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RESEARCH ARTICLE

UN Decade on Ecosystem Restoration

Intra-site sources of restoration variability in severely invaded rangeland: Strong temporal effects of herbicide–weather interactions; weak spatial effects of plant community patch type and litter

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Abstract

1. Invasions by exotic annual grasses (EAGs) are replacing native perennials in semi-arid areas globally, including the vast sagebrush-steppe rangelands of western North America. Efforts to eradicate EAGs and restore perennials have had mixed success, especially in relatively warm and dry areas where EAGs had high dominance prior to intervention. Greater consideration of the ecological sources of variability in EAG treatment outcomes may improve success.
2. We hypothesized that herbicide and restoration outcomes would be influenced by restoration strategy (type of herbicide, seeding or planting, timing of treatment) and underlying spatial variability associated with plant community patch type and litter, all applied in a landscape-scale experiment in a severely invaded area in Southern Idaho, USA.
3. EAGs, specifically medusahead (*Taeniatherum caput-medusae* [L.] Nevski), were strongly reduced for up to 3 years (maximum observation period) by the pre-emergent herbicide indaziflam, whereas the pre/post-emergent imazapic reduced EAGs only when applied twice. Indaziflam effects were greater when post-spray moisture was greater, and also when co-applied with imazapic, but reapplying indaziflam did not lead to additional reduction of EAGs.
4. Imazapic and indaziflam each stimulated species-specific, secondary invasion by exotic and/or invasive tall forbs. Application of the broadleaf herbicide aminopyralid provided only a fleeting 1 year of control of a dominant, highly noxious forb skeletonweed (*Chondrilla juncea* L.).
5. Underlying heterogeneity in plant community patch type (dominant herb species) explained only ~5% of variation in the herbicide effects, and manipulation of litter prior to spraying had no effect. Several years of seedings and planting resulted in no establishment of native perennials.

6. Herbicides, especially indaziflam, appear to be an effective tool for reducing EAGs for multiple years in the challenging restoration conditions we evaluated, particularly if their application coincides with suitable moisture. However, restoring the perennials required for longer term resistance to reinvasion is a serious challenge that could be avoided with preservation of perennials.

KEYWORDS
imazapic, indaziflam, medusahead, sagebrush steppe

1 | INTRODUCTION

The invasion of exotic annual grasses (EAGs) into western North America has contributed to substantial loss of sagebrush steppe habitat (Billings, 1990; Mack, 1981). EAGs create positive feedback loops with wildfire, decreasing natural fire return intervals and altering fire behaviour by increasing the continuity of wildfire fuels, and by establishing more readily in burned areas (Balch et al., 2012; reviewed in Germino et al., 2016). Increased fire disturbance along with direct competition from EAGs has led to decreased plant biodiversity (Davies et al., 2011; Mahood et al., 2019), reduced livestock forage (Major et al., 1960; Pellant, 1990) and loss of wildlife habitat, particularly for steppe-obligate species (Rhodes et al., 2010). EAGs such as cheatgrass (*Bromus tectorum* L.) and medusahead (*Taeniatherum caput-medusae* L. Nevski) are widespread in arid and semi-arid deserts like those found in the Great Basin (D'Antonio & Vitousek, 1992). Cheatgrass and medusahead directly compete with native perennial species by reducing available soil resources, creating microclimates from residual plant litter and by having short, early life cycles that take advantage of shallow soil moisture (Germino et al., 2016).

The most common treatment methods to restore invaded landscapes include herbicide application, reseeding of native vegetation and vegetation or soil manipulation (e.g. plowing, mowing or mechanical thinning; Pilliod et al., 2017). Herbicide treatments are implemented to decrease the occurrence of exotic plant species and thereby reduce competition with surviving or seeded perennials, reducing fuel loads for wildfire and slowing the spread of exotic species. Herbicides are either applied to soils to inhibit germination (pre-emergent) or to the foliar crowns or canopies to reduce growth or eradicate plants (post-emergent).

Imazapic, an acetohydroxyacid synthase inhibitor that has both post- and especially pre-emergent activity, is the most commonly used herbicide for control of EAGs in rangelands. Studies reveal mixed effects of imazapic on EAGs, sometimes providing only 1–2 years of control (Davies & Sheley, 2011; Davison et al., 2007; Kyser et al., 2007), and sometimes longer (e.g. up to 4 years in Lazarus & Germino, 2022). This short duration of control is often inadequate to allow perennial herbs to increase, due to their slower growth and time required for maturation. Indaziflam, an emerging herbicide that may overcome the perceived short duration of control of imazapic, is a cellulose biosynthesis inhibitor that works exclusively as a pre-emergent, inhibiting hypocotyl and initial root growth in germinants (Brabham et al., 2014). Indaziflam is expected to have greater longevity in soils, leading to longer term control of EAGs (Tateno et al., 2016), as indicated by comparisons with imazapic in short-grass steppe (Clark et al., 2020; Sebastian et al., 2016) and as suggested from a 2-year study in sagebrush steppe (Terry et al., 2021). Timing of treatment applications, that is targeting the pre-emergence phase, is non-trivial owing to logistical and weather prediction challenges, and thus there is keen interest in knowing whether combining imazapic and indaziflam may result in an improved combination of short- and longer-term control.

Many sites invaded by EAGs have lost diversity of soil resource use in the native plant community owing to replacement of both short- and deep-rooted perennials with shallow-rooted EAGs, and thus 'secondary' invasion by tap-rooted forbs is common and may result in an invasive community (e.g. Prevéy et al., 2010). Treatments that initially reduce EAGs may increase vulnerability to these forbs, and their presence can be more persistent and noxious owing to their tendency to be longer lived biennials or perennials, and relatively tall statured (e.g. skeletonweed, *Chondrilla juncea* L., and many species of thistles; Lazarus & Germino, 2021).

There are many challenges associated with restoring degraded landscapes and creating generalizable management plans (Svejcar et al., 2017), including environmental variability in space, such as climate, soil characteristics and topography (Chambers et al., 2014) and in time, for example weather (Hardegree et al., 2018). Even after accounting for these environmental factors, there is often large amounts of unexplained variability in models of vegetation responses to treatments (Barnard et al., 2019; Brudvig et al., 2017). Most rangelands and other semiarid landscapes can have important patch-scale variability in plant community composition that could affect inferences on treatment success if not accounted for. EAGs can create dense patches of litter that occlude the soil surface and affect treatment implementation and outcomes through interception of seeds or herbicides or alteration of microclimate for seeds (Clark et al., 2019; Evans & Young, 1970; Kyser et al., 2012; Schantz et al., 2019). Site matching in experimental design or econometric approaches (e.g. propensity score matching; Simler-Williamson & Germino, 2022) is often used to select appropriate un-treated areas to compare with treated areas in light of these spatial variables, but landscape-level evaluations will often entail considerable variability within treatments. This within-plot variation is rarely considered in evaluation of restoration treatment effects.

