Title

Intensification pathways modulate Eragrostis plana invasion trajectories in natural grassland

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Conflict of interest

The authors declare no conflict of interest.

Ethics approval

The animal component of the long-term grazing experiment was approved by the Animal Ethics Committee of the Instituto de Pesquisas Veterinárias Desidério Finamor (CEUA/IPVDF; approval protocol no. 15/2013; official letter no. 16/13–CEUA/IPVDF, dated 4 June 2013). Animal management followed the approved research protocol and applicable Brazilian guidelines for the use of animals in research.

Data availability statement

The datasets generated and/or analysed during the current study are available from the corresponding author on reasonable request.

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Intensification pathways modulate *Eragrostis plana* invasion trajectories in natural grassland

Abstract

Management pathways aimed at increasing forage supply and livestock productivity are often proposed in natural grasslands, but their consequences for established invasive grasses remain uncertain. We evaluated trajectories of an established *Eragrostis plana* Nees (Poaceae) invasion under contrasting pathways in the Brazilian Pampa. From August 2014 to May 2017, vegetation was monitored in eight paddocks arranged in two blocks, two per pathway: managed natural grassland under grazing control, natural grassland with liming and basal fertility correction, natural grassland with fertility correction, Italian ryegrass and forage legumes, and natural grassland with fertility correction, Italian ryegrass and additional urea-based mineral nitrogen. We analysed *Eragrostis plana* frequency using beta-binomial mixed models and evaluated total cover and conditional cover where the species was detected as complementary response layers. Dynamic reference-adjusted summaries described trajectories relative to paddock-specific operational baselines and the contemporaneous reference trajectory, while formal inference was based on the fitted models. Responses did not indicate uniform suppression or promotion across pathways. The clearest pathway-dependent signal occurred in frequency: the reference-adjusted contrast between the Italian ryegrass + additional urea-based mineral-nitrogen pathway and the Italian ryegrass + legume pathway was +9.19 percentage points in the first post-intensification grazing-use year and +5.91 percentage points in the second, and planned contrasts supported greater *Eragrostis plana* frequency under the former in both years. The fertility-correction pathway remained close to the

managed natural-grassland trajectory. Total cover showed the same contrast direction but with smaller magnitude and weaker statistical support, whereas conditional cover showed no corresponding supported difference. Thus, pathway divergence was expressed more clearly through detectable occurrence than through local cover where *Eragrostis plana* was detected. In invaded natural grasslands, intensification pathways should therefore be evaluated not only for production objectives but also for their association with the spatial expression of established invasive grasses.

Keywords: biological invasion; South African lovegrass; grazing management; Pampa biome; grassland intensification.

1. Introduction

Natural grasslands sustain livestock production, biodiversity conservation and cultural landscapes across large areas of the Southern Hemisphere (Bengtsson et al. 2019). In the Pampas and Campos grasslands of southern South America, livestock systems have historically relied on year-round grazing of species-rich natural grasslands that provide forage, sustain biodiversity, and deliver multiple ecosystem services (Modernel et al. 2016; Jaurena et al. 2021). These ecosystems face two connected pressures: the need to increase forage supply and animal production, and the expansion of invasive grasses that are less preferred by livestock and reduce the functional integrity of grazed landscapes. Grassland management intensification is often advocated to increase seasonal forage availability, promote canopy occupation and mitigate degradation. However, whether intensification reduces or increases invasion risk may depend more on the pathway through which it is implemented than on intensification itself.

This question is particularly relevant in the natural grasslands of the Brazilian Pampa, where livestock production occurs in highly heterogeneous vegetation mosaics composed of short inter-tussock patches and taller, less frequently grazed tussock components (Bremm et al. 2012; Silveira et al. 2025). *Eragrostis plana* Nees (Poaceae) is one of the most problematic invasive grasses in the region (Zabala-Pardo and Lamego 2024). It is a perennial C4 species generally poorly selected by livestock; increasing *E. plana* tussock cover can restrict access to preferred forage and alter herbivore diet selection (Bremm et al. 2012, 2016). Increasing *E. plana* cover has also been associated with reduced plant species richness, indicating negative effects on grassland plant biodiversity and community structure (Dresseno et al. 2018).

Once *E. plana* is established, the management problem is no longer preventing colonisation of an uninvaded grassland. Instead, the challenge is to understand how management affects the trajectory of an invader already embedded in the grazed matrix. This distinction matters because invasion responses are often assessed by changes in mean abundance or cover, whereas management responses may also appear as changes in detectable spatial occurrence (Guido and Pillar 2017; Baggio et al. 2018). An invader may be detected in a greater proportion of sampled quadrats without showing greater local cover. Frequency and cover describe different vegetation attributes (Coulloudon et al. 1999) and should therefore be considered together when evaluating management responses in already-invaded grasslands. Frequency captures detectable spatial occurrence, total cover integrates occurrence and local cover, and conditional cover reflects local cover where the species is detected.

Grassland intensification pathways may affect these response layers in contrasting ways. Fertility correction and forage overseeding can alter resident vegetation composition and seasonal forage supply (Jaurena et al. 2016; Jaurena et al. 2021), while grazing and associated disturbance can influence grassland structure and *E. plana* invasion risk (Bremm et al. 2012; Focht and Medeiros 2012; Baggio et al. 2018). These responses may involve changes in resource availability: fluctuating-resource theory predicts greater invasibility when resources become available faster than resident vegetation can capture them (Davis et al. 2000). Pathways differing in additional urea-based mineral N versus forage legumes may differ in the timing and form of N inputs and in the vegetation established during the cool-season phase. We therefore expected contrasting invasion trajectories among these management pathways, while recognising that their component operations could not be isolated experimentally.

Few studies have evaluated how contrasting intensification pathways affect the trajectory of an already established invasive grass in natural grasslands. More specifically, there is limited evidence to determine whether pathway responses are expressed mainly through broader detectable occurrence of the invader or through greater local cover where it is detected. This distinction is important because pathway divergence may be evident in frequency even when changes in total or conditional cover are weak.

Here, we evaluated the post-intensification trajectory of an established *E. plana* invasion in a natural grassland of the Brazilian Pampa. We compared four paddock-level management intensification pathways: managed natural grassland under grazing control; natural grassland with liming and basal fertility correction; natural grassland with fertility correction, Italian ryegrass overseeding and forage legumes; and natural grassland with fertility correction, Italian ryegrass overseeding and additional urea-based mineral N. The study was designed and interpreted at the pathway level because each pathway comprised a coordinated sequence of management operations rather than a single isolated factor.

We hypothesised that intensification aimed at increasing forage supply would not uniformly suppress *E. plana* invasion, because the invader's response would depend on the intensification pathway configuration. Specifically, we predicted that the Italian ryegrass + additional urea-N pathway would show greater *E. plana* frequency than the Italian ryegrass + legume pathway, and that the latter would show a lower frequency trajectory relative to the former rather than absolute suppression of the invader. We further predicted that pathway differences would be clearer for frequency than for conditional cover where *E. plana* was detected, indicating that pathway divergence would be expressed more clearly through detectable occurrence than through local cover where the species was detected.

