Livestock excreta facilitate invasive weed establishment and dominance in pastures through physical niche creation and nutrient pulses

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Abstract

Globally, invasive weeds jeopardize pasture productivity and biodiversity, prompting extensive control efforts which are often hampered by an incomplete understanding of how livestock activities, particularly excreta deposition, facilitate weed invasion. Focusing on southwest Chinese pastures, we combined field surveys and controlled experiments to investigate how livestock excreta facilitate the establishment and dominance of the global invasive weed *Rumex obtusifolius* L. through physical and nutrient-mediated pathways. Field surveys confirmed a strong positive association between excreta deposition and the distribution of *R. obtusifolius* across diverse pasture landscapes. Experimental manipulations revealed a two-stage facilitation mechanism: (1) Initial physical suppression by dung patches (via light exclusion and anaerobic soil) eliminated intolerant species, substantially reducing local richness (61.6% after 30 days) and creating establishment opportunities; and (2) Subsequent multi-nutrient enrichment from overlapping dung and urine deposition promoted *R. obtusifolius* dominance, with dung addition increasing *R. obtusifolius* height ~10-fold and ramet number ~11-fold compared to controls ($p < 0.001$). Combined dung-urine treatments amplified growth by 32.4% ($p = 0.002$) through stoichiometric complementarity, where nitrogen emerged as the primary growth driver (91.3% biomass increase; $p < 0.001$). Crucially, clonal reproduction required concurrent multi-nutrient availability, averaging nearly 4 ramets/plant, compared to less than 1 in nitrogen treatments. These findings directly inform pasture management, highlighting that effective invasive weed control and productivity maintenance in pastoral systems require integrating livestock excretion management. Practical strategies, such as adjusting grazing patterns and targeted excreta removal, limit localized nutrient over-enrichment and help conserve pasture ecosystems in an ecologically sound manner.

Key words: Dung, Urine, Spread, *Rumex obtusifolius*, Pasture

1. Introduction

Pastures cover approximately 30% of the Earth's terrestrial surface, serving primarily as fodder sources for livestock (Alexandratos and Bruinsma 2012, Bengtsson et al. 2019). While the intentional introduction of non-native forage species aims to enhance pasture productivity, this practice frequently results in the unintended introduction of environmental weeds—invasive plants that colonize natural ecosystems, displacing native species and degrading ecological integrity (Neldner et al. 1997, Driscoll and Catford 2014, Driscoll et al. 2014). These weeds pose dual threats: compromising pasture production and encroaching into adjacent native habitats, threatening biodiversity and compromising ecosystem function, and incurring substantial management costs (Driscoll et al. 2014, Catford et al. 2018). The risk of environmental weed spread is particularly high in pastures since some weeds can escape livestock grazing, a risk further exacerbated by improper pasture management (Parker et al. 2006, Driscoll et al. 2014, Gioria et al. 2023). Notable examples include the docks (*Rumex spp.)* and cat's ear (*Hypochaeris radicata*), which can escape grazing and spread aggressively in mismanaged systems and surrounding native ecosystems (Delimat and Kieltyk 2019, Carlin et al. 2023, Lee et al. 2024). Despite widespread control efforts using mechanical, chemical, and biological measures (Bagavathiannan et al. 2019, MacLaren et al. 2020, Diagne et al. 2021), key mechanisms by which livestock behavior facilitates weed invasion remain insufficiently explored, limiting the effectiveness of management strategies.