Abating or reversing the widespread and severe effects of EAGs in the vast sagebrush steppe is a management priority in the United States. Within this broader effort, sites that are relatively low elevation, warmer and drier for sagebrush steppe are often deprioritized for treatment because they have the least resistance to invasion and resilience to disturbances and are the most challenging to restore (Chambers et al., 2014). However, reducing EAGs and restoring deeper rooted less fire-prone perennials, especially native bunchgrasses, is highly desired in degraded areas adjacent to intact habitat requiring protection, or other high-value resources or areas where breaking fire continuity is desired (e.g. fuel breaks; Shinneman et al., 2019). Improving treatment success in these low-resistance resilience sites is thus a continuing need.

Our objective was to evaluate treatment options and underlying sources of variability in treatment effects in a wildland–urban interfacing rangeland that was once sagebrush steppe but had low resistance and resilience and became severely invaded by EAGs. We compared the (i) effectiveness and near-term longevity of herbicide indaziflam, with and without imazapic, for controlling EAGs, (ii) effect of herbicides applied in different years or with re-spraying (temporal variation), with and without removal of litter (spatial variation), (iii) evaluated how underlying plant community variation affected inferences on treatment effectiveness by including plant community patch type as stratification criteria and (iv) evaluated follow-up treatments with the post-emergent aminopyralid to control the exotic perennial forb skeletonweed and possibly provide additional control of EAGs.

2 | MATERIALS AND METHODS

2.1 | Site description

The study area was located in the foothills of the Idaho Batholith in the Boise Wildlife Management Area (latitude = 43°35′31.5″N, longitude = 116°07′37.7″W) in an area referred to as Top Hat that was burned in three separate wildfires, the most recent of which occurred in 1983 (WFIGS, 2021). The area was previously grazed by livestock for decades until several years prior to the study and is currently managed by the Idaho Department of Fish and Game (IDFG), who allowed the experiment and work to be done on the property. The site elevation was 965 m ASL and had a soil type that is predominately vertisol (60% churning clay, 35% loamy 8–12, 5% loamy bottom 8–14; USDA-NRCS, 2014). Annual average precipitation is 37.9 cm with a mean temperature of the warmest month of 30°C (July) and a mean minimum temperature of the coldest month of −1.7°C (January, PRISM; 4-km resolution, 30-year averages). This site is heavily invaded by medusahead, skeletonweed and bulbous bluegrass (*Poa bulbosa* L.) among other non-native grass and forb species. Native species richness and abundance are low, and they include native perennial grasses such as purple three awn (*Aristida purpurea* Nutt.), Sandberg bluegrass (*Poa secunda* J. Presl) and squirrel tail (*Elymus elymoides* [Raf.] Swezey) and native perennial forbs such as common yarrow (*Achillea millefolium* L.), Mexican whorled milkweed (*Asclepias fascicularis* Decne.) and foothill death camas (*Zigadenus paniculatus* [Nutt.] S. Watson).

2.2 | Experimental design

2.2.1 | Main-plot treatments

A full-factorial layout of (1) five different main plots of pre-emergent herbicide treatments including indaziflam, imazapic or their combination, sprayed in different years, and (2) nested subplot treatments of broadleaf/post-emergent herbicide, drill seeding, hand planting and litter removal were applied in three replicate blocks between 2018 and 2019 (Figure 1). To evaluate the effectiveness of the herbicides on longevity and year-of-application effects, ~0.4 ha main-plot areas were treated with either indaziflam (as Rejuvra®) sprayed in the fall of 2018 or 2019 (73 g ai ha^{-1}, = 5 oz per acre), imazapic (as Panoramic®) sprayed in fall 2018 (105 g ai ha^{-1}, = 6 oz per acre) or a tank-mixed treatment of both indaziflam and imazapic (73 + 105 g ai ha^{-1} = 5 + 6 oz per acre) in fall 2018. All treatments applied in 2018 occurred in late October, when temperature ranges were moderate around the time of treatment, ranging from 5 to 21.5°C with no precipitation accumulating in the month post-treatments. Indaziflam applied in 2019 occurred in late August when conditions were warmer and wetter than for the 2018 treatment applications by 11–37°C and 17.78 mm, respectively (Figure 2). Main-plot treatments were applied by Ada County Weed and Pest Department using trucks equipped with a 9-m-wide boom sprayer and Raven's boom control (Raven Applied Technology, SD). All herbicides were sprayed with 187 L water ha^{-1} with 0.25% (v/v) non-ionic surfactant (Super Spread 7000®) to promote uniform coverage and absorption. Spraying was completed under ideal low-wind conditions (<0.5 m s^{-1}), with observers ensuring precise application.

2.2.2 | Aminopyralid herbicide subplots

To assess the effects of the broadleaf herbicide aminopyralid (Milestone®) on the invasive forb, skeletonweed, two, 4 × 4-m nested subplots were added to each main-plot herbicide treatment in August of 2019 (Figure 1). Subplot locations were selected using high-spatial-resolution drone imagery collected in 2019 in which dense skeletonweed stands were evident and could be manually mapped. The subplots were arbitrarily placed within mapped skeletonweed patches of the main-plot treatments. Aminopyralid was then applied to each subplot with a 16-L handpump backpack sprayer calibrated at a rate of 821 L ha^{-1} (122.5 g ai ha^{-1}). The non-ionic surfactant (SprayWet®) was added to the backpack sprayer at 0.25% (v/v) along with 15 ml of blue dye. There was 17.78 mm of accumulated precipitation in the month following herbicide treatment (Figure 2).