2 Methods

2.1 Study site and experimental background

The research was conducted from August 2014 to May 2017 in an invaded natural grassland of the Brazilian Pampa biome at São Gabriel, Rio Grande do Sul, southern Brazil (30°20′19″ S, 54°15′02″ W; 125 m a.s.l.). The experimental area comprised approximately 34 ha of grassland that had been historically grazed by cattle and was already colonised by the invasive perennial C4 grass *Eragrostis plana* Nees before pathway differentiation. Across the three vegetation assessments conducted before pathway-specific fertility interventions (28 August–8 October 2014), *E. plana* frequency averaged 24.5% across paddocks (range 14.7–40.0%), total cover averaged 8.2% (4.2–13.0%), and conditional cover where the species was detected averaged 33.3% (28.4–38.3%). Thus, the study addressed management-associated trajectories of an established, spatially heterogeneous invasion rather than colonisation of an initially uninvaded grassland.

The vegetation represented mixed natural grasslands of the Brazilian Pampa and showed a bimodal structure consistent with moderately grazed Campos grasslands, comprising a mosaic of a shorter, more frequently grazed matrix and spatially discontinuous tussock components (Fedrigo et al. 2018; Silveira et al. 2025). Tussock structure was identified in the field from plant growth form, architecture and structural discontinuity from the lower matrix, rather than from species identity or a fixed height threshold. Typical contributors to the tussock component included *Eryngium horridum* Malme, *Vernonanthura nudiflora* (Less.) H.Rob., *Saccharum angustifolium* (Nees) Trin. and *Acanthostyles buniifolius* (Hook. & Arn.) R.M.King & H.Rob., whereas the lower matrix

was dominated by frequently grazed native grasses and associated species, including *Paspalum notatum* Flüggé, *Axonopus affinis* Chase, *Paspalum umbrosum* Trin., *Paspalum plicatulum* Michx. and *Desmodium incanum* (Sw.) DC. *Eragrostis plana*, itself a tussock-forming grass, could also contribute to the tussock component depending on its structural expression at a given evaluation; its occurrence and cover were recorded independently of this structural classification.

The climate is humid subtropical (Cfa, Köppen–Geiger classification), with warm summers, cool winters and no marked dry season. Mean annual precipitation is approximately 1,430 mm and is relatively well distributed throughout the year, while normal monthly mean air temperature ranges from about 14 °C in July to 25 °C in January. Monthly rainfall and mean air temperature during the experimental period, together with the corresponding climatological normals (Matzenauer et al. 2011), are provided in Appendix S1 (Figure S1a). According to the Brazilian Soil Classification System, the soil is classified as *Argissolo Vermelho Distrófico latossólico* (Santos et al. 2025). Before pathway differentiation, the 0–20 cm layer contained 17% clay, pH-H_2O 5.1, 2.66 mg dm^{-3} P, 125 mg dm^{-3} K, 1.69% organic matter and an effective cation exchange capacity of 6.10 cmolc dm^{-3}, indicating an acidic soil with very low available phosphorus but non-limiting initial potassium availability.

In 2013, the area was subdivided into eight fenced paddocks, ranging from 2.7 to 5.6 ha, arranged in two blocks according to landscape position. Before pathway differentiation, the entire area was managed under a common natural-grassland grazing regime. During grazing-use phases, all paddocks were grazed by heifers under continuous stocking, and stocking rate was adjusted periodically to maintain a moderate target forage allowance (Da Trindade et al. 2012; Da Trindade et al. 2016). This common grazing regime was

maintained across all intensification pathways; therefore, subsequent differences in *E. plana* trajectories were interpreted as pathway-level management contrasts rather than intentional differences in grazing intensity.

2.2 Experimental design and intensification pathways

The experiment followed a randomised-block design with two blocks and four paddock-level management pathways. Within each block, one paddock was allocated to each pathway, yielding two independently allocated paddocks per pathway. These pathways combined coordinated management operations rather than single isolated factors: natural grassland under grazing control (NG); natural grassland with liming and basal fertility correction (NGF); natural grassland with liming, basal fertility correction, Italian ryegrass (*Lolium multiflorum* Lam.) and forage legumes (NGRL); and natural grassland with liming, basal fertility correction, Italian ryegrass and additional urea-based mineral-N fertilisation (NGRN).

The chronology of grazing-use phases, grazing deferments, mowing, sowing, mineral-N applications and vegetation evaluations is detailed in Appendix S1 (Figure S1b). The experiment comprised an operational baseline grazing phase from August 2014 to March/April 2015; grazing deferment from March/April to August 2015; a first post-intensification grazing-use year from August 2015 to April 2016 (Year 1); a second grazing deferment from April to June 2016; and a second grazing-use year from June 2016 to May 2017 (Year 2). Mowing at ≈15 cm was used operationally to reduce accumulated tall tussock biomass and, where applicable, to favour the establishment of overseeded cool-season forage species. Because mowing was applied operationally across the experimental chronology and was not implemented as a separate experimental

factor, it was interpreted as a component of the broader management chronology rather than as an independent treatment.

The NG pathway served as the managed natural-grassland reference trajectory. Like the other pathways, it was maintained under the common grazing regime, but received no deliberate fertility correction or cool-season forage insertion.

The NGF pathway represented soil fertility correction without intentional cool-season forage insertion. This fertility-correction base was also applied to NGRL and NGRN. Dolomitic limestone was surface-applied on 15 October 2014 at 2.5 t ha^{-1}. In 2015, fertilised pathways received 300 kg ha^{-1} of a 5–30–15 N–P_2O_5–K_2O formulation, supplying a small basal N input and correcting P and K availability. In 2016, the shared fertility-correction base was restricted to phosphorus, with 220 kg ha^{-1} of triple superphosphate (46% P_2O_5), consistent with non-limiting soil K status.

The NGRL pathway combined fertility correction with overseeding of Italian ryegrass cv. FEPAGRO São Gabriel and forage legumes. Italian ryegrass was broadcast at 40 kg ha^{-1} in 2015 and 2016. The legume component included red clover (*Trifolium pratense* L.) and arrowleaf clover (*Trifolium vesiculosum* Savi), each broadcast at 6 kg ha^{-1}.

The NGRN pathway combined fertility correction, Italian ryegrass overseeding and additional urea-based mineral-N fertilisation. An additional 100 kg N ha^{-1} was applied as urea (45% N) in 2015 and 2016, split into two applications during early cool-season forage establishment. Therefore, NGRN should be interpreted as the pathway receiving additional urea-based mineral N above the shared fertility-correction base, not as the only pathway exposed to mineral N.

2.3 Monitoring of *E. plana* and response variables

Eragrostis plana was monitored in 32 evaluation rounds spanning the experimental chronology, including 28 rounds covering all eight paddocks and four covering a subset of paddocks. Assessments were conducted at the paddock level using 0.5 × 0.5 m metal quadrats placed systematically along walking transects designed to represent the structural heterogeneity of each paddock. The number of valid quadrats per sampled paddock and evaluation round ranged from 25 to 117 (median = 50). Sampling locations were not permanently marked. Within each quadrat, trained observers recorded the presence of *E. plana* and visually estimated its aerial cover as a percentage of quadrat area. These species-specific records were made independently of the structural classification of the sampled vegetation as lower matrix or tussock component. The same field protocol was maintained throughout the experiment.

Quadrat-level observations were aggregated to the paddock × evaluation-round level before statistical analysis. Quadrats were therefore treated as within-paddock subsamples used to estimate the vegetation state of each experimental unit, rather than as independent replicates. Repeated evaluations characterised temporal trajectories but did not increase the number of independently allocated paddocks per pathway.

