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Abundant Litter Accumulation Decreases Milkweed Abundance While Fire and Grazing May Benefit Milkweed

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Abstract – Current rates of biodiversity loss warrant informed and targeted conservation. Within The United States, rangelands present an opportunity for effective conservation that can promote biodiversity. However, rangelands are susceptible to invasive grasses like *Poa pratensis* L. (Kentucky Bluegrass) and *Bromus inermis* Leyss (Smooth Brome) which can impact native plants such as *Asclepias* spp. (Milkweed), a plant of current conservation interest because of its importance to *Danaus plexippus* L. (Monarch Butterfly). Since fire and grazing shaped the Great Plains rangelands, changes to fire and/or grazing management allowed invasive grasses to expand and take hold. Therefore, reconnecting fire and grazing to the landscape may mitigate invasive grasses, benefiting milkweed and biodiversity. To investigate this, we used a structural equation model (SEM) approach to determine the direct and indirect impacts of invasive grasses (i.e., Kentucky Bluegrass and Smooth Brome) and management (fire and grazing) on milkweed. We found that Kentucky Bluegrass and Smooth Brome themselves did not influence milkweed abundance, but increasing litter abundance strongly decreased it. Increased time since a spring fire was positively associated with Smooth Brome abundance and litter depth which, by extension, increased thatch depth. An increase in time since fire also decreased the utilization by cattle, which thereby indirectly decreased milkweed abundance, as there was less grazing pressure on the vegetation. Collectively, this means that patches that were more recently burned had less Smooth Brome, relatively lower litter depth, more grazing, and more milkweed. Patches with higher utilization had greater milkweed abundance, meaning that despite the possibility of direct consumption by cattle, greater cattle utilization may have benefits that outweigh negative effects on milkweed. Our results suggest that fire and grazing may mitigate invasive grasses and benefit milkweed, with potential positive implications for monarchs and biodiversity.

Introduction

Biodiversity is declining at both local and global scales (Butchart et al. 2010, Pereira et al. 2010), urging broad scale conservation actions (Johnson et al. 2017). Within the United States, rangelands may offer high conservation potential for supporting biodiversity on account of their large scale (MacArthur and Wilson 2001) and relatively natural state (Havstad et al. 2007, Swaty et al. 2011). For instance, rangelands devoted to beef production occupy over a third of U.S. land (Theobald 2014), almost twice as much acreage as croplands (Bigelow and Borchers 2017) and are characterized as lands that are uncultivated and dominated by native plant communities which can support grazing by wild or domestic animals (Williams et al. 1968). However, rangelands are susceptible to invasive woody and herbaceous species (Ruffner and Barnes 2012, Toledo et al. 2014, Gasch et al. 2020, Palit et al. 2021, Palit and DeKeyser 2022), which can shift the plant community from a diverse collection of species to stands of structurally and compositionally homogenous communities. Invasive species invasions within rangelands are products of and/or exacerbated by changes in land management, particularly the loss of historic disturbances (Fuhlendorf et al. 2012), as well

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as shifting climatic factors such as precipitation patterns (Polley et al. 2013). Challenges with invasive species may be mitigated by re-incorporating strategic management actions that favor native plant expression, thus helping species of conservation concern.

Invasive grasses, in particular, may lower the capacity at which rangelands can contribute to biodiversity conservation through a multitude of direct and indirect means (Toledo et al. 2014, Palit et al. 2021, Palit and DeKeyser 2022) and create a positive feedback loop that reinforces their dominance (Jordan et al. 2008, Ellis-Felege et al. 2013). Invasive grasses can directly displace native vegetation (Palit et al. 2021, Palit and DeKeyser 2022) and transform rangelands into near monocultures (Hendrickson et al. 2021). This has been the case for rangelands, often dominated by 2 primary invasive grass species within the Great Plains region, *Poa pratensis* L. (Kentucky Bluegrass) and *Bromus inermis* Leyss (Smooth Brome), the invasive grasses addressed in this article. Both Kentucky Bluegrass and Smooth Brome comprise 10% of plant species cover in the Northern Great Plains, altering plant community structure and functions (i.e., decreases the variability of both; Hendrickson et al. 2019, Toledo et al. 2014). These invasive grasses form dense stands of litter which can lower plant diversity (e.g., forbs; Pei et al. 2023), likely by blocking essential sunlight and moisture from reaching native plant seeds and seedlings on the ground (Toledo et al. 2014, Printz and Hendrickson 2015). Additionally, as Kentucky Bluegrass litter senesces it is compressed by newer litter, and over time these layers of decaying plant material accumulate and form a thatch layer. Thatch, comprised of loosely intermingled decaying litter, dead stems, live buds, and portions of the root mat, is akin to an O-horizon of a soil profile and is a novel addition to the soil profile of prairies in the Northern Great Plains (Fig. 1; Millar et al. 1966, DeKeyser et al. 2015, Kjaer et al. 2024). It has distinctive chemical properties that further facilitate invasive grass expansion, specifically, Kentucky Bluegrass. The entangling effect of thatch alters soil hydrology which can increase runoff (Sanderson et al. 2017, Nouwakpo et al. 2019), suppress new growth and recruitment of native plants (Cardinale et al. 2012) by preventing seed germination (Fowler 1988, Facelli and Pickett 1991), and expedite the transference of viral and fungal infections (Benitez et al. 2022).

The abundance of *Asclepias* spp. (Milkweed), the obligate host plant to *Danaus plexippus* L. (Monarch Butterfly; a species of conservation concern) may be, in a similar manner, directly and indirectly affected by invasive grasses (Fig. 2). While there is minimal research focused on invasive grass effects on milkweed specifically, much of the already discussed negative impacts on native vegetation (e.g., nutrient competition or litter blocking sunlight) would likely extend to milkweed. For instance, invasive grasses may directly compete with milkweed, whose growth is limited by abundant, nearby plants (Dee and Palmer 2019), and when grown in shade, such as with high standing litter, they are less protected against herbivory (Agrawal et al. 2011). Collectively, the characteristics of Kentucky Bluegrass and Smooth Brome create novel grassland systems that are unlikely to be eradicated, but their effects on milkweed and other native vegetation may be attenuated through strategic land management practices, such as prescribed fires and grazing.