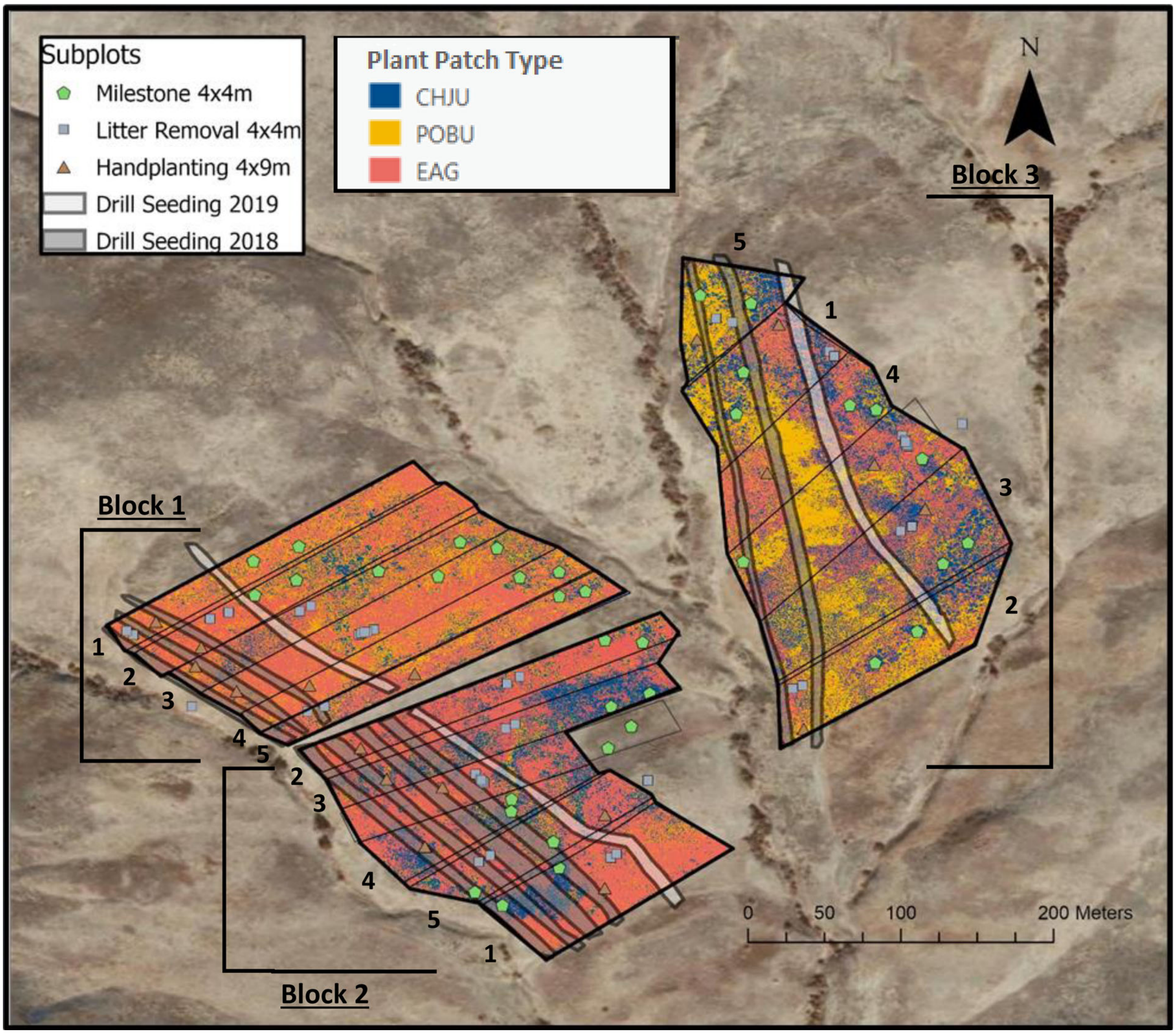

FIGURE 1 Map of the study site, showing main-plot herbicide treatments replicated in three blocks: numbers refer to treatments, specifically 1 = controls, 2 = indaziflam applied in 2018, 3 = imazapic applied in 2018, 4 = indaziflam applied in 2019, 5 = indaziflam and imazapic combined, applied in 2018. The three different colours represent the different plant community patch types inferred from the aerial imagery, specifically matches dominated by skeletonweed (blue, CHJU), bulbous bluegrass (yellow, POBU) or exotic-annual grasses (EAG, pink). Subplots were overlayed on top of main-plot herbicide treatments either in strips (drill seeding) or marked 4 × 4- or 4 × 9-m plots.

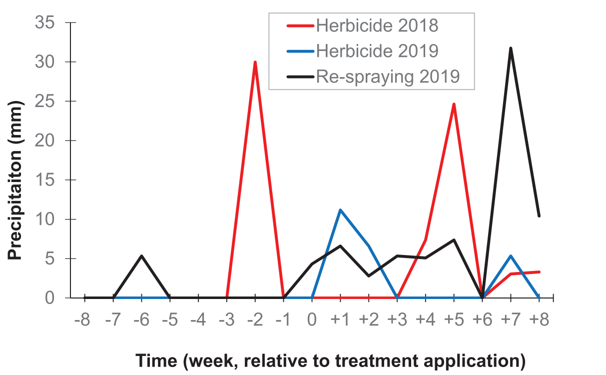

FIGURE 2 Precipitation (mm) accumulated weekly (sum of seven daily values), relative to the time of treatment application. 'Herbicide 2018' includes treatments of indaziflam, imazapic and the indaziflam + imazapic combinations applied in 2018. 'Herbicide 2019' includes treatments of indaziflam applied in 2019. 'Re-spraying 2019' includes applications to 4 × 4-m areas that received herbicides in 2018.

2.2.3 | Litter removal and re-treatment subplots

To assess the influence of litter on herbicide outcomes, we established two, paired, 4 × 4-m nested subplots in December 2019 within all of the main-plot herbicide treatments except the concurrently implemented 2019 indaziflam treatment (i.e. control and the 2018 sprayings of indaziflam, imazapic or their combination; Figure 1). Litter removal subplot locations were selected using the same method as the aminopyralid subplots but targeted on dense EAG patches rather than skeletonweed patches. One of each of the paired subplots was manually raked to remove all standing and surface litter from the subplot, and the adjacent subplot was left undisturbed (unraked). Both paired subplots were then retreated with their respective underlying main-plot herbicide treatment at the same concentrations using a 16-L handpump backpack sprayer calibrated to 328 L ha^{-1} with the non-ionic surfactant (SprayWet®) added to the backpack sprayer at

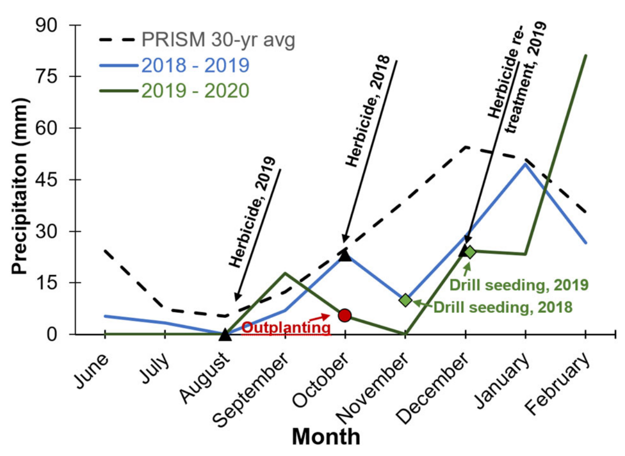

FIGURE 3 Precipitation accumulated within each month before or after treatment application and 30-year precipitation averages from 4-km^2 pixel PRISM data (1991–2020). 'Herbicide 2018' includes treatments of indaziflam, imazapic and the indaziflam + imazapic combinations applied in 2018. 'Herbicide 2019' includes treatments of indaziflam applied in 2019. 'Herbicide re-treatment 2019' includes 4 × 4-m subplots re-sprayed with the respective underlying treatments of indaziflam, imazapic and imazapic + indaziflam applied in 2019 onto areas already treated in 2018. 'Outplants' includes the hand planting of sagebrush and perennial grass seedlings in 2 × 3-m subplots. 'Drill seeding 2018' and 'Drill seeding 2019' include the drill seeding treatments of native perennial grasses and forbs in 2018 and 2019, respectively.

0.30% (v/v) along with 15 ml of blue dye. Temperatures ranged from 28 to 51°C around the time of re-treatment, which was lower than the respective main-plot treatment applications in fall of 2018. There was also a greater amount of precipitation in the month following the litter removal and re-spraying treatments compared to the underlying main-plot treatments applied in 2018, with 19.05 mm total precipitation occurring after re-spraying in 2019 and 0 mm occurring after the main-plot treatment was applied in 2018 (Figure 2).