Livestock, like other large herbivores, exert significant top-down control on non-native plants through grazing and trampling (Guyton et al. 2020, Mungi et al. 2023). Beyond these direct effects, their excreta including dung and urine also play a critical role in shaping vegetation dynamics (Sitters and Venterink 2021a, 2021b) (Figure

1A). Daily excretion rates are substantial, with a high proportion concentrating in high-use zones, such as resting areas (Saggar et al. 1988, Haynes and Williams 1993, Karn 2001). The physical effects of excreta, particularly pronounced for dung pats, which can block light and form a dry, hard, and nonporous crust, leading to anaerobic soil conditions that smother vegetation (Humphreys et al. 1997, Gillet et al. 2010). Nutrient partitioning further differentiates the roles of dung and urine. Generally, urine supplies rapidly available high concentrations of nitrogen (N) and potassium (K) but low phosphorus (P), while dung slowly releases P, calcium (Ca), and magnesium (Mg) because it decomposes slowly (Haynes and Williams 1993, Karn 2001). The dung and urine deposition and divergence creates heterogeneous nutrient hotspots—analogous to ephemeral resource patches (Sitters and Venterink 2021b, Butterworth et al. 2023) (Figure 1A), potentially contributing to the proliferation of nutrient-loving environmental weeds (Qiu et al. 2023, Shan et al. 2024, Tao et al. 2024). While grazing pressure and seed dispersal through endozoochory have been well documented (Campbell and Gibson 2001, Constible et al. 2005, Sullivan and Shaw 2023), the dual mechanisms of excreta—physical stress and multi-nutrient enrichment—remain poorly understood.

Rumex obtusifolius L. native to Europe, has been introduced to multiple regions worldwide including southern China, and became an environmental weed (Figure 1B). This species epitomizes the multifaceted nature of plant invasions in agricultural landscapes, thriving in disturbed habitats and agroecosystems such as roadsides, croplands and pastures with inadequate management practices (Costan et al. 2022, Carlin et al. 2023, Kloetzli et al. 2024). Its invasion success stems from a suite of adaptive traits, including rapid growth, tolerance to anaerobic stress, large stature (40–150 cm), prolific seed output, and clonal reproduction (Gilgen et al. 2010, Hartman et al. 2021, Kloetzli et al. 2024). Notably, its high oxalic acid content poses toxicity risks to livestock, compounding ecological impacts with economic losses (Zaller 2004). Despite its broad dispersal capacity, *R. obtusifolius* exhibits patchy dominance within pastures, showing a strong association with livestock activity hotspots (e.g., resting areas) where excreta deposition is concentrated (Figure 1B). This pattern suggests that factors beyond grazing pressure and trampling are crucial, pointing towards the influence of excreta (Theoharides and Dukes 2007).

We hypothesized that the physical suppression and nutrient enrichment caused by livestock excreta deposition drive the establishment and dominance of *R. obtusifolius* in pastures (Figure 1C). Specifically, we employed a hierarchical methodology, combining field observations and controlled experiments, structured around three predictions: (1) spatial patterns of excreta deposition correlate positively with *R. obtusifolius* abundance and distribution; (2) *R. obtusifolius* will outperform other pasture species (including both native and introduced plants) in establishment success under excreta-induced physical stress; and (3) cattle dung and urine will enhance *R. obtusifolius* growth and clonal reproduction through multi-nutrient synergies. To test these predictions, first, we conducted field surveys in two typical pastures to quantify the relationship between *R. obtusifolius* distribution and excreta deposition patterns. Second, we performed two excreta addition experiments: one in a grazed area to confirm the overall effects of excreta amid other livestock activities, and another in a fenced area to isolate the physical and nutrient impacts of excreta and distinguish the individual and interactive effects of dung and urine. These experiments allowed comparison between grazed versus fenced conditions. Finally, we conducted laboratory pot experiments to identify the key nutrients in excreta that promote *R. obtusifolius* growth and clonal reproduction.