Fire and grazing can each directly and indirectly impact invasive grasses and milkweed. For example, spring prescribed fires directly remove aboveground biomass, which can limit Kentucky Bluegrass and Smooth Brome expansion by stunting their early-season growth (Curtis and Partch 1948, Blankespoor and Bich 1991) and reducing litter and thatch (Menke 1992, Limb et al. 2016). At the same time, it can also generate new milkweed growth (e.g., above-ground stem removal can promote same-year re-growth or increase floral expression one-year post-fire; Baum and Sharber 2012, Duquette et al. 2022a). Fire can also indirectly affect milkweed by altering the soil nitrogen content (Goergen and Chambers 2009, Toledo et al. 2014) or stimulating germination (e.g., smoke water; Mojzes and Kalapos 2015). Grazing, like fire, directly removes biomass as cattle eat, which can limit the spread of invasive grasses (Hendrickson et al. 2020, Rhodes et al. 2021), but it can also damage or remove milkweed stems (Dickson et al. 2023, Johnson 2023, Pietola et al. 2005, Ricono et al. 2018). However, cattle may also trample milkweed seeds into the ground, possibly increasing the population via sowing (Jackson 1999), or generate growth by increasing soil

Figure 1. Thatch at the Central Grasslands Research Extension Center in July 2022. Thatch is a loosely compressed mixture of decaying litter, buds, dead stems, and roots that accumulates over time following Kentucky Bluegrass invasion. This layer resembles a pseudo O-horizon in the soil profile. Notably absent in the historical northern Great Plains landscape, this thatch layer now acts as a physical barrier, significantly altering soil hydrology, nutrient cycling, and temperature, ultimately suppressing native species growth and germination (Printz and Hendrickson 2015, Nouwakpo et al. 2019, Kjaer et al. 2024). Anything above the upper line is the aboveground plant material, while below the lower line is the non-thatch bound root mass and mineral soil. Although thatch and the bulk of the root mat are distinct layers, roots often intertwine with the lower portion of the thatch. For this study, thatch depth is measured as the distance between aboveground biomass and non-thatch bound root mass (i.e., between the two dashed lines).

nitrogen content via dung (Jungnitsch et al. 2011). Considering certain clonal milkweed species like *Asclepias syriaca* L. (Common Milkweed) and *Asclepias speciosa* Torrey (Showy Milkweed) are resilient against disturbance (Liu et al. 2007), most milkweed can likely tolerate management actions such as prescribed fires and grazing.

Invasive grasses limit ecosystem function within rangelands by altering native ecosystem structure (e.g., thatch; Kjaer et al. 2024), composition (e.g., monoculture; Hendrickson et al. 2021), and processes (e.g., hydrology; Sanderson et al. 2017, Nouwakpo et al. 2019). As such, investigating the extent to which varying management strategies may impact invasive grasses and in turn how invasive grasses may directly (e.g., interspecific competition of resources and physical space) or indirectly (e.g., litter accumulation and thatch formation)

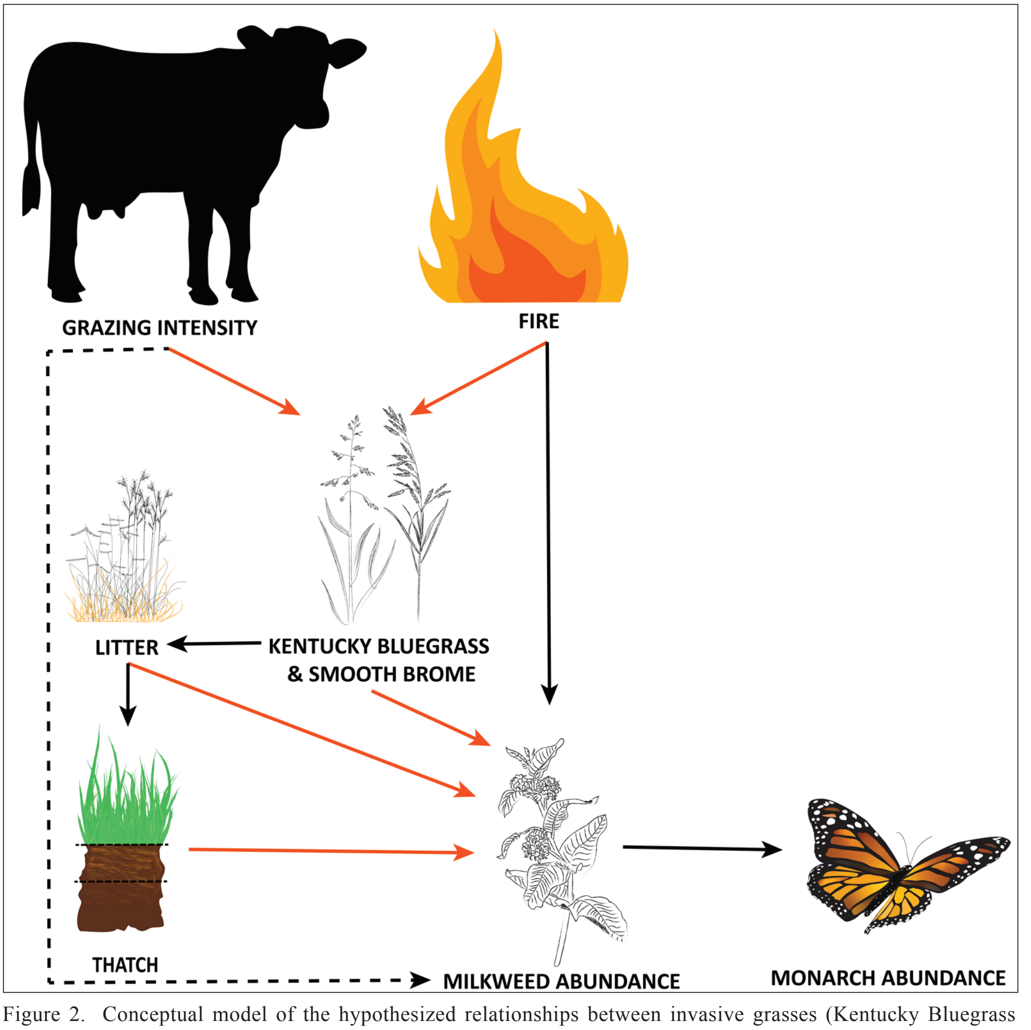


Figure 2. Conceptual model of the hypothesized relationships between invasive grasses (Kentucky Bluegrass and Smooth Brome), litter, thatch, land management actions (fire and grazing), and milkweed that can indirectly influence monarch populations (not measured). Litter refers to dead vegetation, represented by yellow lines. Black, dashed lines on the thatch image enclose the thatch layer. Orange lines indicate a net negative directional relationship (e.g., fire decreases Kentucky Bluegrass and Smooth Brome) while solid black lines indicate a positive, directional relationship (e.g., litter increases thatch). Dashed lines represent uncertainty for a net positive or negative relationship.