2.2.4 | Drill seeding subplots

Drill seeding subplots were implemented to assess the effects of herbicide timing on drill seeding treatments. In fall of 2018, within a week of the main-plot herbicide applications, three 5-m-wide drill seeding strips containing a mix of native perennial grasses and forbs (37 kg ha^{-1}) were applied with a standard rangeland drill across all three replicate blocks (Figure 1; Table S1 for species and amounts). The same treatment was repeated in fall of 2019 with residual seed mix from 2018. The drill seeding in 2019 only installed a single, 5-m-wide drill strip across the three treatment blocks. Both drill seeding treatments occurred in similar weather windows. Temperatures ranged from 16 to −7°C in early November of 2018 and 16 to −9°C in late December of 2019. Both drill seeding installations experienced freezing temperatures (<0°C) and received precipitation in the month following application (17.02 and 33.27 mm, respectively; Figure 3).

2.2.5 | Hand planting subplots

Sagebrush and perennial grass seedlings were hand planted to assess the effectiveness of this revegetation method as well as to examine the influence of herbicides on nursery stock seedlings (Figure S2). In the fall of 2019, nursery stock grass and shrub seedlings were hand planted into 2 × 3-m subplots within each main-plot treatment (Figure 1). These species included Sandberg's bluegrass (POSE, *Poa secunda* J. Presl), bluebunch wheatgrass (PSSP6, *Pseudoroegneria spicata* [Pursh] Á. Löve), bottlebrush squirreltail (ELEL5, *Elymus elymoides* [Raf.] Swezey), purple three-awn (ARPU9, *Aristida purpurea* Nutt.) and basin big sagebrush (ARTRT, *Artemisia tridentata* Nutt. ssp. *tridentata*). All seedlings were grown for 6 months and were 98 cm^3 (grasses) or 164 cm^3 (shrubs) in size. In the month following seedling planting, temperatures ranged from 20 to −9°C and accumulated precipitation was very low, with a total of 5.3 mm (Figure 3).

2.3 | Sampling methods

2.3.1 | Line point intercept for plant cover

Plant cover was determined using a line–point intercept (LPI) method. Five, 20-m-long transects were oriented diagonally across each main-plot treatment and were monitored annually at the time of peak biomass (June) from 2019 to 2021. Cover of litter (previous-year growth), bare soil or rock and current-year growth to species for each canopy layer were recorded at 0.5-m intervals along the transects. Data were recorded directly into a database (USDA DIMA form, in Microsoft Access software) with Mesa2 field tablets (~3 m accuracy, Juniper Systems, UT) and ESRI ArcGIS Collector software was used to aid in geo-locating plots and subplots, which were permanent.

2.3.2 | Seedling counts for plant density

Seedlings (new emergents) of all plant species were counted in the spring and fall (March or late November to early December, respectively) beginning in fall 2019 and ending in spring 2021. The number of emergent plants was counted by species in three 1-m^2 quadrats per monitoring plot in 2019 (resulting in 15 quadrats per replicated main-plot treatment), but thereafter, in 2020 and 2021, sampling occurred in one 1-m^2 quadrat per monitoring plot. Species with high seedling densities were counted in smaller subquadrats within the designated 1-m^2 areas, specifically either in two 30 × 30-cm areas (e.g. large exotic forb skeletonweed) or in four 10 × 10-cm areas (e.g. small EAGs). Final calculations of seedling density (number of plants m^{-2}) were averaged by species and monitoring plot.

2.3.3 | Density counts for large-statured exotic or invasive forbs

In the late summer of 2021, density counts of large-statured (i.e. plants 0.5 to >2 m height, depending on species) exotic or invasive forbs were recorded to investigate non-target herbicide effects on species unrepresented in LPI methods or spring/fall seedling density counts. The exotic or invasive, tall-statured species skeletonweed, prickly lettuce (*Lactuca serriola* L.), yellow salsify (*Tragopogon dubius* Scop.), sunflower (*Helianthus annuus* L.) and moth mullein (*Verbascum blattaria* L), and prostrate and laterally spreading field bindweed (*Convolvulus arvensis* L.) were counted in five monitoring plots per replicated main-plot treatment. The number (count) and height of each species present within a plot was recorded incrementally beginning with a 1-m^2 plot and extending to 5.5-, 9- or 13-m-radius areas as needed until at least three individuals were detected. Total species density was extrapolated to a 10-m^2 area per monitoring plot.

2.3.4 | Mapping plant community patch types

Accounting for vegetation heterogeneity within treatments was accomplished by first identifying and mapping dominant plant community patch types using high-spatial-resolution imagery obtained. In August of 2019 (1-year post-treatment), a red–green–blue orthophotograph with 2.5-cm pixel resolution was obtained of the plots from an unmanned aerial vehicle operated by Donna Delparte of Idaho State University (Figures 1 and S1). The imagery was delineated into a map of three different plant community patch types using classification and regression trees (CART; Breiman et al., 2017) in the 'classifier' package of Google Earth Engine, which assigned either 'POBU' (bulbous bluegrass), 'CHJU' (skeletonweed) or 'EAG' (exotic annual grass) areas within the image.

To train our classifier, 30 randomly located 1-m-radius plots were monitored at the time of image acquisition. Visual estimates of percent plant cover (to species) were recorded within each monitoring plot. Each plot was later designated as 'POBU' or 'CHJU' if their respective covers of bulbous bluegrass and skeletonweed were >25% or 'EAG' if both bulbous bluegrass and skeletonweed cover was <25%. In the few cases where both species had >25% cover, the species with the highest percent cover was selected as the plant community patch type for the classification (Table S1).

To test the accuracy of our classified map, 30 additional sample areas were added as training points for validation. Using the same classifier package, a confusion matrix was created using the 'errorMatrix' tool to test the accuracy of the classifier (Stehman, 1997). The overall accuracy was 86% with a Kappa score of 0.82. Of 30 samples for each species, six CHJU were classified incorrectly as EAG, two POBU were classified incorrectly as EAG and three and two EAG were incorrectly classified as CHJU and POBU, respectively (Table S2).

Prior to treatment, the dominant species within the Top Hat site were bulbous bluegrass, skeletonweed and EAG. LPI data collected in 2019 suggested neither skeletonweed nor bulbous bluegrass cover was initially affected by treatments, therefore imagery of those two patch types obtained in 2019 would be representative of pre-treatment patches and all other areas were assumed to be dominated by EAGs. At the time the imagery was obtained (1-year post-treatment), EAG patches had been influenced by treatment and included cover from EAGs, perennial bunch grasses, bare soil, plant litter and non-skeletonweed forbs (Table S2).

2.4 | Data analysis

2.4.1 | Main-plot treatments

To compare EAG cover responses to treatments, we used a generalized linear mixed effects model (beta distribution) with the 'glmmTMB' package in R Studio (R Core Team, 2021; Magnusson et al., 2017). Three different models for EAG cover were compared to determine if plant community patch type helped explain variability in treatment responses (Table 1): (i) The 'base model' included EAG cover (from LPI) as the response variable and treatment type (main-plot treatments), sample year (year of monitoring; 2019–2021) and the interaction between the two as fixed effects; (ii) The 'block model' added random intercepts for treatment block and monitoring transect to the base model; (iii) The 'patch model' added plant community patch type as a fixed effect to the block model.