2. METHODS

2.1 Field survey 1

To investigate the relationships between *R. obtusifolius* spread^{-} and the distribution of livestock excreta, we conducted field surveys at two typical pastures invaded by *R. obtusifolius* in September 2023: Dushan pasture (in Guizhou province) and Nanshan pasture (in Hunan province) (Figures 1D and S1). The two pastures were exploited and utilized from the 1980s. The plant community in Dushan pasture is dominated by annual plants, such as ryegrass (*Lolium multiflorum Lamk.*) and oat (*Avena sativa L.*). Nanshan pastures are dominated by perennial plants, such as Yorkshire fog (*Holcus lanatus L.*) and white clover (*Trifolium repens L.*). The study sites exhibited contrasting topographies: Dushan pasture is characterized by gentle terrain (slopes < 10°) with rotational grazing management, while Nanshan pasture comprises rolling to steep terrain (slopes 15-45°) under free continuous grazing (Figures S1A, B). The two pastures also have different grazing regime and intensities (Table S1) as well as soil properties. The Nanshan pasture exhibited acidic topsoil (pH approx. 5) with high organic carbon (52.81 g kg^{-1}) and mineralizable N (58.95 g kg^{-1}), while the Dushan pasture featured near-neutral soils (pH approx. 6.2) containing substantially low organic carbon (24.36 g kg^{-1}) and mineralizable N (43.98 g kg^{-1}). These contrasting conditions provided a robust background for confirming the observed association between *R. obtusifolius* spread and excreta distribution.

We conducted a detailed survey of *R. obtusifolius* spread using systematic transect sampling (McGarvey et al. 2016). Transects (1–2 km in length, approx. 0.5 km in width) were established extending outward from cattle milking shed (Figures 1D, S1B). Along each transect, we documented *R. obtusifolius* distribution in relation to livestock movement routes. We established sixty 2 m × 3 m plots at stratified random locations within each transect to measure *R. obtusifolius* density and height. Additionally, we surveyed four feeding sites in Nanshan pastures, and one site in Dushan pasture because of smaller area compared to Nanshan pastures.

2.2 Field survey 2

To further explore the relationship between *R. obtusifolius* distribution and cattle excreta, we conducted a paired-plot survey on the Nanshan pasture, focusing on areas already subject to cattle grazing and trampling. We randomly selected eight hillocks with high *R. obtusifolius* density (Figure S1B). At each hillock, we established three paired plots (1 m × 0.25 m). Each pair consisted of one plot with visible cattle dung and one immediately adjacent plot without visible dung. Within dung-present and dung-absent plots, we assessed *R. obtusifolius* abundance, density, and height (Figure 1E). To understand the broader community context in which *R. obtusifolius* occurred, we also quantified plant community composition and biomass. Specifically, we identified and recorded the presence and abundance of each plant species to determine community composition, and measured total aboveground shoot biomass for each species by clipping, drying, and weighing the harvested material. Average plant height was determined for all species by measuring five randomly selected individuals, or all if fewer than five were present.

2.3 Experiment 1

To directly test the effect of cattle dung on *R. obtusifolius* spread, we conducted a dung addition experiment in a grazed area at the Nanshan site (Figure 1F). In June 2023, five hillocks were selected, where *R. obtusifolius* was colonized but had not established despite ongoing cattle grazing and trampling (Theoharides and Dukes 2007). This initial condition suggests that grazing and trampling alone were insufficient for *R. obtusifolius* establishment and dominance at these locations. At each hillock, three pairs of plots (1 × 0.5 m) were established (six plots total per hillock): within each pair, one plot received an application of cattle dung (~4 kg dry matter), approximating the average mass of naturally deposited pats, and the other served as an untreated control.

To assess the impact of dung addition, we conducted weekly visual monitoring of the plant community to track dynamic changes, and measured selected parameters at day 0 (pre-treatment), 30, and 120 days (post-treatment). For *R. obtusifolius*, we measured height and the number of clonal individuals (ramets, counted directly within each plot). For the recipient community response, we determined species richness by identifying and counting all plant species present within each plot. We also measured overall plant height (excluding *R. obtusifolius*) and calculated it by a weighted average based on the height and abundance of each species.