Figure 3. Final SEM model for the effects of fire coupled with grazing, grazing alone, and invasive grass abun-

impact native vegetation like milkweed is essential to monarch conservation and promoting biodiversity. The goal of our study is to identify the direct and indirect influences of varying fire and grazing on the invasive grasses Kentucky Bluegrass and Smooth Brome and to identify the role of these species and management on milkweed. We hypothesize that (1) Kentucky Bluegrass and Smooth Brome will displace milkweed and indirectly affect milkweed abundance through litter and thatch accumulation, (2) Fire accompanied by grazing will directly affect milkweed abundance by creating openings for expression and indirectly by altering Kentucky Bluegrass and Smooth Brome abundances and grazing behavior, and (3) Grazing will have both a direct and an indirect influence on milkweed abundance by decreasing Kentucky Bluegrass and Smooth Brome (Fig. 2; Fig. S1, available online at https://eaglehill.us/prnaonline/suppl-files/prna-039e-Johnson-sf1.pdf). Understanding the interplay between invasive grasses, fire and grazing management, and milkweed in rangelands might elucidate options for addressing milkweed decline and its possible repercussions on Monarch Butterfly populations.

Methods

Site description

This study took place in 2022 at the North Dakota State University Central Grasslands Research Extension Center (CGREC). Our sites are located in the Missouri Coteau ecoregion, an area composed of rolling hills interspersed with small glacial lakes (USDA Soil Conservation Service 1982). This area experiences a continental climate with average temperatures ranging from −0.4° C to 11.5° C (NDAWN 2024). Sites received a total of 342.77 mm in 2022 (60.9 mm below the 30-year average; NDAWN 2024). Historically, the sites were comprised of northern mixed-grass prairies, consisting of cool-season grasses such as *Pascopyrum smithii* Rydberg À. Löve (Western Wheatgrass), warm-season grasses, such as *Schizachyrium scoparium* Michaux Nash (Little Bluestem), and various forbs, such as *Artemisia* spp. and *Solidago* spp. (Limb et al. 2018). Milkweed species, particularly *A. syriaca* and *A. speciosa*, are also found throughout the CGREC (Limb et al. 2018). However, deviations from historic grazing and fire regimes have allowed Kentucky Bluegrass and Smooth Brome to dominate these sites.

Experimental design

Our study utilized four 65-ha replicates (pastures) of three different grazing practices: season-long grazing, patch-burn grazing, and heterogeneity-based rotational grazing. Season-long and patch-burn pastures were established in 2017 and contained no interior fencing. Under season-long grazing, cattle were turned out to pasture in mid-May (in 2022 cattle turnout for all treatments was May 19) and allowed to graze and move freely. The patch-burn grazing treatment was designed so a different quarter (approximately 16 ha) of each patch-burn pasture (approximately 65 ha) was burned every spring prior to cattle turn out, and cattle could graze and move freely, with the expectation that they would preferentially graze the recently burned areas (Allred et al. 2011). Prescribed fires were typically conducted between mid-April and late-May each year but were not conducted in 2022 due to a lack of fuel accumulation from an exceptional drought in 2021 (NDAWN 2024). Fires were always conducted after Kentucky Bluegrass and Smooth Brome had begun growing for the year. However, the amount of green plant material and completeness of the fires varied with time. Fires that occurred toward the end of May tended to have more green plant material (specifically Kentucky Bluegrass and Smooth Brome) and subsequently had less complete fires.

As an alternative way of creating landscape-level heterogeneity, we developed a heterogeneity-based rotational grazing system in the form of a modified twice-over rest-rotational grazing system in 2018. Heterogeneity was created by restricting cattle movement to one of four different 16-ha paddocks within each 65-ha pasture at a given time. Each paddock was stocked and grazed for different lengths of time twice in a year to create different levels of grazing disturbance. The different levels of disturbance were achieved by altering the number of grazing days cattle would spend in a paddock to achieve (1) no utilization by cattle (rested), (2) moderate utilization (20–40% degree of disappearance), (3) full use (40–60% degree of disappearance), and (4) heavy use (>60% degree of disappearance. See Duquette et al. (2022b) and Kjaer et al. (2024) for a full description of this grazing practice. Prior to the creation of the heterogeneity-based rotational grazing system these pastures were involved in patch-burn grazing and early intensive grazing experiments (Dornbusch et al. 2020).

Stocking rates were similar among each treatment, ranging from 2.37 to 2.48 animal unit months per hectare (AUM/ha). After turnout cattle grazed each pasture until October 22 in 2022. Patch-burn patches and the initial location of the different levels of use within the heterogeneity-based rotational pastures were randomized. For data collection purposes, each pasture was further subdivided into 16 hypothetical 8-ha sub-patches (sub-paddocks).

Data collection

We established 96 60-meter transects on loamy soils spread across our 12 pastures with 1 transect per sub-patch and 32 transects per treatment (Sedevic et al. 2021). Each transect was sampled every other meter starting at 0, for a total of 31 sample points per transect. To assess changes in the relative abundance of all plant species between sample points, we recorded plant community composition data by identifying every species in a 1-m^2 quadrat and assigning them a modified Daubenmire cover class, allowing us to detect small changes in abundance for both minor and major abundant species:

1 = trace–1%; 2 = 1–2%; 3 = 2–5%; 4 = 5–10%; 5 = 10–20%; 6 = 20–30%; 7 = 30–40%; 8 = 40–50%; 9 = 50–60%; 10 = 60–70%; 11 = 70–80%; 12 = 80–90%; 13 = 90–95%; 14 = 95–98%; 15 = 98–99%; 16 = 99–100% (Daubenmire 1959, Dornbusch et al. 2020).

Cover is commonly used to measure the abundance of plant species in grasslands (Damgaard 2014, Dornbusch et al. 2020, Floyd and Anderson 1987, Watson et al. 2024). We also recorded basal litter (primarily horizontal) and standing litter (primarily vertical) abundances using the same modified Daubenmire cover classes, as well as thatch depth and litter depth at each point. All cover classes were converted to cover midpoints prior to data analysis. We sampled litter depth by placing a ruler vertically on the ground and recording the height of the horizontal litter layer to the nearest 0.1 cm. We recorded thatch depth by taking soil cores at every sample point. Using a 1.9-cm diameter soil probe to a depth of 20 cm we took soil cores and recorded the length of the thatch layer present in each core to the nearest 0.1 cm (Kjaer et al. 2024). To be precise, thatch depth was measured as the length between the aboveground biomass and the non-thatch bound root mass (Fig.1). Data collection occurred from July to mid-August each year to allow us to capture the greatest variation in the plant community, as this time window corresponds to the portion of the growing season when cool-season plants begin to senesce and warm season plants are beginning to grow and reach peak biomass for the year. Prior to sampling the heterogeneity-based rotational grazing pastures, all non-rested paddocks had been grazed once. All observers were trained in plant identification each year and observers calibrated cover estimations to one another prior to each bout of data collection to minimize observer bias. One graduate student served as the calibration metric each year to further reduce observer bias. Finally, the time since the last known fire event was recorded for each transect: 1 to 5 years for patch-burn transects, 8 years for heterogeneity-based rotational grazing transects, and 41 years for season-long transects.