Three response variables were derived for each paddock and evaluation round. *E. plana* frequency was calculated as the percentage of valid quadrats in which the species was detected and was used as the primary response describing detectable above-ground occurrence across sampled quadrats at the paddock scale. Total cover was calculated as mean *E. plana* cover across all valid quadrats, with quadrats where the species was not detected assigned zero cover. Conditional cover was calculated as mean cover only among quadrats where *E. plana* was detected at that evaluation and described local cover where the species occurred. Total and conditional cover were treated as complementary cover

responses. Because sampling locations were not permanent microsites, changes in frequency cannot be attributed directly to recruitment, colonisation or vegetative expansion of previously unoccupied locations. The three responses describe related attributes derived from the same quadrat observations and should not be interpreted as independent lines of evidence.

2.4 Functional chronology and analytical dataset

Evaluation rounds were assigned to functional phases of the experimental protocol rather than treated as a simple sequence of calendar observations. This distinction was necessary because the experiment alternated active grazing and grazing-deferment periods, while mowing, sowing and fertilisation events were not uniformly distributed through time.

The initial pre-intervention condition reported in Section 2.1 was characterised from the three vegetation assessments conducted before pathway-specific fertility interventions (28 August–8 October 2014). This descriptive initial condition was distinct from the operational baseline used in the analyses. The operational baseline comprised grazing-phase evaluations from August 2014 to the first grazing deferment: 12 March 2015 in NG and NGF and 6 April 2015 in NGRL and NGRN. It preceded cool-season forage establishment but included the October 2014 liming of the fertilised pathways and therefore did not represent an entirely untreated period. All paddocks returned to grazing on 5 August 2015. In Appendix S1, grazing deferment I is displayed using the mean graphical start date of 25 March 2015.

The primary analytical dataset was restricted to evaluations conducted during the two post-intensification grazing-use years: Year 1, from the return to grazing on 5 August 2015 to the terminal pre-deferment evaluation in April 2016; and Year 2, from the return

to grazing on 15 June 2016 to the final evaluation in May 2017. Evaluations conducted during grazing-deferment phases were retained in the experimental chronology but excluded from the primary grazing-use inference to avoid pooling vegetation states measured under active grazing with those measured during deferment.

For each paddock and response variable, the mean across evaluations within the operational baseline grazing phase was used as the paddock-specific analytical baseline. Within each post-intensification grazing-use year, time was expressed as the number of days elapsed since the corresponding return to grazing, calculated separately for Year 1 and Year 2. The analytical roles of the operational baseline and temporal variables are described in the dynamic NG-adjusted framework and statistical analyses below.

2.5 Dynamic natural-grassland adjustment

To account for seasonal and interannual background variation represented by the managed natural-grassland reference, post-intensification responses were summarised using a dynamic NG-adjusted framework. This approach expressed pathway-associated deviations relative to both the paddock-specific operational baseline and the contemporaneous NG trajectory.

For each response variable, the operational baseline for each paddock was calculated as the mean across evaluations within the operational baseline grazing phase defined in Section 2.4. A corresponding NG operational baseline was calculated across operational-baseline observations from the two NG paddocks. Then, for each evaluation round, the dynamic NG-adjusted response was computed as:

$$\Delta_{\mathrm{NG-adjusted},i,e} = \left(Y_{i,e} - \bar{Y}_{i,\mathrm{baseline}}\right) - \left(\bar{Y}_{\mathrm{NG},e} - \bar{Y}_{\mathrm{NG,baseline}}\right)$$

where $Y_{i,e}$ is the observed value for paddock i in evaluation round e, $\bar{Y}_{i,\text{baseline}}$ is the paddock-specific operational baseline, $\bar{Y}_{\text{NG},e}$ is the mean value of the NG pathway in the same evaluation round, and $\bar{Y}_{\text{NG,baseline}}$ is the corresponding operational baseline for the NG pathway.

Positive values indicate that the response in a paddock increased more, or declined less, than the contemporaneous NG trajectory after each was referenced to its respective operational baseline. Negative values indicate a smaller increase or greater decline relative to NG, whereas zero indicates the same baseline-relative change as NG and does not necessarily represent absolute stability. For frequency and cover responses expressed as percentages, NG-adjusted values are expressed in percentage points.

The metric was calculated for *E. plana* frequency, total cover and conditional cover where the species was detected. This adjustment provided a baseline- and reference-adjusted temporal response that incorporated paddock-specific baseline differences and contemporaneous variation in the managed natural-grassland reference. Dynamic NG-adjusted summaries were used to describe pathway trajectories and response magnitudes in percentage points, whereas formal inferential tests were based on the models described in Section 2.6. The NGRN − NGRL contrast compared the Italian ryegrass + additional urea-N pathway with the Italian ryegrass + legume pathway, both built on the shared fertility-correction base.

2.6 Statistical analyses

All analyses were conducted in R version 4.3.3 (R Core Team 2024). The analytical workflow preserved the paddock as the experimental unit and accounted for repeated

measurements through time. Models were fitted at the paddock × evaluation-round level after aggregation of quadrat-level observations within each paddock and field evaluation.

E. plana frequency was analysed using beta-binomial generalised linear mixed models with a logit link, fitted with the *glmmTMB* package (Brooks et al. 2017). Frequency was represented by the number of quadrats in which *E. plana* was detected relative to the number of valid quadrats evaluated within each paddock and evaluation round, and the beta-binomial distribution allowed for extra-binomial variation. The primary pathway × post-intensification grazing-use year model for frequency was:

$$n_{\text{present},i,e} \sim \text{BetaBinomial}(n_{\text{valid},i,e}, p_{i,e}, \theta)$$

$$\text{logit}\left(p_{i,e}\right) = \beta_0 + \text{pathway}_i * \text{post_year}_e + \beta_1 \,\text{baseline}_i + b_{\text{paddock}(i)} + b_{\text{evaluation}(e)}$$

where *i* denotes paddock and *e* denotes field evaluation round. pathway represented the four paddock-level intensification pathways, post_year represented post-intensification Year 1 and Year 2, and baseline was the centred and scaled paddock-specific operational frequency baseline on the logit scale. Here and in the temporal model below, the asterisk denotes inclusion of the main effects and all lower-order interactions. Paddock identity was included as a random intercept to account for repeated measurements within the same experimental unit. Evaluation round was included as a crossed random intercept to account for temporal and operational conditions shared by paddocks sampled during the same field evaluation.

A second beta-binomial model included the temporal trajectory within each post-intensification grazing-use year:

$$\text{logit}\left(p_{i,\text{e}}\right) = \beta_0 + (\text{pathway}_i * \text{post_year}_e * T_e) + \beta_1 \,\text{baseline}_i + b_{\text{paddock}(i)} + b_{\text{evaluation(e)}}$$

where post_year$_e$ denotes the post-intensification grazing-use year and T_e denotes the centred and scaled number of days elapsed since the corresponding return to grazing. The full pathway × post-intensification-year × time interaction was used to evaluate whether pathway differences changed through grazing-use time within Year 1 and Year 2. A quadratic temporal formulation was also fitted as a sensitivity analysis, but interpretation was based primarily on the pathway × year model and on the pathway × year × linear within-year time model.

Total *E. plana* cover and conditional cover where the species was detected were analysed as complementary Gaussian response layers after logit transformation of percentage values. Percentages were first converted to proportions and constrained to the open interval before transformation to avoid undefined logits at 0 or 1. For each cover response, models included pathway, post-intensification grazing-use year, their interaction and the corresponding centred and scaled operational baseline as fixed effects. Temporal versions also included days since return to grazing and its interaction with pathway and year. Paddock-level random-intercept models were fitted using *lme4* and *lmerTest* when estimable (Bates et al. 2015; Kuznetsova et al. 2017); when the mixed-model formulation could not be fitted, the corresponding reduced Gaussian model was fitted using *lm*. Cover models were interpreted as complementary support for frequency-based inference.