2.4 Experiment 2

To determine the individual and combined effects of dung and urine on *R. obtusifolius* invasion, distinguishing between physical and nutrient impacts, we conducted a controlled field experiment in a fenced pasture, excluding livestock grazing and trampling effects (Figure 1G). In early May 2023, we established a randomized block experiment with five replicates on a flat, *R. obtusifolius*-colonized area at the bottom of a hillock on Nanshan pasture. Each block contained five 1 × 1 m plots separated by 1 m buffers. To standardize initial conditions, four similarly-sized *R. obtusifolius* plants were transplanted into each plot from adjacent grassland. After successful colonization (mid-July), two plants of similar height were retained diagonally within each plot. Plant community characteristics were measured before treatment application.

Treatments were then randomly assigned to each plot within the blocks, consisting of an untreated control and four cattle excreta treatments: dung, urine, dung and urine combined, and a water-diluted dung solution (to isolate the nutrient effects of dung by minimizing its physical impacts) (Figure 1G). The dry mass of dung applied was approx. 0.55 kg across all dung-containing treatments. For all dung applications, it was applied evenly as a simulated cattle pat to each *R. obtusifolius* plant. For the dung solution treatment, the same mass of dung was mixed with approx. 0.55 L water and applied evenly. Post-treatment, plant community was monitored as described in Experiment 1. Finally, plant species within the recipient community were classified as either 'tolerant' (present after dung addition) or 'intolerant' (absent after dung addition) to analyze changes in community composition.

2.5 Pot experiment

To determine which nutrient in excreta plays a crucial role in promoting the spread of *R. obtusifolius*, we conducted a pot experiment with different nutrient addition treatments (Table 1 and Figure 1H). Pots (24 cm diameter, 20 cm depth) were filled with soil collected from the study pasture. Seeds of *R. obtusifolius* were planted in the pots at a density of 1 seedling per pot, approximating the observed field density. Plants were grown for approximately two weeks under regular watering and ambient outdoor conditions. Nutrient addition treatments (detailed in Table 1) were initiated once the seedlings reached approx. 10 cm in height. The nutrient addition rates were based on our previous analysis of cattle excreta samples from the study site. Each treatment had five replicates, and the pots were arranged randomly within a field block. Plant height and the ramet number of *R. obtusifolius* were measured every two months post-fertilization to assess growth and clonal reproduction.

2.6 Statistical analysis

To explore the relationships of livestock activity with *R. obtusifolius* invasion in field survey 1, we applied segmented regression (using the 'segmented' package in R) (Muggeo 2017). We expected a non-linear relationship, potentially exhibiting a threshold effect, between distance from the milking shed and *R. obtusifolius* invaded area, density, and height. In field survey 2, paired t-tests were employed to compare biomass and density of *R. obtusifolius* and of all other species combined between dung and non-dung plots. Separate t-tests were conducted for each variable.

In experiment 1, paired t-tests were used to compare between dung addition and control treatments for *R. obtusifolius* height, ramet number, and overall plant height (excluding *R. obtusifolius*). Additionally, within both the dung addition and control treatments, paired t-tests compared the height of *R. obtusifolius* to the overall plant height. One-way ANOVAs followed by post-hoc Tukey's HSD tests were conducted to examine the effect of time (0 day, 30 days, and 120 days) on the relative abundance of *R. obtusifolius* (calculated as the species' abundance divided by the total abundance of all species within a plot) and on species richness within the dung addition treatment.

We applied linear mixed-effects models (LMMs) to analyze the data from both experiment 2 and the pot nutrient addition experiment. In the respective LMMs, the specific treatments for each experiment (excreta or nutrient additions) were treated as fixed factors, and plot identity (for experiment 2) or pot identity (for the pot experiment) was treated as a random factor. For experiment 2, the response variables included measures of *R. obtusifolius* performance (height, biomass, and clonal reproduction) and the height of other plants. To account for initial variation in plant traits and community composition among plots, change ratios of measured parameters were calculated as $(X_{t2} - X_{t1})/ X_{t1}$, where X_{t2} and X_{t1} represent the values after and before treatment, respectively. For the pot experiment, the response variables were measures of *R. obtusifolius* growth and development. In Experiment 2, we analyzed the response of *R. obtusifolius* and other plants (as either 'tolerant' or 'intolerant') to different dung and urine treatments. We calculated the relative change rate of height for *R. obtusifolius,* tolerant plants and intolerant plants (calculated as a weighted average based on the height of each species). Linear mixed effects models, followed by post-hoc Tukey's HSD tests, were used to compare these relative change rates across the different treatments. Post-hoc Tukey tests were also used for pairwise comparisons among the nutrient treatments. Model assumptions were checked by inspecting the residuals and no apparent violations were found. All statistical analyses were performed in R (v4.4.1), with the significance level set at 0.05.