To compare EAG density responses to treatments, we used the same model formula from our cover analysis with a zero-inflated negative binomial distribution rather than a beta distribution. The zero-inflated model accounted for both the structural and sampling zeros in our seedling count data, and it created a better model fit to our data, which was over dispersed with many zero values (Blasco-Moreno et al., 2019). To evaluate non-target effects of treatments on exotic forb height and density, we used our block model with monitoring transect excluded as a random effect. The model for exotic forb height had a gamma distribution (log link) and the model for exotic forb density had a negative binomial distribution. Modelled cover, density and height predictions for EAG or exotic forbs were all made with the package 'ggeffects' (Lüdecke, 2017). Akaike's information criterion (AIC) was used to compare model fit and identify the best models. We also calculated root mean square error (RMSE) for each model type (base, block and patch; Table 1).

2.4.2 | Subplots to inform on planting, seeding, litter, and broadleaf herbicide effects

Non-parametric Kruskal–Wallis tests (R package 'dplyr') were used to determine the significance of differences in plant cover among the treatments applied in subplots, compared to their respective control subplots, for each year (2020, 2021; no germinants from seeding in 2019), because the data were not normally distributed (Shapiro–Wilk, $p > 0.05$)

TABLE 1 Model descriptions for responses of exotic annual grass density (negative binomial) and cover (beta)

Response variable	Model name	Distribution	Model statement	df	AIC	RMSE
Density	'Patch'	Negative binomial (zero-inflated)	Treatment Type × Year + Plant Patch Type + Transect ID + Treatment Block	18	962.6	12.9
	'Block'		Treatment Type × Year + Transect ID + Treatment Block	17	931.9	15.3
	'Null'		Treatment Type × Year	16	−929.6	21.7
Cover	'Patch'	Beta	Treatment Type × Year + Plant Patch Type + Transect ID + Treatment Block	35	4424	1135.7
	'Block'		Treatment Type × Year + Transect ID + Treatment Block	31	4455	1295.8
	'Null'		Treatment Type × Year	32	4462	1300.7

Note: Both models are generalized linear mixed effects models fitted with a maximum likelihood estimation via 'TMB' (Template Model Builder). 'Plant Patch Type' = three different plant communities identified through imagery classification of the site, 'Year' = sample year and 'Season' = Fall or Spring sampling.

3 | RESULTS

3.1 | Main-plot treatments

3.1.1 | Response of EAGs in EAG community patch types

Compared to controls, EAG cover was reduced (1) by 20%, 51% and 44% in 2019, 2020 and 2021, respectively, following the first (2018) indaziflam treatment (95% confidence interval [CI] = 9%, 8% and 9%) and (2) by 53% and 71% in 2021 following the second (2019) indaziflam treatment (95% CI = 8% and 7%; Figure 4). EAG cover was reduced 61%, 87% and 84% respectively, over all three years following the combination treatment of indaziflam + imazapic (95% CI = 6%, 2% and 3%). All indaziflam treatments reduced EAG cover an additional 17%–30% in the second year post-treatment. Imazapic had no effect on EAG cover in any post-treatment year.

Reductions of EAG densities were also evident following indaziflam application, specifically with 34% greater reductions in the second compared to the first post-spray year (95% CI = 13%) (Figure 5). Unlike the treatment responses observed for EAG cover, EAG seedling densities (plants m^{-2}) were reduced 35%–40% by imazapic for the first 2 years post-treatment compared to controls (95% CI = 14%; Figure 5). No significant differences were observed in EAG seedling densities between controls and imazapic treatments the third year post-treatment. Similar to EAG cover responses, EAG seedling densities were reduced most by the indaziflam + imazapic treatments, specifically 67%, 88% and 96% in 2019, 2020 and 2021, respectively (95% CI = 11%, 5% and 2%).

3.1.2 | Forb response

Skeletonweed density was not significantly influenced by indaziflam, imazapic or indaziflam + imazapic; however skeletonweed heights were a mean 20 cm greater in all four treatments (95% CI = 5 cm; Figure 6). Sunflower (*Helianthus annuus* L., a native but invasive species), on average, were three to five times denser in all other treatments other than treatments sprayed in 2019 with indaziflam and were 10 times denser (per 10 m^2) in imazapic + indaziflam treatments compared to controls. Mean sunflower heights were 23 cm greater in the indaziflam and imazapic + indaziflam treatments sprayed in 2019 than in unsprayed controls (95% CI = 25 cm). The exotic biennial forb prickly lettuce was a mean five times denser within the imazapic treatments compared to the control and twice as dense in the

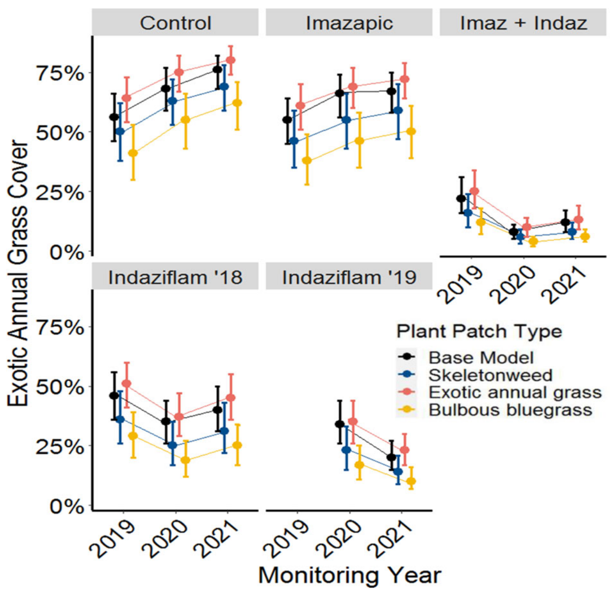

FIGURE 4 Mean ± 95% CI cover predictions of exotic annual grasses by treatment and sample year, estimated from generalized linear mixed effects models with a beta distribution fitted with line–point intercept data. 'Plant Patch Type' groups represent the three different plant community patch types identified through imagery classification along with the base model (which did not include plant community patch type as predictor). Indaziflam applied in 2019 was considered untreated for the 2019 monitoring year and excluded from the figure. 'Imaz' refers to imazapic and 'Indaz' refers to indaziflam; ''18' and ''19' refer to 2018 and 2019, respectively.