Estimated marginal means and planned contrasts were obtained using the *emmeans* package (Lenth and Piaskowski 2026). The planned priority contrast was NGRN − NGRL, evaluated separately for Year 1 and Year 2, because it compared the Italian ryegrass + additional urea-N pathway with the Italian ryegrass + legume pathway, both built on the shared basal fertility-correction base. Additional contrasts involving NG and NGF were retained for completeness. For temporal models, pathway-specific slope

differences were estimated using marginal trend contrasts for within-year grazing-use time.

Model diagnostics for beta-binomial models were assessed using simulated residuals from the *DHARMa* package (Hartig 2024). Uniformity, dispersion and outlier diagnostics were inspected. Evaluation round was retained as a crossed random intercept in the final frequency models because it represented a biologically meaningful source of shared evaluation-level variation. Because the experiment included only two blocks, block was not fitted as a random effect. Instead, the robustness of the priority frequency contrast was evaluated using sensitivity models that included block as a fixed effect. Additional sensitivity analyses recalculated the operational baselines using a common truncated baseline window ending on 12 March 2015, the earliest grazing-deferment date, to verify that the NGRN − NGRL inference did not depend on the paddock-specific operational-baseline definition. Model structures, residual diagnostics and sensitivity checks are summarised in Appendix S3.

Model estimates and P-values were used to support inferential conclusions about pathway-level patterns, whereas ecological interpretation emphasised effect direction and magnitude, temporal consistency and the decomposition of the invasion response into detectable occurrence and local cover where the species was detected.

3 Results

3.1 Post-intensification trajectories of *E. plana* across intensification pathways

Eragrostis plana was detected throughout the post-intensification period in all intensification pathways, indicating that the experiment followed trajectories of an

already established invasion. Across the two post-intensification grazing-use years, frequency, total cover and conditional cover where detected showed marked temporal variation (Figure 1). This variation was not synchronous across pathways, indicating that responses did not reflect a uniform temporal shift throughout the experimental area.

Observed mean frequency varied from 33.2 to 39.0% in Year 1 and from 32.8 to 41.6% in Year 2. However, pathway trajectories differed in direction and amplitude, indicating that similar annual mean ranges concealed distinct within-year dynamics. The managed natural-grassland reference pathway (NG) also showed temporal fluctuations, reinforcing the need to interpret post-intensification responses relative to the contemporaneous NG trajectory.

Total *E. plana* cover varied over a narrower range, with pathway means from 10.1 to 13.6% in Year 1 and from 9.1 to 12.8% in Year 2. Conditional cover where *E. plana* was detected was higher than total cover, ranging from 30.0 to 38.1% in Year 1 and from 26.1 to 30.3% in Year 2, but showed weaker pathway separation. Thus, at the descriptive level, pathway differences were more apparent in frequency than in conditional cover.

3.2 Dynamic NG-adjusted pathway responses

After accounting for paddock-specific operational baseline conditions and the contemporaneous NG trajectory, pathway differences in *E. plana* frequency became more evident. The Italian ryegrass + additional urea-N pathway (NGRN) showed the largest positive NG-adjusted frequency response, whereas the Italian ryegrass + legume pathway (NGRL) remained closer to, or below, the dynamic NG trajectory (Figure 2).

For frequency, the mean dynamic NG-adjusted response in NGRN was +7.74 percentage points (p.p.) in Year 1 and +0.15 p.p. in Year 2. In contrast, NGRL showed negative

deviations in both years, with −1.45 p.p. in Year 1 and −5.75 p.p. in Year 2. Consequently, the dynamic NGRN − NGRL contrast was positive in both years, reaching +9.19 p.p. in Year 1 and +5.91 p.p. in Year 2 (Figure 3; Appendix S2). This pattern was supported by the planned beta-binomial contrast for frequency, which indicated greater *E. plana* frequency in NGRN than in NGRL in both Year 1 (estimate = 0.420, SE = 0.128, P = 0.0011) and Year 2 (estimate = 0.262, SE = 0.129, P = 0.0427). The frequency contrast was robust to block adjustment and the common truncated-baseline sensitivity analysis (Appendix S3, Table S3.4).

The fertility-correction pathway without cool-season forage insertion (NGF) remained comparatively close to the NG trajectory for frequency. Its dynamic NG-adjusted frequency response changed direction between years, from +3.85 p.p. in Year 1 to −3.71 p.p. in Year 2. Thus, relative to NG, frequency showed the clearest positive deviation under NGRN in Year 1, was negative under NGRL in both years, and changed direction under NGF.

Dynamic NG-adjusted total-cover deviations were small and positive in NGRN (+1.21 and +0.09 p.p. in Year 1 and 2, respectively), small and negative in NGF (–0.20 and –0.39 p.p.), and negative in NGRL (–2.58 and –1.80 p.p.; Appendix S2). Consequently, the dynamic NGRN − NGRL contrast for total cover was +3.79 p.p. in Year 1 and +1.89 p.p. in Year 2. However, modelled support for this contrast was weak in Year 1 (estimate = 0.360, SE = 0.230, P = 0.124) and Year 2 (estimate = 0.113, SE = 0.223, P = 0.616).

Dynamic NG-adjusted conditional-cover deviations were negative in all three intensified pathways in Year 1 (NGF –4.15, NGRL –6.65 and NGRN –6.17 p.p.) and mixed in Year 2 (NGF +3.92, NGRL +0.92 and NGRN −1.62 p.p.; Appendix S2). The dynamic NGRN − NGRL contrast was +0.48 p.p. in Year 1 and −2.54 p.p. in Year 2, with no modelled

support for a difference in either Year 1 (estimate = −0.009, SE = 0.256, P = 0.973) or Year 2 (estimate = −0.138, SE = 0.252, P = 0.588). Thus, the greater frequency under NGRN relative to NGRL was not accompanied by evidence of higher conditional cover.

3.3 Temporal trajectories within post-intensification grazing-use years

Temporal models indicated that pathway differences were also expressed through within-year trajectories, particularly for *E. plana* frequency (Figure 4). The model including days since return to grazing showed that post-intensification responses involved not only differences in annual mean status, but also differences in how frequency changed during grazing-use years.

In Year 1, the strongest predicted increases in frequency occurred in the two Italian ryegrass-based pathways, NGRN and NGRL, with NGRN showing the steepest slope. However, because NGRL also increased during this year, the NGRN − NGRL slope contrast was not statistically supported (estimate = 0.046, SE = 0.153, P = 0.766). In Year 2, NGRN maintained a positive frequency slope, whereas NGRL was nearly stable or slightly negative. Consequently, the NGRN − NGRL slope contrast was positive and statistically supported (estimate = 0.272, SE = 0.108, P = 0.0118). The same qualitative interpretation was retained under the quadratic-time sensitivity analysis (Appendix S3, Table S3.7).

Temporal slope contrasts for total cover and conditional cover did not show the same NGRN − NGRL separation and were not statistically supported in either year (Appendix S3, Table S3.6).

Overall, frequency provided the clearest pathway-dependent temporal signal. NGRN showed greater detectable *E. plana* occurrence than NGRL, whereas total cover followed

the same direction with weaker support and conditional cover showed no corresponding supported difference.