3. RESULTS

3.1 Relationships between the spread of *R. obtusifolius* and cattle excreta

Consistent with field observations showing higher *R. obtusifolius* presence near sheds (associated with higher excreta), segmented regression analysis confirmed significant linear decreases in infested area and density with increasing distance (Figure 2) (Nanshan pastures: $p = 0.001 – 0.03$, $R^2 = 0.17 – 0.59$; Dushan pastures: $p = 0.03$ for both area and density, $R^2 = 0.99$ for area, $R^2 = 0.95$ for density). Plant height showed a similar linear decrease pattern (Figure S2), though not statistically significant across all locations. Moreover, the paired plots survey further demonstrated that the excreta deposition plots with higher concentrations of N, P, Ca, K, and Mg had significantly higher biomass, height, and density of *R. obtusifolius* compared to the adjacent plots without excreta (Figures 3, S3 and S4). On the contrary, these deposition plots had significantly lower plant diversity than plots without excreta (Figure 3).

3.2 Effect of experimental excreta

Our dung addition experiments also showed that dung addition had larger positive effects on the height and density of *R. obtusifolius* than on those of the other species in the recipient community in both grazed and fenced area (indicated by relative change rate of height) (Figures 4A, 5A and S5). The addition of water-diluted dung had similar effects on the growth of *R. obtusifolius* and tolerant species compared to dung addition alone (Figure 5A). However, intolerant species exhibited a contrasting response: water-diluted dung promoted their relative height growth, whereas dung addition alone suppressed it (Figure 5A). The dung addition also significantly increased the ramet number of *R. obtusifolius,* and the proportion of *R. obtusifolius* in the community, particularly after 30 days of treatment (Figures 4B, C). However, the number of other plants in the recipient community decreased significantly after 30 days of dung addition and partially recovered after 120 days, but still remained lower than pre-treatment levels (Figures 4D, S5A).

The growth of *R. obtusifolius* and other plants in recipient community responded differently to the additions of dung, urine, dung and urine (Figure 5A). There were significant positive effects of dung, rather than urine, on *R. obtusifolius* growth, and the simultaneous addition of cattle dung and urine had the largest effects (Figure 5A). In contrast, the growth of intolerant species was significantly inhibited by the addition of dung, while urine had no significant impact on their growth (Figure 5A). However, while the positive effects on tolerant species were similar between the two treatments, the negative effects of dung addition on intolerant species were significantly moderated by the simultaneous addition of urine (Figure 5A).

Additions of both NH_4^+-N and NO_3^--N exerted similar significant and positive effects on the growth of *R. obtusifolius*, while combined additions of P, K, Ca, and Mg alone had no effect (Figures 5B and S6). The combined addition of N with Ca, Mg, K, and P further enhanced the growth of *R. obtusifolius* by 17.8% to 66.1% compared to

N addition alone (Figure 5B). Although NH_4^+-N and NO_3^--N additions did not significantly affect *R. obtusifolius* clonality, the combined addition of NH_4^+-N with Ca, Mg, K, and P had the strongest effects, resulting in an average of four ramets compared to only two or no ramet in other treatments and control plots, respectively (Figure 5C).