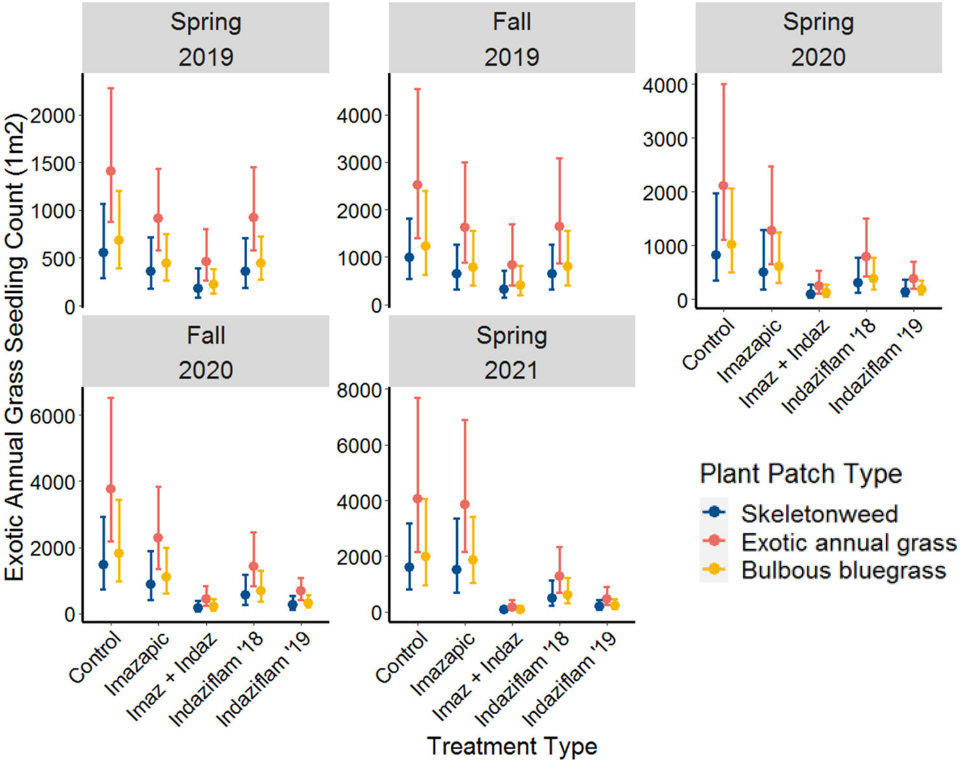

FIGURE 5 Mean ± 95% CI seedling count predictions (1 m^2) of exotic annual grasses by treatment and sample time, based on a generalized linear mixed effects model with a zero-inflated negative binomial distribution. 'Plant Patch Type' groups represent the three different plant community patch types identified through imagery classification of the site. 'Imaz' refers to imazapic and 'Indaz' refers to indaziflam; ''18' and ''19' refer to 2018 and 2019, respectively.

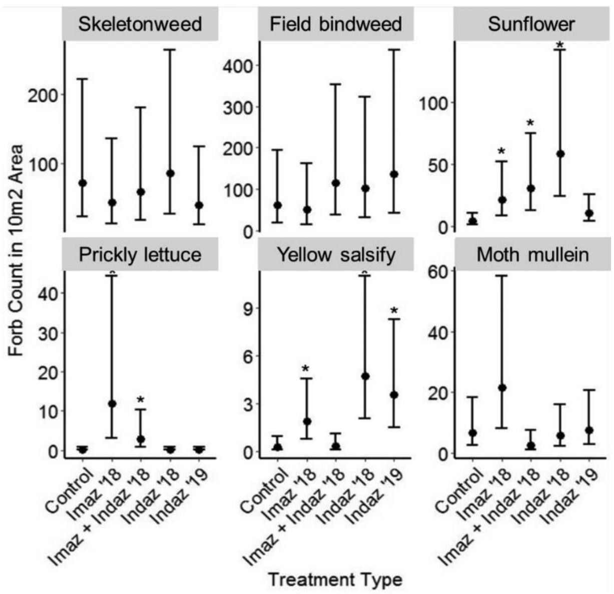

FIGURE 6 Mean ± 95% CI count prediction of exotic forbs per 10 m^2 based on predictions from a generalized linear mixed effects model with a negative binomial distribution and fitted with density count data collected in summer of 2021. Starred treatments are significantly different from their respective controls based on 95% confidence interval overlap. 'Imaz' refers to imazapic and 'Indaz' refers to indaziflam; ''18' and ''19' refer to 2018 and 2019, respectively.

imazapic + indaziflam treatments. Yellow salsify was found at higher densities (three to seven times denser) in all treatments except for the imazapic + indaziflam compared to controls.

3.1.3 | Differences in EAG response among plant community patch types

Treatment effects on EAG cover were not uniform across the plant community patch types within the main-plot herbicide treatments and tended to be least in bulbous bluegrass (POBU) community patch types, intermediate in skeletonweed (CHJU) community patch types and greatest in EAG community patch types (Figure 4). Compared to our base model, the inclusion of treatment block and monitoring transect as a random intercept accounted for 1% and 6% of model error, respectively (Table 1). Plant community patch type explained an additional 2% of model error as indicated by the calculated RMSE (Table 1). Parsing treatment effects by plant community patch type increased detectable treatment effects by a 5% change in EAG cover. EAG cover differed considerably amongst the community patch types, irrespective of herbicide treatments, with 18% of the mean reduction in EAG cover attributed to the presence of bulbous bluegrass (confidence intervals did not overlap) and 12% reduction in EAG cover attributed to skeletonweed (95% CI = 6%).

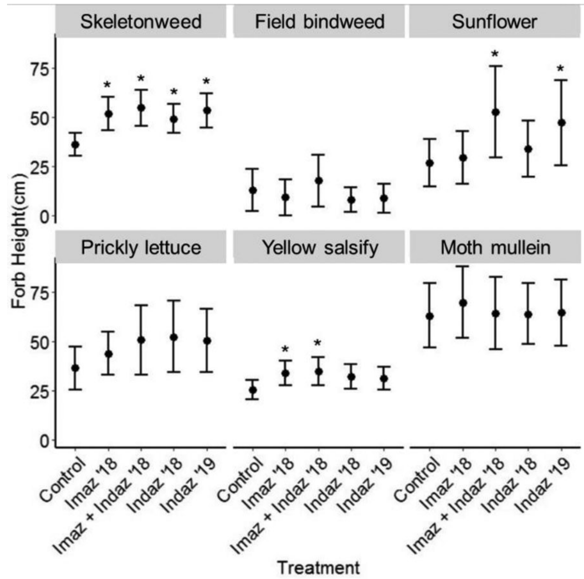

FIGURE 7 Mean ± 95% CI height predictions (cm) of exotic forbs, based on predictions from a generalized linear mixed effects model with a gamma distribution and fitted with density count data collected in summer of 2021. Starred treatments are significantly different from their respective controls based on 95% confidence interval overlap. 'Imaz' refers to imazapic and 'Indaz' refers to indaziflam; ''18' and ''19' refer to 2018 and 2019, respectively.

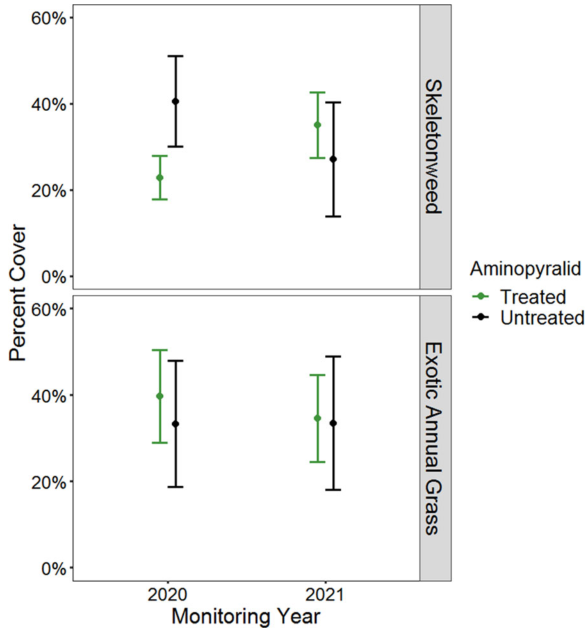

FIGURE 8 Response of skeletonweed or exotic annual grass cover in 2020 and 2021 to aminopyralid applied in fall 2019

3.2 | Subplot treatments

3.2.1 | Aminopyralid herbicide subplots

Aminopyralid treatments reduced skeletonweed cover by an average of 18% (SE for untreated, 10%; SE for treated, 5%) the first year post-treatment (40% reduction compared to controls). By the second year post-treatment, there were no significant differences in skeletonweed cover between treated and untreated areas (Figure 7). EAG cover was not significantly different between the treated and untreated subplots either year post-treatment (Figure 7). Additionally, we did not observe any significant interactions between aminopyralid and the underlying herbicide treatments.