To assess grazing intensity after the grazing season, we established 1.5-m^2 exclosures within each 8-ha sub-patch to compare aboveground biomass in grazed and ungrazed areas. In patch-burn and season-long pastures, each 16-ha unit had eight exclosures, totaling 32 per pasture. Heterogeneity-based rotational pastures had 10 exclosures per sub-patch, resulting in 80 per pasture. Exclosures were placed on loamy ecological sites, at least 20 m from plant community transects (USDA-NRCS 2021). This placement ensured that the plant communities inside and outside the exclosure were similar to those found on the vegetation transects, while minimizing the influence of high cattle traffic as cattle travelled to exclosures to rub on them or eat near them.

After cattle removal, we collected 0.25-m^2 samples of annual production (i.e., vegetation that had grown that year) both inside and outside each exclosure. Clipped vegetation was dried at 60° C for at least 48 hours until reaching a constant weight. Cattle utilization was calculated as the difference between average biomass inside and outside each exclosure. Percent utilization at the sub-patch level was calculated by dividing total utilization by total standing crop biomass and multiplying by 100, accounting for natural variation in biomass production. Average percent utilization for a patch within a pasture was calculated by averaging percent utilization across sub-patches. In one patch-burn pasture that lacked exclosures, the other sub-patch's average percent utilization represented the entire patch.

Data analysis

Statistical analyses were preformed using the piecewiseSEM package in R 4.2.3 (Lefcheck 2016, R Core Team 2023). Eight response variables were included in our structural equation model (SEM; Table S1, available online at https://eaglehill.us/prnaonline/suppl-files/prna-039e-Johnson-st1.pdf). Before running the SEM we examined each using a Shapiro-Wilks test to assess normality. Of the 8 variables in the model only "utilization" and "Kentucky Bluegrass abundance" were normally distributed, the other 6 were not. This lack of normality, coupled with a relatively low sample size for each treatment (n = 16 per treatment, four pastures with 4 distinct patches) led us to use piecewiseSEM's local estimation, rather than global estimation, to calculate our SEM (Lefcheck 2016).

Local estimation allows us to model response variables that are not normally distributed without transformation, in a manner to how generalized linear models allow for the modeling of non-normally distributed response variables (Table 1; Lefcheck 2016). Relationships where the response variable was non-normal and continuous were assessed using a gamma distribution and log link-function (Table 1). However, milkweed abundance did not fit a gamma distribution prior to our initial model and could not be easily transformed to a normal distribution. As such, milkweed abundance was transformed using a square root transformation and was then assessed using a gamma distribution and log link-function (Table 1). Years since fire was the only discrete variable, and as it was an exogenous predictor, no transformations or non-normal distributions were needed. All data were transformed and averaged to the patch level prior to model initialization.

Also, while local estimation can be relatively robust against small sample sizes, we further accounted for small sample sizes by combining data from all grazing treatments, giving us a total sample size of 48. While this eliminates our ability to draw conclusions on

Table 1. Pathways included in the initial SEM model. The table includes response variables, the distribution used to model each response, their predictor variables for each response, justification for including each pathway (i.e., response-predictor relationship), citations for specific pathways, as well as pathway identifiers that match pathways shown in Figure S1.

Response Variable	Distribution	Explanatory Variable(s)	Justification	Citation	Pathway
Kentucky Bluegrass Abundance	Normal	Time Since Fire	Kentucky Bluegrass decreases after a fire.	Dornbusch et al. (2018)	a
		Grazing Intensity	Intense grazing can temporarily decrease Kentucky Bluegrass abundance.	Duquette et al. (2022)	b
Smooth Brome Abundance	Gamma	Time Since Fire	Smooth Brome decreases after a fire.	Dornbusch et al. (2018)	c
		Grazing Intensity	Intense grazing can temporarily decrease Smooth Brome abundance.	Duquette et al. (2022)	d
Litter Abundance	Gamma	Time Since Fire	Fire removes litter from grasslands.	Limb et al. (2016)	e
		Grazing Intensity	Cattle occasionally eat litter and compress/move litter through trampling.	Vermeire *et al*., (2004)	f
		Smooth Brome Abundance	Smooth Brome senesces, creating dense litter.	Palit and DeKeyser (2021)	g
		Kentucky Bluegrass Abundance	Kentucky Bluegrass senesces, creating dense litter.	Palit et al. (2021)	h
Litter Depth	Gamma	Time Since Fire	Fire removes litter from grasslands.	Limb et al. (2016)	i
		Grazing Intensity	Cattle occasionally eat litter and compress/move litter through trampling.	Vermeire *et al*., (2004)	j
		Smooth Brome Abundance	Smooth Brome senesces, creating dense litter.	Palit and DeKeyser (2021)	k
		Kentucky Bluegrass Abundance	Kentucky Bluegrass senesces, creating dense litter.	Palit et al. (2021)	l

Table 1. Continued.

Response Variable	Distribution	Explanatory Variable(s)	Justification	Citation	Pathway
Thatch Depth	Gamma	Grazing Intensity	High grazing intensity may compress thatch.		m
		Smooth Brome Abundance	Smooth Brome alters nutrient cycling, potentially increasing thatch decomposition	Palit and DeKeyser (2021)	n
		Kentucky Bluegrass Abundance	Kentucky Bluegrass forms thatch.	Palit et al. (2021)	o
		Litter Abundance	Litter compresses to form thatch.	Palit et al. (2021); Printz and Hendrickson (2015)	p
		Litter Depth	Litter compresses to form thatch.	Palit et al. (2021); Printz and Hendrickson (2015)	q
		Litter Abundance X Litter Depth	Deeper more abundant litter may more readily form thatch than deep or abundant litter on their own.		r
Milkweed Abundance	Gamma	Time Since Fire	Forb expression/growth increases the year after a fire.	Duquette et al. (2022)	s
		Grazing Intensity	Cattle eat forbs, including milkweed.	Dickson et al. (2023)	t
		Kentucky Bluegrass Abundance	Kentucky Bluegrass may compete with milkweed for resources, including light, soil nutrients, and water.	Palit et al. (2021)	u
		Smooth Brome Abundance	Smooth Brome may compete with milkweed for resources, including light, soil nutrients, and water.	Palit and DeKeyser (2021)	v
		Litter Abundance	High litter abundance may shade out milkweed species, reducing expression and germination	(Bailey and Brown 2011)	w
		Litter Depth	Deep litter may shade out milkweed species and alter water cycling, reducing expression and germination.	Nouwakpo et al. (2019)	x
		Litter Abundance X Litter Depth	Deeper more abundant litter may more readily shade out and negatively affect milkweed than deep or abundant litter on their own.		y
		Thatch Depth	Thatch accumulation prevents milkweed germination.	Palit et al. (2021); Printz and Hendrickson (2015)	z
Litter Abundance and Litter Depth Covariance			More abundant litter is likely to also be deeper.		aa

how specific management practices influence milkweed abundance, it allows us to safely draw conclusions on how "time since fire", "grazing alone", and "invasive grasses" influence milkweed abundance. Additionally, by calculating utilization as a measure of grazing intensity, while also recording time since the most recent fire on a transect, allows us to tease apart the effects fire and grazing, it is important to note that all pastures were grazed the year of the study.