4 Discussion

Our results supported the central expectation that the trajectory of *E. plana* would depend on the configuration of the intensification pathway rather than respond uniformly to intensification. As predicted, *E. plana* frequency was greater under the Italian ryegrass + additional urea-N pathway (NGRN) than under the Italian ryegrass + legume pathway (NGRL) in both post-intensification grazing-use years. Total cover showed the same directional NGRN–NGRL contrast but with weaker support, whereas conditional cover showed no supported difference between these pathways. Thus, pathway divergence was expressed most clearly in detectable *E. plana* occurrence across the sampled paddock area, rather than in the magnitude of local cover where the species was detected. This response structure supported our prediction that pathway effects would be stronger for frequency than for conditional cover and showed that the trajectory of the established invasion differed among intensification pathways.

4.1 Intensification pathways and invasion trajectories

This divergence is ecologically relevant because frequency and conditional cover represent different dimensions of invasion. Frequency captures the proportion of sampled quadrats in which *E. plana* was detected, whereas conditional cover represents local cover where the species was detected (Coulloudon et al. 1999; Guido and Pillar 2017). The absence of a consistent or model-supported NGRN − NGRL difference in conditional cover indicates that the greater frequency under NGRN was not accompanied by evidence

of greater local cover. Thus, pathway divergence was expressed primarily through broader detectable occurrence across the sampled paddock area.

The managed natural-grassland reference pathway (NG) also changed over time, reinforcing that invasion dynamics in grazed grasslands cannot be interpreted against a static background (Baggio et al. 2018; Zabala-Pardo and Lamego 2024). Temporal fluctuations in NG plausibly reflected seasonal and interannual climatic variation, particularly changes in rainfall and temperature, together with grazing and other paddock-level variation (Appendix S1, Figure S1a). Because climatic conditions were experienced by all pathways and were not isolated experimentally, they are interpreted here as components of background temporal variation rather than as pathway-specific drivers. The dynamic NG-adjusted framework was therefore useful because it expressed pathway responses relative to both their own operational baselines and the contemporaneous background trajectory. This approach does not isolate mechanisms, but it provides a baseline- and reference-adjusted description of pathway-associated deviations rather than relying only on raw post-intensification means.

4.2 Divergence between the two Italian ryegrass-based pathways

The contrast between NGRN and NGRL was central because both pathways were built on the same basal fertility-correction framework and included Italian ryegrass, but differed principally in their N-input strategy and forage composition. NGRN received additional urea-based mineral N, whereas NGRL included forage legumes. Mowing, grazing deferment and subsequent grazing-use dynamics formed part of the broader experimental management context and therefore cannot be interpreted as components specific to either pathway. Accordingly, the greater *E. plana* frequency under NGRN should be interpreted as a compound pathway-level contrast with NGRL rather than as

the isolated effect of any single management operation. This distinction is also important because all fertilised pathways received a small basal mineral-N input from the compound fertiliser in 2015; NGRN differed by receiving additional urea-based mineral N above this shared fertility-correction base.

The behaviour of NGF helps to delimit this interpretation. Because NGF shared the liming and basal fertility-correction base with NGRL and NGRN but did not include intentional cool-season forage insertion, its proximity to the managed natural-grassland trajectory indicates that basal fertility correction alone did not reproduce the stronger *E. plana* frequency response observed under NGRN. The NGRN response should therefore be interpreted in relation to the broader configuration of that intensification pathway rather than to fertility correction per se.

During Year 1, the strongest predicted increases in *E. plana* frequency occurred in the two Italian ryegrass-based pathways, with NGRN showing the steepest slope, but the NGRN − NGRL slope contrast was not statistically supported. The shared cool-season forage establishment phase may have contributed to this common response, although it was not isolated experimentally. Mowing, grazing, deferment and seasonal variation in resource availability occurred more broadly across the experiment and therefore formed part of the management and environmental context rather than pathway-specific explanations. In Year 2, the pathways diverged more clearly: NGRN maintained a positive frequency slope, whereas NGRL was nearly stable or slightly negative, and the NGRN − NGRL slope contrast was positive and statistically supported. This indicates a lower frequency trajectory under NGRL relative to NGRN in Year 2, not absolute suppression or reversal of *E. plana* within NGRL.

Several non-exclusive mechanisms could underlie this divergence, but they were not tested independently. NGRL and NGRN differed in the form of N input and in the vegetation established during the cool-season phase, differences that could affect the timing of N availability, resource capture and canopy reorganisation (Davis et al. 2000; Jaurena et al. 2016; Jaurena et al. 2021). Companion botanical assessments from the same experimental platform also indicated changes in resident sward composition, including perennial C4 grass groups and lower species diversity under the N-based strategy (Carvalho 2018). These observations provide plausible context for the pathway divergence, but the experimental design supports inference at the compound pathway level rather than causal attribution to mineral N, legumes or any other individual component.

4.3 Detectable spatial occurrence rather than local cover was the clearest invasion signal

The decomposition of the invasion response into occurrence and local-cover components was one of the most informative outcomes of this study. Frequency captures the proportion of sampling units in which *E. plana* is detected, total cover integrates occurrence and local cover, and conditional cover describes local cover among quadrats where the species is detected at a given evaluation (Coulloudon et al. 1999; Guido and Pillar 2017). In our study, these response layers behaved differently: *E. plana* frequency was greater under NGRN than under NGRL, whereas conditional cover showed no corresponding supported difference between these pathways. Thus, the pathway contrast was expressed more clearly through broader detectable occurrence across the sampled paddock area than through greater local cover where the species was detected.

For management, the contrasting behaviour of the three response layers shows why cover alone may provide an incomplete diagnosis of invasion trajectory. Frequency provided the clearest pathway separation: NGRN showed greater detectable occurrence than NGRL in both post-intensification grazing-use years, whereas NGF remained comparatively close to the NG trajectory and changed direction between years. Total cover followed the same NGRN–NGRL direction with smaller magnitude and weaker statistical support, while conditional cover showed no corresponding supported difference. Thus, the pathway-dependent signal would have been less evident if monitoring had relied only on cover. Monitoring frequency together with total and conditional cover therefore provides complementary information on changes in detectable spatial occurrence and local cover.

4.4 Management implications and inferential limits

Our findings indicate that productive intensification in invaded natural grasslands should not be assumed to reduce invasion risk through increased forage production, soil fertility or canopy occupation alone. In this study, NGRN was associated with greater detectable *E. plana* occurrence than NGRL, whereas the legume-based pathway showed a lower frequency trajectory than the additional urea-N pathway. Pathway choice should therefore be considered as part of invasion-risk management in already-invaded natural grasslands, especially where the target invader is less preferred by livestock and capable of reducing the functional value of the grazing landscape (Focht and Medeiros 2012; Bremm et al. 2016).

This does not imply that fertilisation, annual forage insertion or mineral N should be broadly avoided in invaded grasslands. Rather, as proposed for conservation-oriented use of Brazilian grassy ecosystems, the relevant management question is how grazing and

associated practices are configured (Baggio et al. 2021). Where established *E. plana* infestation warrants direct intervention, intensification-pathway selection may also need to be integrated with targeted control. MIRAPASTO is one such integrated pasture-recovery approach, combining selective control of adult *E. plana* with soil-fertility correction, forage introduction and adjustment of forage allowance (Perez 2015; Zabala-Pardo and Lamego 2024). The present experiment did not test MIRAPASTO or other targeted-control methods, so their efficacy, costs or interactions with the intensification pathways evaluated here cannot be inferred from our data.

