woody plant restoration efforts (Holl & Quiros-Nietzen 1999; McAdoo et al. 2013; Forsyth et al. 2015).

The effects of lagomorphs on sagebrush dominance compared to recovery suggest contrasting outcomes depending on recent disturbance history. Lagomorphs likely contribute to the perpetuation of sagebrush dominance and a depleted understory in the absence of a disturbance to sagebrush, but if sagebrush is disturbed and has to recover by recruiting new individuals, lagomorphs may also suppress sagebrush recovery. This indicates that management will also need to consider the composition and recent disturbance history of a plant community when determining and accounting for potential effects of lagomorphs.

Lagomorph herbivory also appears to influence competitive relationships within plant communities. This was most evident when evaluating their effect on exotic annual grasses in areas seeded with perennial grasses after sagebrush reduction. Unlike Sandberg bluegrass and perennial bunchgrasses, exotic annual grasses decreased with lagomorph exclusion in these areas. This was likely because greater perennial bunchgrass cover and abundance with lagomorph exclusion suppressed exotic annual grasses. Perennial bunchgrasses are highly competitive with exotic annual grasses and overlap substantially in resource acquisition (Chambers et al. 2007; Davies 2008; James et al. 2008). Thus, increases in perennial bunchgrasses produce consequential decreases in annual grasses. Similarly, lagomorphs shifted grass composition from a species they consumed more to a species they preferred less in New Mexico (Gibbens et al. 1993). In our study, annual forbs were greater with lagomorph herbivory, further suggesting that lagomorphs alter competitive relationships. This implies that lagomorphs can indirectly, as well as directly, influence plant community composition.

The effects of lagomorphs on plant community characteristics would likely affect other higher trophic levels. For example, lagomorphs substantially decreased perennial forbs in all three vegetation treatments (i.e. sagebrush reduction, seeded sagebrush reduction, and untreated controls). Perennial forbs are a critical food source for sage-grouse, a species of conservation concern (Crawford et al. 2004; Pennington et al. 2016), and other wildlife (Stephenson et al. 1985; Beck & Peek 2005). Lagomorphs' effects on sagebrush recovery could therefore impact sagebrush-associated species. Sagebrush recovery after disturbance is critical for the conservation of sagebrush-associated organisms (Crawford et al. 2004; Suring et al. 2005; Shipley et al. 2006). Lagomorph-induced habitat alterations could influence other species populations and affecting their conservation. Thus, conservation efforts for some wildlife species may need to account for the effects of lagomorphs on wildlife habitat.

Our study provides some important insights into the potential effects of lagomorphs. The long-term nature of our experiment was extremely valuable; however, the robustness of our study was restrained by only being applied at two sites. More replications across a broader array of conditions would be valuable. Another limitation of our study was that lagomorph densities and the intensity and frequency of their use, which probably largely determines effects, were not measured. Our study highlights that lagomorphs can be important drivers of plant community dynamics, but did not determine under what circumstances these effects will be realized. There are also likely many situations where their effects could be inconsequential, in particular if they are not abundant or other disturbances are larger drivers of plant community dynamics. These caveats of our study should be recognized when considering potential effects of lagomorph on management and restoration. Regardless, lagomorphs and likely other native herbivores can have substantial effects on plant community dynamics, restoration attempts, and likely, through their effects on habitat, other wildlife species. Lagomorphs can also alter the amount and composition of livestock forage. Therefore, management, conservation, and restoration plans could be improved by also considering and accounting for the potential effects of lagomorphs and other noncharismatic herbivores.

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### Supporting Information

The following information may be found in the online version of this article:

**Table S1.** Cover group results from mixed model repeated-measure ANOVA.

**Table S2.** Density group results from mixed model repeated-measure ANOVA.

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