4. DISCUSSION

Moving beyond traditional views focusing on direct grazing, trampling, and seed dispersal, our study uncovers the critical role of livestock excreta in facilitating *R. obtusifolius* invasion within pastures. We identify a novel two-stage mechanism: initial physical effects create an establishment window which the weed exploits due to its anaerobic tolerance, while subsequent multi-nutrient enrichment (especially from the overlapping deposits of dung and urine) fuels its rapid growth and clonal spread. This demonstration of invasion driven by the synergy between the sequential impacts of excreta and the weed's specific adaptations underscores a significant and potentially underestimated pathway in landscape management (Figure 6A).

4.1 Excreta distribution as a key mechanism driving livestock-mediated weed spread

Field surveys across diverse pasture landscapes revealed a strong association between *R. obtusifolius* abundance and proximity to milking sheds, independent of environmental variables. This spatial correlation indicates that areas with higher excreta deposition are more vulnerable to invasion. This finding was further confirmed by manipulative experiments, which also demonstrated that dung, rather than urine, plays a key role in *R. obtusifolius* establishment. Integrated with results from the water-diluted dung solution and nutrient addition experiments, these findings underscore the dual role of livestock-induced physical disturbance and nutrient enrichment in shaping plant community dynamics and facilitating invasion processes. Livestock, through their movement and natural excretion behaviors, create localized "hotspots" of dung and urine enrichment (Ahmed et al. 2018, Koch et al. 2018), providing a mechanistic explanation for our findings. Consequently, our study provides compelling evidence that livestock-mediated excretion patterns are crucial in facilitating *R. obtusifolius* invasion within grazed pastures. This finding therefore highlights the necessity of targeted livestock excreta management strategies in these areas to effectively mitigate invasive species spread.

In the context of hilly pastures, this mechanism of excretion accumulation is likely to be amplified due to livestock behavioral preferences. Livestocks preferentially graze slopes while congregating and excreting disproportionately in flat terrain such as valley tops or bottoms (Haynes and Williams 1993, Aarons et al. 2017, Koch et al. 2018), creating hyper-enriched zones that favor nutrient-demanding weeds. For example, a study in New Zealand upland grasslands found that 60% of dung and 55% of urine accumulated in areas constituting only 15% of the total land area (Saggar et al. 1988). While our results strongly suggest that excreta influence *R. obtusifolius* distribution through deposition patterns, we acknowledge that the impact of these excretion patches on plant invasion dynamics may be further modulated by excretion deposition activities (e.g., repeated deposition events), which adds layers of complexity to the spatial heterogeneity and repeated disturbance of dung and urine enrichment.

4.2 Synergistic physical and nutrient pathways in excreta-facilitated invasion

Building on the spatial patterns identified above, our findings demonstrate that livestock dung and urine synergistically drive *R. obtusifolius* invasion through coupled physical and nutrient mechanisms (Figure 6B). Dung pats initiate establishment windows by forming a hard crust that smothers existing vegetation and creates anaerobic soil conditions, while urine can scorch grass blades (Humphreys et al. 1997, Gillet et al. 2010). These physical disturbances act as environmental filters, eliminating intolerant species while providing establishment opportunities for stress-tolerant species such as *R. obtusifolius* (Gillet et al. 2010, Gallien et al. 2014, Kraft et al. 2015). *R. obtusifolius* exhibits remarkable anaerobic tolerance likely through ethylene-mediated adaptive mechanisms, emerging as the dominant species in colonization after one month of dung deposition, while other plant species remain virtually absent (Hartman et al. 2021).

The nutrient pathway, particularly N enrichment, amplifies invasion success. As a fast-growing and nitrophilic invasive weed, *R. obtusifolius* efficiently exploits these nutrient pulses (Stilmant et al. 2012). This is demonstrated by markedly increased biomass and clonal expansion of *R. obtusifolius* in dung-enriched areas and of other similar invaders in nutrient-enriched areas (Seabloom et al. 2015, Liu and van Kleunen 2017, Tao et al. 2024). The high nutrient exploitation efficiency further enhances the competitive advantage of the invader over resident species. This advantage is further amplified through a positive feedback loop: the decomposition of smothered vegetation releases additional nutrients, creating optimal conditions for establishment (MacDiarmid and Watkin 1971). Moreover, the spatial overlap of nutrient-rich dung (rich in P, Ca, and Mg) and urine (rich in N and K) creates balanced nutrient profiles that maximize *R. obtusifolius* establishment (Haynes and Williams 1993, Agren and Weih 2012). These findings are supported by results from our pot experiment, where N was identified as the primary driver, increasing growth by 91.3% and triggering clonal reproduction when combined with other nutrients. Although urinary N emerged as the primary growth driver, weaker effects from isolated urine treatments emphasize the primacy of dung-mediated physical modification during initial establishment. These physical and nutrient mechanisms work synergistically, as concentrated livestock activity intensifies both physical disturbance and nutrient enrichment effects, accelerating the invasion process.