After developing an initial causal or hypothesized model based on the aforementioned hypotheses (Fig. S1, Table 1), piecewiseSEM (Lefcheck 2016) was used to evaluate the initial model for convergence. After initial convergence, fit measures (Fisher's C), tests of directed separation, and parsimony were used to assess and guide model selection. There was one significant test of directed separation between Kentucky Bluegrass and Smooth Brome abundance. While there is likely a negative correlation between the 2 invasive grasses (i.e., as Kentucky Bluegrass increases in abundance, Smooth Brome decreases, and vice versa; Grant et al. 2020), we cannot determine the causality of such a relationship at this time. Instead, this relationship was then included as a covariance structure in the model. No other significant tests of directed separation were reported.

Afterwards, starting with the pathway with the largest *p*-value, non-significant pathways were dropped iteratively from the model (Hooper et al. 2008). If dropping a non-significant pathway from the model resulted in non-linearity in the basis set, the pathway was instead retained. Dropping non-significant pathways typically caused both the Fisher's C score and the *p*-value associated with it to increase slightly. This process was repeated until the *p*-value associated with the Fisher's C score began to shrink, and the final model was decided. Because our model contained paths that were assessed with different distribution families and link functions, all pathway coefficients were standardized by multiplying the initial pathway coefficient for a path by the standard deviation of the predictor divided by the standard deviation of the response variable (Equation 1; Lefcheck 2016).

$$Standardized\ Coefficient = Pathway\ Coefficient * \frac{Predictor\ SD}{Response\ SD}$$

Results

Structural equation model fitting of causal/hypothesized paths for milkweed abundance

We began the model selection process with a highly saturated SEM (i.e., almost all possible pathways were included in the initial model; Table 1, Fig. S1, and Data Analysis Section). Our initial model converged and was relatively well supported (Fisher's C = 2.564, *df* = 2, *P* = 0.277). Through 10 iterations, poorly supported paths were individually removed to improve model fit. Resulting in a final model that was well-supported upon convergence (Fisher's C = 8.524, *df* = 16, *P* = 0.932; Table 2) and further removal of unsupported pathways either did not improve model fit or decreased model fit.

SEM results

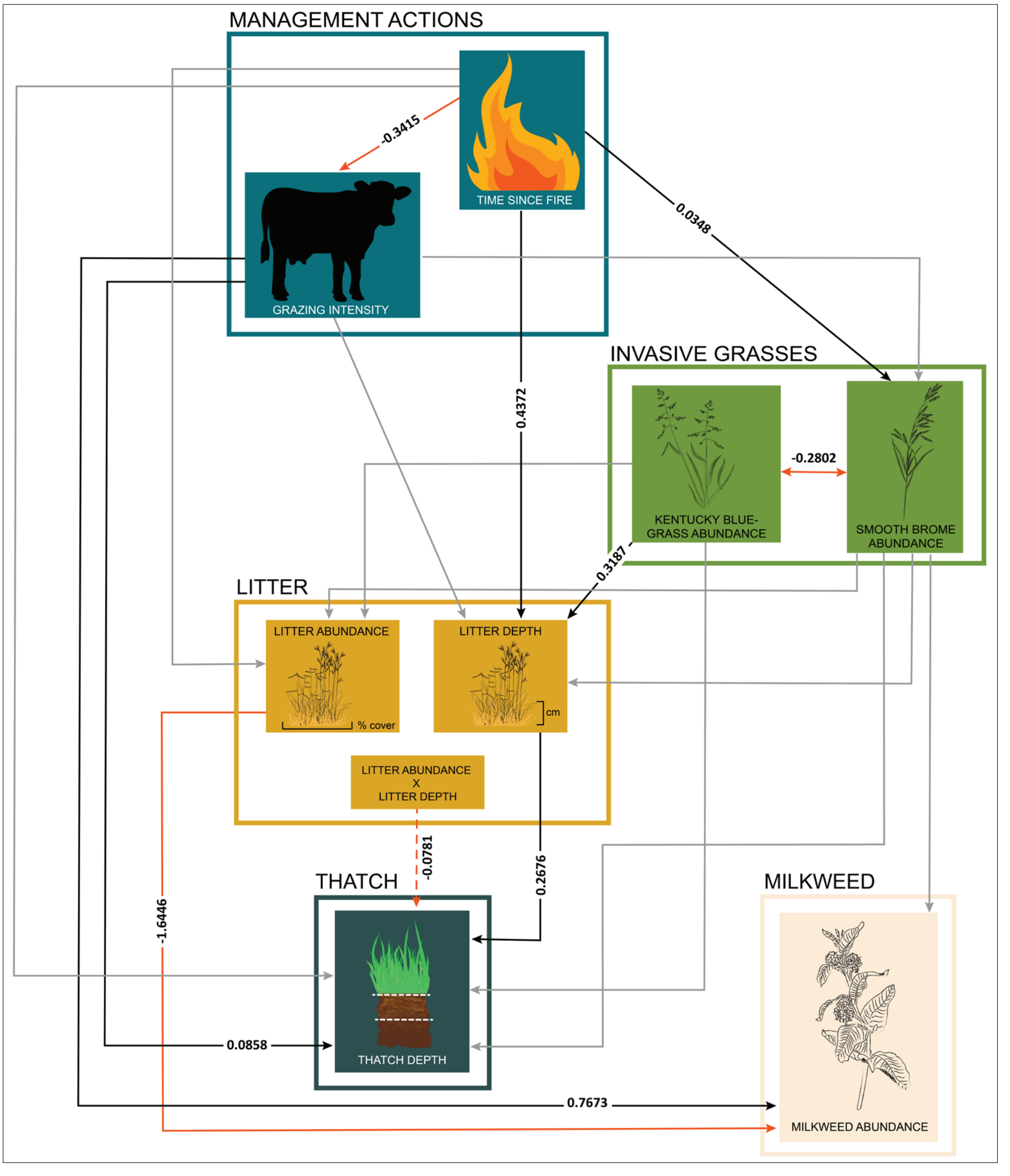
The final model supported our hypotheses that grazing intensity in the form of utilization has a direct impact on milkweed abundance, and that fire coupled with grazing and grazing by itself indirectly affects milkweed abundance (Fig. 2, Fig. 3).