3.2.2 | Litter removal (raking and re-treatment) subplots

Within each main-plot treatment, EAG cover was similar between the re-treated, raked and re-treated, unraked subplots for both years post-treatment (Figure 8). This was in spite of litter being common on the landscape, occurring under nearly all point-intercepts. Re-treatment of imazapic plots greatly reduced EAG cover by 67.5% (SE = 5%) relative to the initial treatments, and re-treatment of imazapic + indaziflam plots reduced EAG cover by 99%.

3.2.3 | Drill seeding and hand planting

Neither drill seeding nor hand planting treatments led to perennial plant recruitment (either for the 2018 or 2019 drill seedings) and there was nearly 100% mortality of hand planted individuals within 1 year post-treatment. Only three of 108 sagebrush seedlings survived, two of which were located within the herbicide treatment indaziflam + imazapic and another was in the 2018 indaziflam treatment.

4 | DISCUSSION

Our study site presented unique restoration challenges with unfavourable soil quality (churning clays) in a low resistance and resilience site with established populations of both invasive forb and grass species as well as a highly mosaiced and heterogenous plant community structure. Reducing exotic species while simultaneously increasing native perennials is a well-known challenge in heavily disturbed areas, with many cases of low success (e.g. Brabec et al., 2015; Knutson et al., 2014; Monaco et al., 2016). We observed multiple installations of drill seedings fail along with the hand plantings of greenhouse grown seedlings. The herbicide treatment effects varied by herbicide type and timing of application (Figures 4–8). Indirect effects were also observed with the increased establishment of exotic forbs (Figures 6 and 7). Variability in vegetation responses were not attributed to litter and were only partially attributed to the plant community patch heterogeneity between treatment areas (i.e. ~5% error; Figures 4, 5, and 9; Table 1). Despite the variability observed within treatments, there were still significant differences in EAG control between the indaziflam and imazapic treatments (Figures 4

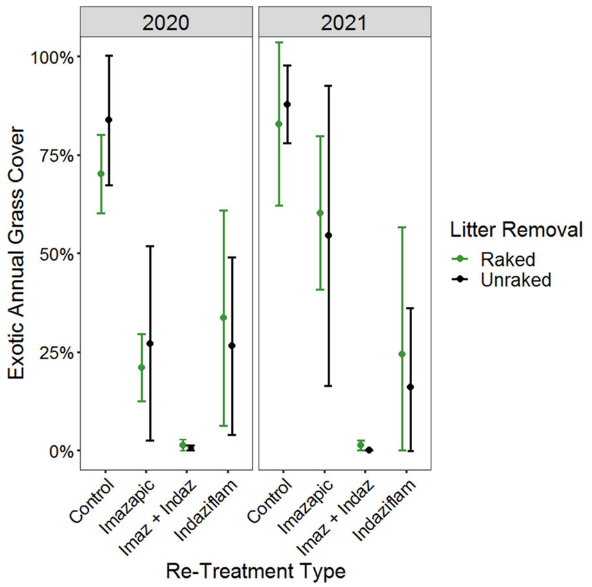

FIGURE 9 Response of exotic annual grass cover to raking prior to re-treatment of each herbicide type in 2019, by sampling year (2020, 2021). 'Imaz' refers to imazapic and 'Indaz' refers to indaziflam.

and 5). Indaziflam had the greatest control of EAGs when precipitation occurred within a month post-treatment, and our results suggested that the combination of indaziflam and imazapic is a more effective treatment than indaziflam alone, including serial respraying of indaziflam (Figures 2–5). Indaziflam also provided a minimum of 3 years of EAG control compared to 0 or 1 year of control from imazapic-treated areas (Figure 4).

Other studies evaluating imazapic effects on EAGs have reported mixed results, ranging from little or no control in Clark et al. (2019) or positive effects, including near our study site (Applestein, Germino, & Fisk, 2018; Germino & Lazarus, 2020; Lazarus & Germino, 2021). The 105 g ai ha^{-1} application rate we used is standard. Studies using lower imazapic application rates tended to observe few and only short-term effects (Clark et al., 2019; Koby et al., 2019; Sebastian et al., 2016 in grasslands). Lazarus and Germino (2022) was the one other study, to our knowledge, that observed some portion of plots treated with imazapic to have reduced EAGs up to 4 years post-treatment, although some of their treatment types had as few as 2 years of control. The lack of a reduction in EAG cover by imazapic in our first trial, in spite of reduced seedling densities (Figures 4 and 5), may have an important explanation that provides insight on demographic mechanisms by which the herbicide may not lead to control. We suggest that the few EAGs that escaped imazapic grew larger foliar crowns, possibly due to greater soil resource availability, and thereby created a similar canopy cover to those found in untreated controls. This mechanism could be verified with additional study and, if supported, would indicate that seed production by EAGs could potentially be greater in situations where removal of EAGs is incomplete. As our results suggest, re-application of imazapic may greatly improve treatment outcomes, perhaps owing to the need to remove 'escaped' EAGs. In comparison, a single application of indaziflam reduced EAG density for 3 years following application in our study, supporting the findings in studies conducted in wetter and more temperate grasslands (Clark et al., 2019; Sebastian et al., 2016; Terry et al., 2021).

4.1 | Exotic forb response

Non-target effects of herbicides are another important factor to consider when evaluating the efficacy of an herbicide as a restoration treatment. A reduction in EAGs could potentially lead to a reduction in native forb abundance and richness, thereby reducing the benefit of EAG control. Additionally, the reduced abundance of otherwise dominant EAGs could also lead to an increase in exotic forb density, particularly in highly degraded areas where pre-existing exotic forb communities can easily spread and take advantage of soil resources without competition from grasses. The forbs invading our plots have relative tall stature, or can spread laterally (field bindweed), and thus have a conspicuous presence in the plant community. The invasion of forbs after herbicide has been observed in several studies including Lazarus et al. (2021), Reid et al. (2009) and Pearson et al. (2016); however, we observed that exotic forb responses to the herbicides varied considerably among the species. Invaders such as prickly lettuce increased >10-fold in density in response to imazapic but not indaziflam, and invaders such as sunflower increased in response to both herbicides. Overall, imazapic had higher exotic forb invasion than the indaziflam-only treatments, suggesting that the increased resource availability hypothesis for explaining post-emergent herbicide invasion by exotic forbs cannot explain the full response.