The study also has clear inferential limits. The experimental unit was the paddock, with only two independently allocated paddocks per management pathway at a single experimental site. Quadrat subsampling and repeated vegetation assessments increased temporal resolution but did not increase experimental replication. Accordingly, the results provide evidence of pathway-associated *E. plana* trajectories within this experimental system, whereas the magnitude and generality of those differences should be extrapolated cautiously to other sites, years or management contexts. Replicated tests across additional sites and environmental conditions are now needed. A particularly useful next step would be to incorporate this response framework into long-term grassland experiments and vegetation-monitoring programmes across the Campos and Pampas, where repeated observations could test whether pathway-dependent changes in detectable occurrence are consistent across management contexts, soils and climatic conditions, and whether the joint analysis of frequency, total cover and conditional cover improves diagnosis of invasive-grass trajectories.

Treatments were also compound management pathways rather than isolated factorial components, so the results do not identify the independent causal effects of mineral N,

legumes, mowing, grazing deferment or Italian ryegrass establishment. Because quadrats were not permanent microsites, changes in frequency cannot be attributed specifically to recruitment, vegetative expansion or changes in above-ground detectability. Finally, the two post-intensification grazing-use years provide a relatively short window for evaluating long-term dynamics of a persistent perennial invader (Guido and Pillar 2017; Zabala-Pardo and Lamego 2024).

Despite these limits, the study provides evidence that intensification pathways can differentially influence the trajectory of an established *E. plana* invasion. The central finding is not that intensification uniformly suppressed or promoted the invader, but that pathway configuration mattered: NGRN showed greater detectable occurrence than NGRL, while total cover provided weaker separation and conditional cover did not differ correspondingly. In invaded natural grasslands, productive forage intensification should therefore be evaluated not only by its production objectives but also by whether the chosen pathway is associated with a broader spatial expression of established invasive grasses.

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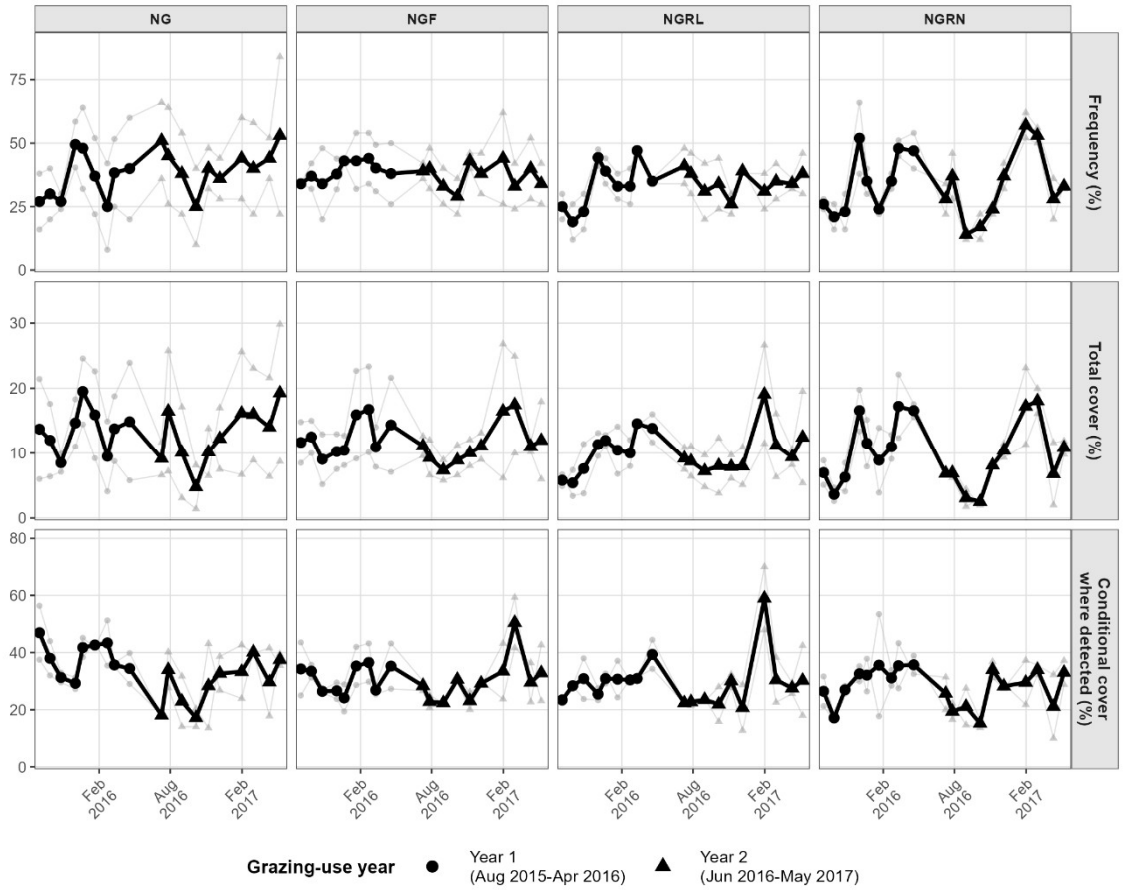
Supporting Information

Appendix S1. Weather conditions and experimental chronology.

Appendix S2. Dynamic NG-adjusted response summaries and NGRN − NGRL contrasts.

Appendix S3. Statistical model outputs, diagnostics and sensitivity analyses.

679 **Figures**



680

681 **Figure 1.** Observed post-intensification trajectories of *Eragrostis plana* frequency, total
682 cover and conditional cover where detected. Panels show the four intensification
683 pathways: managed natural grassland under grazing control (NG), natural grassland with
684 liming and basal fertility correction (NGF), natural grassland with fertility correction,
685 Italian ryegrass and forage legumes (NGRL), and natural grassland with fertility
686 correction, Italian ryegrass and additional urea-based mineral N (NGRN). Grey lines
687 show paddock-level trajectories and black lines show pathway means by evaluation
688 round. Y-axis scales differ among response layers but are held constant across pathways
689 within each response layer.