SEM – direct and indirect impact of invasive grasses on milkweed abundance

Counter to our conceptual model (Fig. 2) and our initial causal or hypothesized model (Fig. S1), our final SEM did not support a direct or indirect path from either Smooth Brome or Kentucky

Table 2. This table represents each pathway in the final structural equation model. The table lists each response variable, predictor or explanatory variable, standardized pathway coefficients (effect sizes), standard errors, *p*-values, R^2 estimates for each pathway, and justification for inclusion in the final model.

Response Variable	Predictor Variable	Standardized Coefficients	Standard Error	p-value	R^2	Justification
Grazing Intensity	Time Since Fire	-0.3415	0.1620	0.023	0.11	Allred et al. (2013)
Smooth Brome Abundance	Time Since Fire	0.0000	0.0058	<0.001	0.35	(Palit and DeKeyser 2022)
	Grazing Intensity	-0.0004	0.0049	0.954		(Duquette et al. 2022)
Litter Abundance	Smooth Brome Abundance	-0.0274	0.0079	0.133	0.11	(Palit and DeKeyser 2021)
	Kentucky Bluegrass Abundance	-0.0214	0.0093	0.113		(Palit et al. 2021)
	Grazing Intensity	0.0139	0.0033	0.205		(Vermeire et al. 2004, Bailey and Brown 2011)
	Time Since Fire	0.0184	0.0055	0.266		(Limb et al. 2016)
Litter Depth	Smooth Brome Abundance	-0.1584	0.0082	0.114	0.55	(Palit and DeKeyser 2022)
	Kentucky Bluegrass Abundance	0.3187	0.0096	<0.001		(Palit et al. 2021)
	Time Since Fire	0.4372	0.0056	<0.001		(Vermeire et al. 2004)
Thatch Depth	Smooth Brome Abundance	0.1017	0.0040	0.148	0.56	Smooth Brome litter causes other litter and thatch (compressed decaying litter) to decompose quickly. Palit and DeKeyser (2021)
	Kentucky Bluegrass Abundance	0.0680	0.0055	0.26		(Printz and Hendrickson 2015, Palit et al. 2021)
	Grazing Intensity	0.0858	0.0016	0.045		Cattle waste promotes nutrient cycling, resulting in increased thatch formation (Jungnitsch et al. 2011)
	Time Since Fire	0.1152	0.0032	0.118		Fire can burn off the top portion of the thatch layer.
	Litter Depth	0.2676	0.0606	0.004		(Printz and Hendrickson 2015, Palit et al. 2021)
	Litter Depth X Litter Abundance	-0.0781	0.0049	0.06		(Printz and Hendrickson 2015, Palit et al. 2021)
Milkweed Abundance	Smooth Brome Abundance	0.4480	0.0112	0.274	0.13	Smooth Brome competes with milkweed for nutrients and other resources.
	Grazing Intensity	0.7673	0.0069	0.041		(Jungnitsch et al. 2011, Dickson et al. 2023)
	Litter Abundance	-1.6446	0.0324	0.003		Abundant litter reduces light availability for milkweed.
Kentucky Bluegrass Abundance - Smooth Brome Abundance Covariance		-0.2802	-	0.028	-	Kentucky Bluegrass and Smooth Brome are both perennial invasive cool-season grasses, occupying the same niche.



dance on milkweed abundance. Components are grouped inside colored boxes to mimic the broad groups created in Figure 1 (i.e., management actions, invasive grasses, litter, thatch, and milkweed). Arrows represent relationships or pathways between variables. Orange and black paths indicate negative and positive relationships, respectively. Solid lines indicate paths with significant support ($p < 0.05$) and dashed lines indicate paths with marginal support ($0.1 > P > 0.5$). Solid grey paths are paths that were included in the final model but did not have significant or marginally significant support ($p \geq 0.1$). Pathway coefficients are standardized regression coefficients. These values indicate the magnitude and direction (positive or negative) of relationships in our final model and allow for us to make direct comparisons between model pathways. Additionally, we are able to assess the magnitude and direction of indirect pathways by multiplying the pathway coefficients involved in the indirect effect together. Pathways included in the model that did not have significant support do not have pathway coefficients listed. Increasing grazing intensity increases milkweed abundance, while increasing time since a fire decreases grazing intensity, subsequently decreasing milkweed abundance. Smooth Brome and Kentucky Bluegrass abundance do not directly or indirectly affect milkweed abundance.

Figure 4. Relationship between a) litter abundance and the square root of milkweed abundance and b) utilization and the square root of milkweed abundance. Even though milkweed composed a relatively small portion of the plant community found along vegetation transects, both relationships presented here are present in the final SEM. Specifically, litter abundance negatively impacted the square root of milkweed abundance and utilization positively impacted the square root of milkweed abundance. Shaded regions represent standard error.

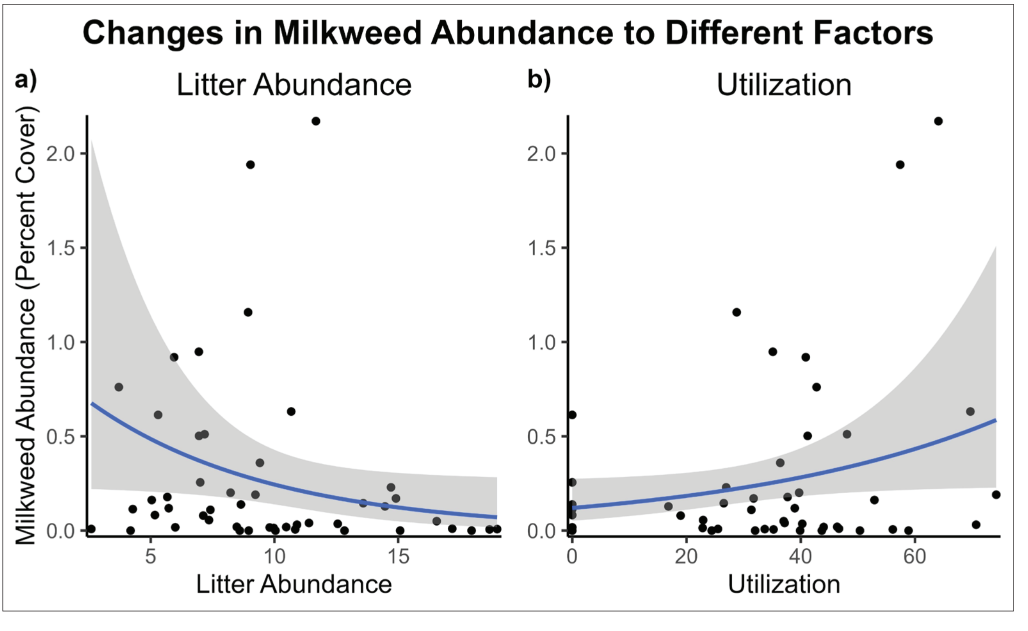
Bluegrass abundance to milkweed abundance (Fig. 3). While neither invasive grass directly nor indirectly affected milkweed abundance, our model supported a strong direct negative relationship between litter abundance and milkweed abundance (−1.6446, P= 0.002; Fig. 3 and 4a), indicating that abundant litter accumulation decreases milkweed abundance. This was the strongest relationship in our final SEM (Fig. 3). Our model did support an indirect path that went from Kentucky Bluegrass abundance to litter depth (0.3187, $P < 0.001$; Fig. 3), and litter depth to thatch depth (0.2676, $P = 0.004$; Fig. 3), indicating that high Kentucky Bluegrass abundance indirectly leads to high levels of thatch accumulation (0.0853; Fig. 3). There was also marginal support for a negative pathway from the interaction of litter depth and litter abundance to thatch depth (−0.07814, P = 0.060; Fig. 3). We also found support for a negative covariance structure between Smooth Brome and Kentucky Bluegrass abundance (−0.2802, $P = 0.028$; Fig. 3), suggesting that certain patches either have high Kentucky Bluegrass abundance and low Smooth Brome abundance or vice versa.