4.3 Managing excreta distribution to control invasive weeds in pastoral systems

The excretion-invasion mechanism identified here provides a foundation for developing targeted excretion management strategies in pastoral systems. First, we recommend implementing intensive rotational grazing with shortened grazing periods, particularly in mountainous terrain, as this approach can promote uniform excreta distribution while maintaining pasture productivity and diversity. Second, building on evidence that prolonged overnight grazing exacerbates dung/urine deposition and induces spatial overlap of dung and urine in resting areas (Aarons et al. 2017, Ahmed et al. 2018, Koch et al. 2018). Our findings further suggest that reducing nocturnal pasturing duration could minimize concentrated nutrient enrichment and spatial overlap in resting areas. Finally, given persistent excreta accumulation observed even under reduced grazing durations (particularly nocturnal regimes), the precision removal or strategic dispersion of highly enriched excretion patches is also needed to break the invasion feedback loop while maintaining pastoral productivity.

Our findings also provide broader implications for invasion ecology and policy development. The demonstrated role of concentrated nutrient pulses in facilitating invasion of *R. obtusifolius* suggests that similar mechanisms may operate in other contexts, such as manure fertilization practices and wild animal carcasses (Loydi and Martin Zalba 2009, Barton et al. 2016, Blumenthal et al. 2017). This understanding calls for an integrated approach to invasion management that considers both grazing intensity and nutrient redistribution patterns. We advocate integrating excretion management into environmental protection frameworks and developing policies addressing animal-mediated invasion risks, thereby enhancing both the effectiveness of environmental weed control and the sustainability of ecosystems.

4.4 Study limitations

We acknowledge several key limitations. First, the short experimental timeframe restricted our analysis to initial responses, precluding insights into longer-term ecological dynamics and potentially overlooking slower adaptations within the native plant community. Second, our focus on cattle excretion limits direct generalization to systems with other small ruminants (e.g., sheep/goats), which exhibit higher N excretion rates per metabolic body weight and different morphological characteristics of dung (Haynes and Williams 1993, le Roux et al. 2020, Sitters and Venterink 2021c). Third, by concentrating on the target species, *R. obtusifolius*, we did not comprehensively analyze the responses of residual species, thus missing finer details of community interaction under treatments. Finally, the minimal herbivory pressure on *R. obtusifolius* in our invasive-range system shaped our focus on the physical and nutrient effects on excreta-mediated facilitation. This context is crucial, as our findings on facilitation mechanisms are most applicable where consumption pressure is low and may differ significantly from scenarios where herbivory provides substantial *R. obtusifolius* control (e.g., Zaller 2006). Addressing these points requires future studies employing longer durations, incorporating diverse livestock and plant community analyses, and examining outcomes across varying herbivory regimes.

4.5 Conclusions

Our study demonstrates how livestock excreta create critical invasion opportunities enabling invasive weed establishment and dominance in pastures through dual mechanisms: initial physical suppression and subsequent multi-nutrient enrichment.

These findings advance pasture management by shifting focus beyond traditional grazing-centric models and dung-mediated seed dispersal to highlight the critical role of excreta-mediated invasion pathways driving pasture degradation. We demonstrate that managing excretion distribution patterns is just as crucial as controlling grazing intensity for preventing weed spread in pastures and even the adjacent roadside ecosystem. The mechanistic understanding gained from this study advances the theory of weed invasion while providing evidence-based strategies for sustainable pasture management.