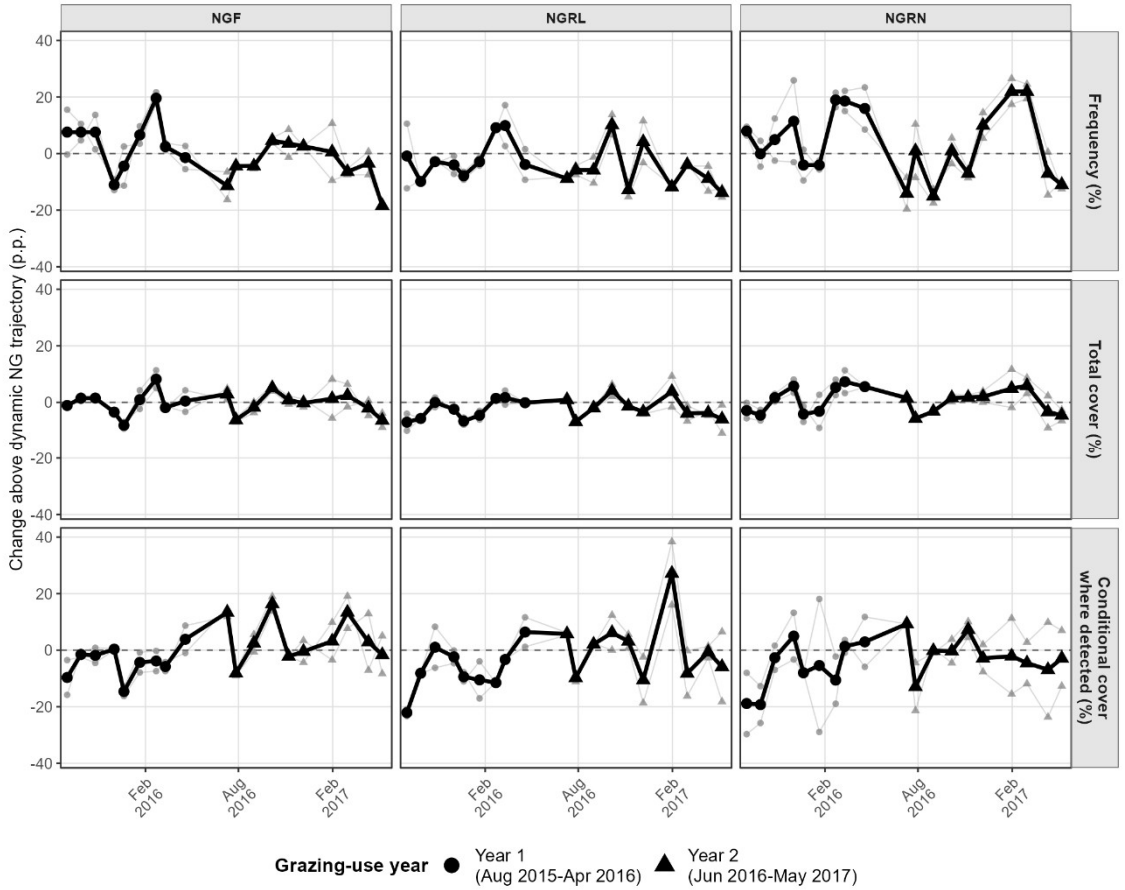
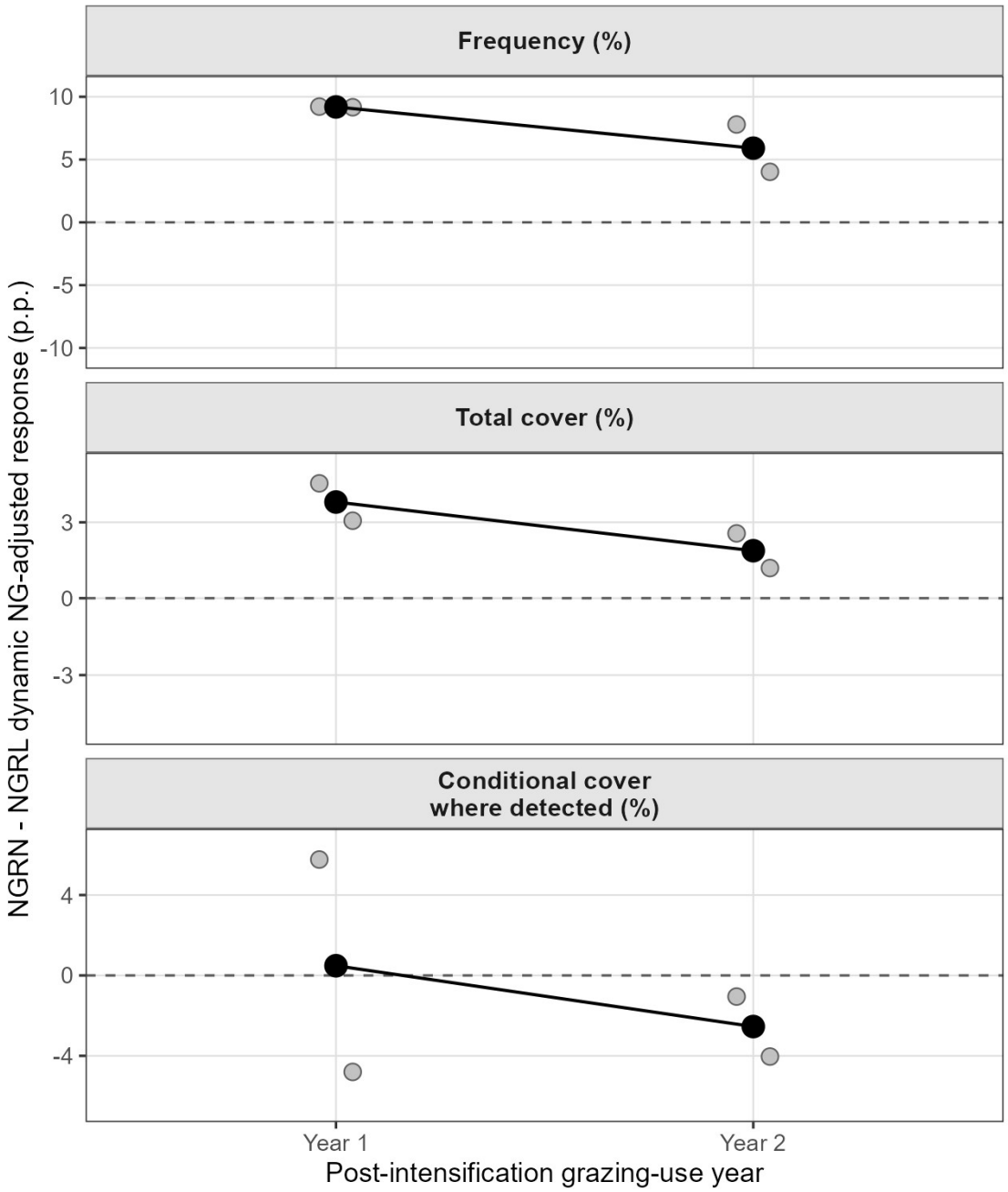


Figure 2. Dynamic NG-adjusted responses of *Eragrostis plana* frequency, total cover and conditional cover where detected. Panels show NGF, NGRL and NGRN responses relative to the contemporaneous managed natural-grassland trajectory after accounting for paddock-specific operational baselines. Positive values indicate that the response increased more, or declined less, than NG after each was referenced to its operational baseline; negative values indicate a smaller increase or greater decline. Grey lines show paddock-level trajectories and black lines show pathway means by evaluation round. The dashed horizontal line indicates the same baseline-relative change as NG, not absolute stability. NG = managed natural grassland under grazing control; NGF = natural grassland with liming and basal fertility correction; NGRL = natural grassland with fertility correction, Italian ryegrass and forage legumes; NGRN = natural grassland with fertility correction, Italian ryegrass and additional urea-based mineral nitrogen.



703

704 **Figure 3.** Dynamic NG-adjusted NGRN − NGRL contrasts for *Eragrostis plana*
705 frequency, total cover and conditional cover where detected. Positive values indicate a
706 greater response in the Italian ryegrass + additional urea-N pathway (NGRN) than in the
707 Italian ryegrass + legume pathway (NGRL), after accounting for paddock-specific
708 operational baselines and the contemporaneous NG trajectory. Grey points show block-
709 level paired contrasts, black points show the means of the block-level paired contrasts,
710 and the black line connects these means across post-intensification grazing-use years. The
711 dashed horizontal line indicates no difference between pathways.