4.2 | Formal assessment of vegetation heterogeneity

Prior to treatment, the Top Hat site was predominately a mosaic of bulbous bluegrass, medusahead and skeletonweed with plant community patch sizes ranging from 2 to 50 m radii (Figure 1). We expected to observe improved predictive model accuracy by accounting for vegetation heterogeneity as a variable. However, including plant community patch type as a fixed effect only marginally increased our model accuracy compared to our random effects (repeated transects; Table 1). This suggests that there was variability occurring at the transect level that was not measured or accounted for in our model. Munson et al. (2015) also accounted for monitoring transect as a random effect and found that it explained more variability in vegetation cover than any of their fixed effects (excluding treatments). It is possible that classifying the site into only three community patch types was too course (i.e. insufficient categorical resolution) given the spatial diversity of plant community patch types. Additionally, there was still 13% of error in model predictions of EAG response to treatments that was not explained by plant community patch type or random effects. High model error is common in ecological systems as there are a multitude of biotic and abiotic factors that affect biological responses (Barnard et al., 2019; Brudvig et al., 2017). However, our in-sample model accuracy of 87% is above the standard (approx. 80% accuracy) for landscape-scale predictive models (Applestein, Germino, Pilliod, et al., 2018). The findings of our study as well as Dickens et al. (2015) suggest that plant community composition could be an important predictor for vegetation response to treatment; however, more research is needed to fully understand how to capture this variability in a predictive model.

4.3 | Litter removal effects and yearly precipitation differences on herbicide effects

We expected, but did not observe, litter removal effects on herbicide re-treatments (Figure 9). However, other studies have shown significant differences in herbicide effects when a disturbance, such as raking, is used to expose the soil surface (Kyser et al., 2013). Controlled fire is sometimes used to remove litter, although this method carries increasing risks as warming and high-value development exacerbate fire risk exposure. In a nearby site, pre-burning increased the interactive effects of imazapic and seeding in reducing EAGs and increasing perennials (although only in a particular year and with very high seeding rates; Schantz et al., 2019). One possibility for our negative raking results could be that the layer of medusahead thatch was not thick enough on the areas we raked (which we had previously applied herbicide to) to alter EAGs or the effects of herbicide application on EAGs.

Imazapic re-treatment had stronger negative effects in comparison to either initial treatments or untreated controls (Figure 9, compared to Figure 4). Whether this is due to accumulating more imazapic in the soil or some temporal factor such as weather causing the second spraying to be more effective is an important question. It is possible that higher precipitation after treatments applied in 2019 was the primary factor in herbicide success. Specifically, nearly 30 mm of precipitation was received preceding the 2018 treatments but none in the month after, which contrasted the nearly opposite patterns in 2019 (30 mm of precipitation received after treatments and none in the month prior; Figures 2–6 and 9). Our findings that post-treatment precipitation may enhance herbicide effectiveness contrast with Morris et al.'s (2009) findings that treatment outcomes are better predicted by pre- rather than post-treatment precipitation, due to greater infiltration on pre-wetted soils.

4.4 | Aminopyralid effects on skeletonweed and EAGs

Aminopyralid provided transient control of skeletonweed with only 1 year of cover reductions and quickly regained skeletonweed cover the second year post-treatment (Figure 8). Other studies are mixed in whether they found aminopyralid control of skeletonweed (Spring et al., 2018; Thorne & Lyon, 2021). Specifically, Spring et al. (2018) observed strong control of skeletonweed in both of two years post-treatment (97% and 84%, respectively), while Thorne & Lyon (2021) did not observe any significant control of skeletonweed from aminopyralid (Figure 8). Findings for aminopyralid control of EAGs is also mixed. Our study did not provide evidence for aminopyralid control of medusahead, whereas other studies have suggested that the broadleaf herbicide has potential for medusahead reduction (Kyser et al., 2012; Rinella et al., 2018). However, timing of aminopyralid application may be an important factor, for example Rinella et al. (2018) observed improved control of EAGs with spring applications compared to fall applications.

4.5 | Re-vegetation and herbicide treatments

The failed drill seeding in our study precluded assessment of indaziflam effects on drill seeding. Factors that commonly explain drill seeding failures were all observed in our study including (1) below average precipitation in the months just before and after seeding, although germination was not stimulated by a wet winter and spring (Figures 2 and 3; Hardegree et al., 2018), (2) unfavourable soil types (churning clay) and (3) competition from multiple invasive species (Davies, 2010; Young et al., 1999). There is a potential conflict between pre-emergent herbicides and seeding which we initially attempted to avert by seeding both before or after herbicide application, but the lack of emergence in unsprayed control plots clearly indicates that herbicides were not the cause of seeding failure that were evident in previous work (Terry et al., 2021). Also, the same seed mix was used for both years of application (2018 and 2019) and had a tested viability of 60%–85%, suggesting that variation in seeds or poor viability was unlikely to explain the results. Perennial establishment from drill seeding was observed in a nearby study, but only in plots using fivefold greater seeding densities and only in one of 4 years that had a very snowy winter (120 mm of precipitation, compared to a maximum of 83 mm in the current study), and where pre-burning and imazapic application had been previously applied (Schantz et al., 2019). The comparison between our data and Schantz et al. (2019) is confounded such that pre-burning cannot be compared to raking, and there is some possibility that burning but not raking removed EAG seeds and thereby improved the treatment outcome. We suggest that it is more likely that over 4 years the required precipitation for seeds was not observed in our study, even though water-year precipitation recorded at the Boise airport (<7 km) was above the mean annual precipitation of 300 mm (30-year average) for two years (423 and 330 mm in 2019 and 2020, respectively) and not severely below average in the other years (265 mm in each of 2018 and 2021). Instead, the timing of the wetting events may have not met the seed requirements (Figure 3), even in the wetter water years (Hardegree et al., 2018). Planting of perennials is often done to circumvent the demographic bottleneck of weather- and herbicide-sensitive seed germination and seedling survival, but the planting trial applied here also failed. Like for our seeding, hand planting of seedlings may have resulted in more perennial establishment with improved environmental conditions, which appears possible only with sustained re-application of treatments in sequential years to increase odds of coinciding with required weather.

5 | SUMMARY

Our data suggests that indaziflam, particularly when combined with imazapic, can be an effective method for providing at least 3 years of EAG control, although methods of control for secondary invasions by non-target invaders may be necessary for more comprehensive restoration strategies. Additionally, a lack of revegetation success is highly problematic in sites where native perennials are scarce (such as the Top Hat study site) and thus are weak sources for desired plant recovery. More intensive revegetation strategies and establishment of perennial bunchgrasses are vital to conservation and in preventing further invasion by EAGs and forbs (Davies & Svejcar, 2008). Lastly, our results indicated that only some of the variability in treatment outcomes could be explained by vegetation heterogeneity between treatments and pre-existing plant community effects. Further investigation is needed into the underlying causes of variation in treatment outcomes to improve predictions for vegetation response to treatment and to help inform successful management strategies.

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AUTHOR CONTRIBUTIONS

Matthew Germino conceived of the project and the experimental design, oversaw the implementation of treatments, procured funding and supervised the project. Rebecca Donaldson collected and analysed the data. Both authors wrote the manuscript and gave final approval for publication.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available at https://doi.org/10.6084/m9.figshare.20349510 (Donaldson & Germino, 2022).

PEER REVIEW

The peer review history for this article is available at: https://publons.com/publon/10.1002/2688-8319.12172.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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