SEM – direct and indirect impact of grazing on milkweed abundance

In line with our initial hypothesized model (Table 1, Fig. S1), our final model supported a direct positive relationship between utilization and milkweed abundance (0.7673, P = 0.041; Fig. 3 and 4b). However, we did not find any significant indirect effects of utilization on milkweed availability (Fig. 3). Instead, we found that grazing had a relatively weak direct effect on thatch depth, with thatch depth increasing with utilization (0.0858, $P = 0.045$; Fig. 3), but thatch depth not affecting milkweed abundance.

SEM – direct and indirect impact of fire followed by grazing on milkweed abundance

We expected fire to have both direct and indirect impacts on milkweed abundance (Fig. 2). However, our final SEM found no support for a direct effect of time since fire on



milkweed abundance (Fig. 3). Despite the lack of a direct effect, fire did indirectly affect milkweed abundance (Fig. 3). Increasing time since fire had a negative effect on utilization (−0.3415, $P = 0.023$; Fig. 3). Because increasing utilization had a positive effect on milkweed abundance (0.7673, $P = 0.041$; Fig. 3), this meant that increasing the time since a fire event decreased the utilization in an area, subsequently decreasing milkweed abundance (−0.2620). In addition to its effects on milkweed abundance, increasing time since a fire event had a direct positive impact on Smooth Brome abundance (0.0345, $P < 0.001$) and litter depth (0.4372, $P < 0.001$; Fig. 3).

Discussion

In an era marked by biodiversity loss (Tilman et al. 2017), targeted conservation is increasingly important (Johnson et al. 2017). Rangelands may support such conservation goals, but they are threatened by invasive grasses such as Kentucky Bluegrass and Smooth Brome which tend to create monocultures (Hendrickson et al. 2021) and limit native plant abundance. Certain management actions like fire and grazing show promise for maintaining or decreasing invasive grass abundances (Towne and Owensby 1984, Gasch et al. 2020), but there is little known of the degree to which native vegetation such as milkweed is impacted by invasive grasses and their management. Through structural equation modeling, we examined the direct and indirect impacts of invasive grasses (Kentucky Bluegrass and Smooth Brome) on milkweed abundance, as well as the direct and indirect effects of management actions (time since fire and utilization) on invasive grasses and milkweed abundance. We found that invasive grasses did not impact milkweed directly, but that litter derived from any source decreased milkweed abundance. Additionally, more recent fires effectively decreased Smooth Brome abundance and litter depth, which by extension decreased thatch depth and increased utilization. Lastly, grazing led to an increase in milkweed abundance and surprisingly increased thatch depth. Management actions such as fire and grazing hold potential in mitigating invasive grasses and aiding conservation of milkweed, monarchs, and biodiversity.

The SEM did not support the idea that Kentucky Bluegrass and Smooth Brome reduce milkweed abundance. This could be because Kentucky Bluegrass and Smooth Brome growth periods do not overlap much with that of Common and Showy Milkweed (Bennett et al. 2019), meaning they may not directly compete with one another, and/or that milkweed is structurally different from the grasses (e.g., taller with broader leaves), which may give milkweed a growth advantage. Given that Kentucky Bluegrass and Smooth Brome are both cool-season (C3) grasses (Palit et al. 2021, Palit and DeKeyser 2022), they predominantly grow in the spring and senesce or go dormant by mid-summer (Ode et al. 1980). Milkweed, on the other hand, blooms in mid-summer, though increased temperatures can shift bloom date earlier (Howard 2018), meaning their peak productivity occurs past the peak of Kentucky Bluegrass and Smooth Brome. These niche and life history differences likely contribute to why these invasive grasses do not appear to directly impact milkweed. Additionally, Common and Showy Milkweed can reproduce via rhizomes (Wilbur 1976). This ability may allow for the internal redistribution of nutrients from ramets without local stressors, due to neighboring plants, to those under external pressures (Tao and Hunter 2012). In this way, the milkweed species included in this study (Common and Showy) may have bypassed any direct resource competition and indirect soil alteration effects of Kentucky Bluegrass and Smooth Brome.

Litter abundance directly decreased milkweed abundance. While litter abundance and litter depth had minor correlation prior to running the initial SEM, the correlation was removed during the model selection process. This implies that in the context of changes in milkweed abundance, litter abundance and litter depth act independently. Despite both invasive grasses being associated with copious amounts of litter (Piper et al. 2014, Toledo et al. 2014, Hendrickson et al. 2021), our model did not support a pathway between either grasses or litter abundance. Kentucky Bluegrass directly increased litter depth, which directly increased thatch depth. Litter abundance having the strongest negative influence on milkweed abundance, but not being influenced by either invasive grass, suggests that milkweed may not be influenced by species-specific litter, but that litter from any source has the potential to negatively impact milkweed abundance. It is also possible that litter from some other species that we did not account for negatively impacts milkweed abundance. However, this is unlikely, as Kentucky Bluegrass and Smooth Brome were consistently the most abundant plant species across our transects (34.8 ± 8.2 SE and 16.7 ± 13.1 SE; Table S1), and no others were as abundant. Abundant litter most likely blocks essential sunlight from reaching young milkweed stems, thus preventing or stunting their development (e.g., heavy shade negatively affects milkweed growth; Silva et al. 2022). How deep the litter layer is, regarding milkweed, does not appear to matter. A relatively shallow litter layer could be enough to have adverse outcomes, meaning any additional depth may not produce compounding effects. In short, increasing litter abundance results in less exposed ground and less sunlight reaching the soil (Jessen et al., 2023). Since high litter abundance negatively impacts milkweed, management actions that reduce litter cover may be of benefit.