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Author contributions

Conceptualization: X.S. Investigation: H.W., T.T., Y.L., Y.G., and X.S. Formal Analysis: Q.Y., H.W., X.L. and X.S. Visualization: Q.Y., H.W., X.L. S.Z., and X.S. Writing (original draft): X.L. and X.S. Writing (review and editing): H.C., X.L., D.J., Z.Z., W.Z., S.Z., and X.S..

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Table 1. Treatments applied in the pot experiment investigating nutrient effects on *Rumex obtusifolius* growth, showing the different combinations and amounts of nutrients (g m^{-2}) (nitrogen [N], phosphorus [P], potassium [K], calcium [Ca], magnesium [Mg]) and nitrification inhibitor (3,4-dimethylpyrazole phosphate [DMPP]) were added.

Treatments	N	P	K	Ca	Mg	DMPP
Control						
NH_4^+ + DMPP	15					0.45
NH_4^+ + DMPP + P	15	8				0.45
NH_4^+ + DMPP + P + K + Ca + Mg	15	8	10	57.1	28.6	0.45
P + K + Ca + Mg		8	10	57.1	28.6	

Figure captions

Figure 1 Conceptual framework, experimental hypotheses tested, experimental design. (A) the possible effects of livestock excreta on invasion dynamics by regulating the invasion of environmental weeds and the invasibility of native plants. (B) Global distribution of *Rumex obtusifolius* (source: powo.science.kew.org), and the spread of *R. obtusifolius* related to cattle activities in Nanshan pasture. (C) The hypotheses of the effects of cattle excreta on the invasiveness of *R. obtusifolius* and resistance of the recipient community. Line thickness and arrows represent their relative strength and direction. (D) Survey and experimental designs for testing the mechanism of livestock excreta facilitating the spread of *R. obtusifolius* in pasture. See Methods for details.

Figure 2 The variation patterns of spread of *Rumex obtusifolius* in relation to livestock excreta in pastures. (A, B) Variation in spread area and density of *R. obtusifolius* in four breeding sites, respectively, with distance from shed in Nanshan pastures (JZP, Jizhuaping, SWA, Siwenao, WJWC, Wangjiawochang, XJA, Xinjianao). (C, D) Variation in spread area and density of *R. obtusifolius*, respectively, with distance from shed in Dushan pasture. The asterisks denote significance: $^{*} = p < 0.05$; $^{**} = p < 0.01$, $^{***} = p < 0.001$.

Figure 3 Biomass and density differences of *Rumex obtusifolius* and other species, as well as plant diversity between grazing area without dung and congregating area with dung. The asterisks denote significance: $^{*} = p < 0.05$; $^{**} = p < 0.01$, $^{***} = p < 0.001$.

Figure 4 (A, B) Differences in height and ramet number of *Rumex obtusifolius* between control and cattle dung addition. (C, D) Changes in relative abundance of *R. obtusifolius* and species richness within the dung addition treatment. Bars sharing the same letter are not significantly different ($p > 0.05$).

Figure 5 Effects of livestock excreta additions on *Rumex obtusifolius*, tolerant plants and intolerant plants in recipient ecosystems. (A) Changes in height of *R. obtusifolius*, tolerant, and intolerant plants after 30 days of treatment with different excreta additions compared to control. (B, C) Differences in height and ramet number of *R. obtusifolius* among different nutrient addition treatments. Bars sharing the same letter are not significantly different ($p > 0.05$).

Figure 6 Conceptual framework illustrating the mechanisms of livestock influence on *Rumex obtusifolius* invasion. (A) The magnitude and pathways of cattle effects on native species and invasive species. Line thickness and arrows represent their relative strength and direction of grazing and excreta effects, respectively. (B) Nutrient and physical effects of cattle excreta on *R. obtusifolius* along the two periods of dung decomposition.