Increasing time since fire resulted in an increase in litter and Smooth Brome abundance. In other words, fire appears to reduce litter (Menke 1992, Limb et al. 2016) and limit cool-season growth (Curtis and Partch 1948, Blankespoor and Bich 1991; as exemplified by Smooth Brome in our study), both of which prevent the spread of invasive grasses. Specifically, we found that increasing time since fire directly led to an increase in litter depth, which is consistent with other literature (DeKeyser et al. 2009). Fire suppression allows a build-up in fuel load (e.g., standing and basal litter), which can be favorable for Smooth Brome by chemically altering the soil (Jordan et al. 2008), blocking sunlight thereby preventing native plant seed germination (Toledo et al. 2014, Printz and Hendrickson 2015), and reinforcing the spread of disease (Benitez et al. 2022). Decreasing time since fire increased utilization due to a burst of nutritionally dense plant growth which herbivores preferentially graze (Coppedge and Shaw 1998, Fuhlendorf and Engle 2004, Anderson 2006, Fuhlendorf et al. 2009). However, time since fire itself did not directly impact milkweed abundance, possibly due to the high disturbance-resistant nature of Common and Showy Milkweed (Liu et al. 2007).

Increased utilization directly increased milkweed abundance but did not have an impact on Kentucky Bluegrass or Smooth Brome. It is almost certain that some transects had more time to experience regrowth than others, especially in the heterogeneity-based rotational grazing pastures where cattle were physically excluded from some areas. This time for regrowth differential may have influenced our results. However, grazed plants rarely, if ever, become more abundant than non-grazed plants in the same system (Strauss and Agrawal 1999). Meaning that even if some areas had more time to experience regrowth, the overall effect of grazing (i.e., utilization) on milkweed abundance would be negative and result in the highest milkweed abundances occurring within low to no utilization areas (e.g. Dickson et al. 2023). Instead, we see the opposite, where highly utilized areas have higher milkweed abundances (Figure 4b). Likely what is happening is that when cattle graze certain areas, they remove dominant vegetation (i.e., Kentucky Bluegrass and Smooth Brome) and decrease competition for light and other nutrients, allowing milkweed to increase in abundance (Borer et al. 2014). This idea is further supported by the negative relationship we observed between litter abundance and milkweed abundance (Figure 4b). Reducing litter abundance, regardless of the method, leads to an increase in milkweed abundance, likely because of an increase in access to light and other resources, which were not captured as pathways in our model. Our results are encouraging as they suggest management that reduces litter abundance, such as both fire and grazing, is consistent with more milkweed.

Although our model informs how management may attenuate the effects of invasive grasses and how these grasses and management actions impact milkweed, there may be missing key pathways that warrant further research. There are likely absent intermediary pathways and limited temporal and precipitation information that may help explain the relationships between variables. First, there is certainly a missing pathway between grazing and thatch (or indirectly Kentucky Bluegrass). Though the relationship was relatively weak, it is unclear why there was a significant positive relationship between utilization and thatch depth. It follows that increasing time since fire directly led to increased litter depth which then increased thatch depth. However, it seems contradictory that more intense grazing would also increase thatch depth. It is possible cattle waste can accelerate tissue production via nutrient deposition (Aarons et al. 2008), but due to the high C:N ratio of cow waste, this likely would not also increase thatch accumulation rates (Smiley 1981). However, we expect there are additional or different means in which cattle impact thatch that were not captured by our model. Second, there are probably numerous ways in which cattle impact milkweed that could not be investigated given our data constraints. For example, cattle graze milkweed (Dickson et al. 2023; Johnson 2023), which may promote new growth (e.g., Haan and Landis 2019) through the allocation of resources to undamaged ramets (Tao and Hunter 2012). During the data collection process, however, damaged stems (i.e., grazed) were categorized the same as undamaged (i.e., not grazed) stems, restraining analysis of the relationship between cattle and milkweed. Additional aspects of cattle grazing that could enhance milkweed abundance include a reduction in competitive species (Dee and Palmer 2019), curtailment of litter and subsequent sun exposure (Vermeire et al. 2004, Bailey and Brown 2011), or the addition of nutrient deposition from cattle waste (Aarons et al. 2008).

Cattle directly consume milkweed (Dickson et al. 2023, Johnson 2023), and although we do not have ungrazed data to compare the absence of grazing to our results, our data from grazed pastures indicates the benefits of more intense grazing outweigh any drawbacks of milkweed consumption by cattle. Additionally, our model only explained a modest amount of variation in milkweed abundance, further suggesting that there are likely additional pathways that we were unable to consider (Fig. S2, available online at https://eaglehill.us/prnaonline/suppl-files/prna-039e-Johnson-sf2.pdf). Third, plant communities vary year-to-year in accordance with both pre-growing season snowfall and growing season precipitation, which can then also influence fire and grazing responses. Evaluating data over multiple years would provide further insight into how the relationships between invasive grasses, milkweed, and management fluctuate not only through time but also with water availability. Lastly, it is worth noting that our study was not designed to explicitly examine how invasive grasses, fire, and grazing impact monarchs, and that a more comprehensive study would be needed to better understand how these factors may advise monarch conservation efforts. While our study demonstrates how structural equation models can be used to link invasive species, management actions, and species of conservation interest, future analyses should include additional variables such as frequency of milkweed regrowth post-grazing or pre-growing season snowfall depth to better delineate biological mechanisms.

Conclusions

Using an SEM, we found that milkweed is not directly affected by the invasive grasses Kentucky Bluegrass or Smooth Brome, but rather that litter abundance, which becomes more pronounced following Kentucky Bluegrass and Smooth Brome invasion, decreased milkweed abundance. Additionally, we found that increasing the utilization of an area led to an increase in milkweed abundance. In both instances, milkweed is likely responding to increased access to light and other nutrients that follow reductions in either litter or the dominant plant species (i.e., Kentucky Bluegrass and Smooth Brome; Borer et al. 2014), suggesting that any management practice that removes either litter or the dominant plant species may benefit milkweed abundance. Though explicit research needs to be done on the topic, the synergistic application of both fire and grazing, such as in patch-burn grazing (Fuhlendorf and Engle 2004, Fuhlendorf et al. 2009) is particularly effective at removing litter, and altering the abundance of dominant species (Menke 1992, Limb et al. 2016) and may prove to be one of the most effective management strategies to directly and indirectly benefit milkweed abundance in rangelands.

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Statements and Declarations

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Data Availability

The datasets analyzed during the current study are available in the figshare repository, Vegetation Data: https://doi.org/10.6084/m9.figshare.28296317, Utilization Data: https://doi.org/10.6084/m9.figshare.28296755. R code for data analyses associated with the current study are available on GitHub: https://github.com/elkjaer1745/Milkweed_InvasiveGrasses.

Author Contributions

Ellysa Johnson contributed to the study conception and design. Esben Kjaer performed data collection and analysis. The first draft of the manuscript was co-written by Ellysa Johnson and Esben Kjaer, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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