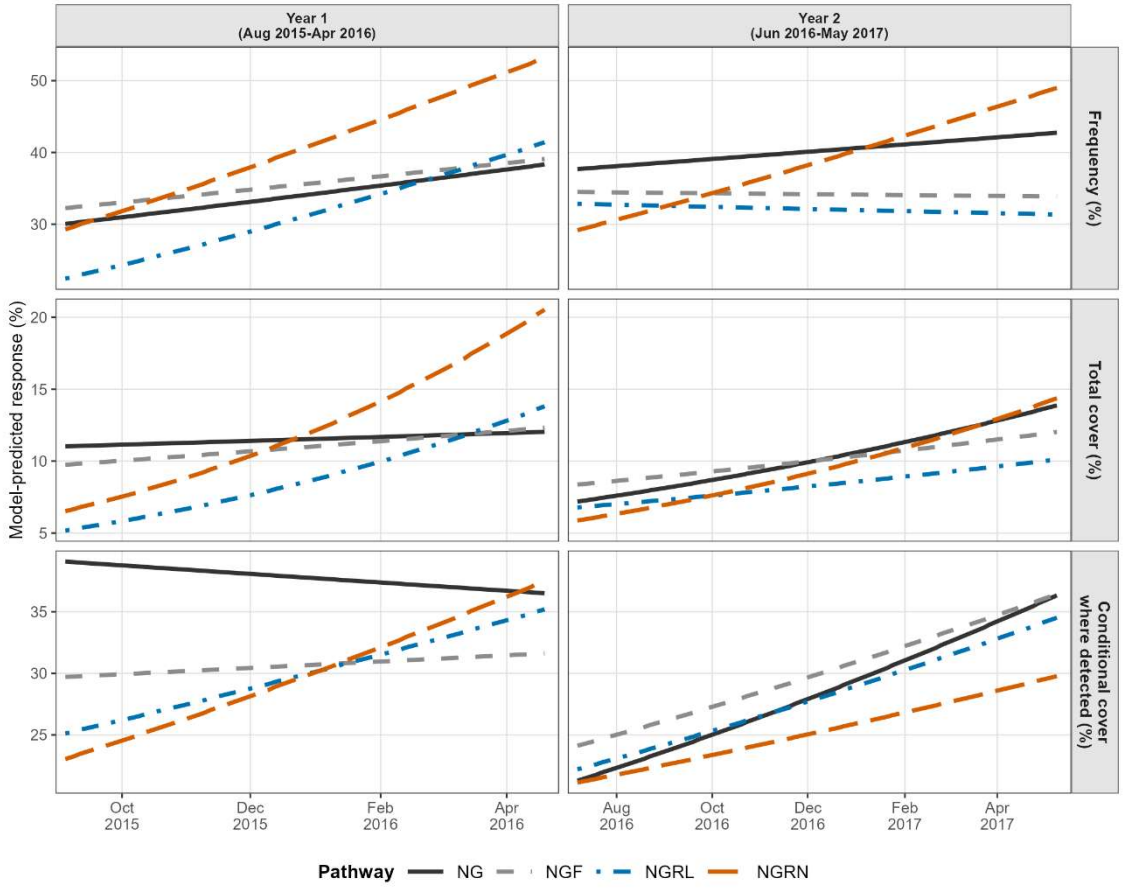


Figure 4. Population-level model-predicted temporal trajectories of *Eragrostis plana* frequency, total cover and conditional cover where detected. Lines show pathway-specific predictions for NG, NGF, NGRL and NGRN during the two post-intensification grazing-use years, obtained from temporal models including the pathway × post-intensification grazing-use year × linear days-since-return-to-grazing interaction. Predictions were generated from the fixed-effects component of the fitted models, with baseline covariates set to their centred values. Time was fitted as centred and scaled days since return to grazing and is displayed on the calendar-date axis for ecological interpretability. The relative steepness of the lines represents the estimated within-year temporal slopes. Formal slope contrasts are reported in the Results and Appendix S3. NG = managed natural grassland under grazing control; NGF = natural grassland with liming and basal fertility correction; NGRL = natural grassland with fertility correction, Italian ryegrass and forage legumes; NGRN = natural grassland with fertility correction, Italian ryegrass and additional urea-based mineral nitrogen.

Supporting Information

Title

Intensification pathways modulate *Eragrostis plana* invasion trajectories in natural grassland

Appendix S1. Weather conditions and experimental chronology.

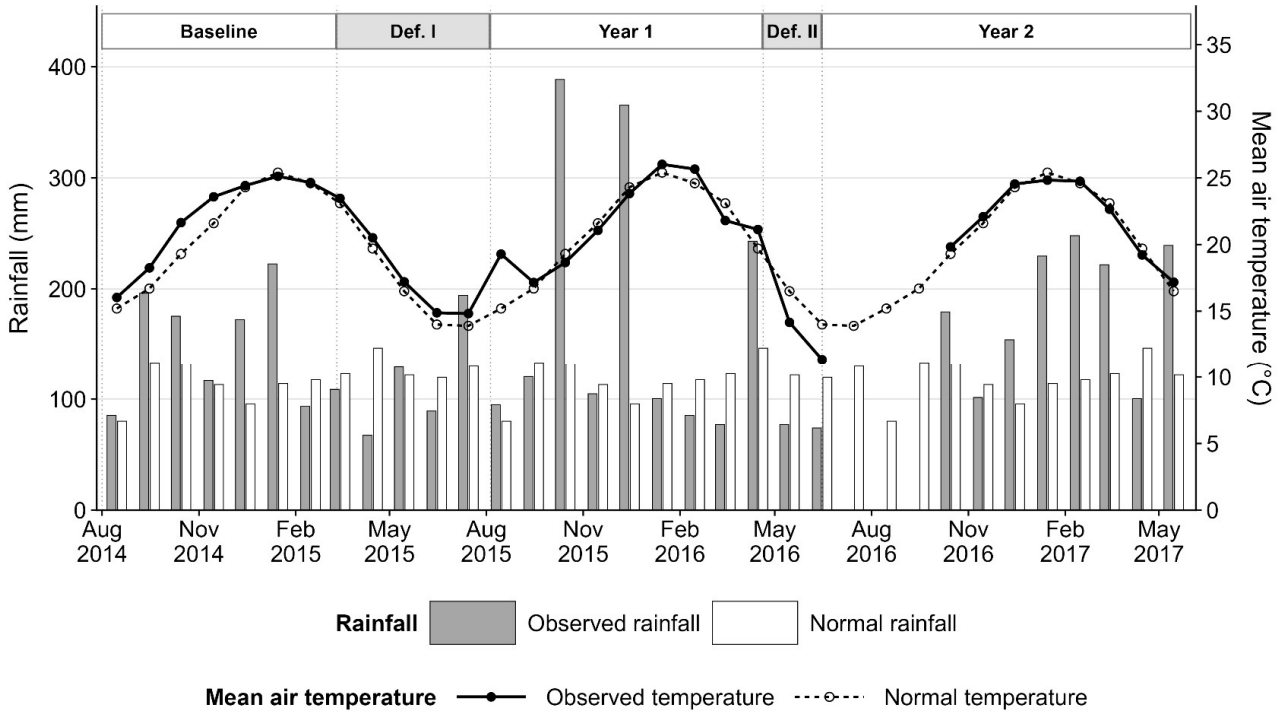


Figure S1a. Monthly rainfall and mean air temperature recorded at the Brazilian National Institute of Meteorology (INMET) weather station in São Gabriel (30°20'29.1"S 54°18'39.2"W) during the experimental period, together with monthly climatological normals for São Gabriel, Rio Grande do Sul, Brazil. The top strip indicates the operational baseline phase, the two grazing-deferment phases and the two post-intensification grazing-use years; Def. I and Def. II denote the first and second grazing-deferment phases, respectively. Observed weather data were unavailable from July to September 2016 owing to gaps in the INMET station records. Climatological normals correspond to the 1976–2005 period reported in the *Atlas Climático do Rio Grande do Sul* (Matzenauer et al. 2011).

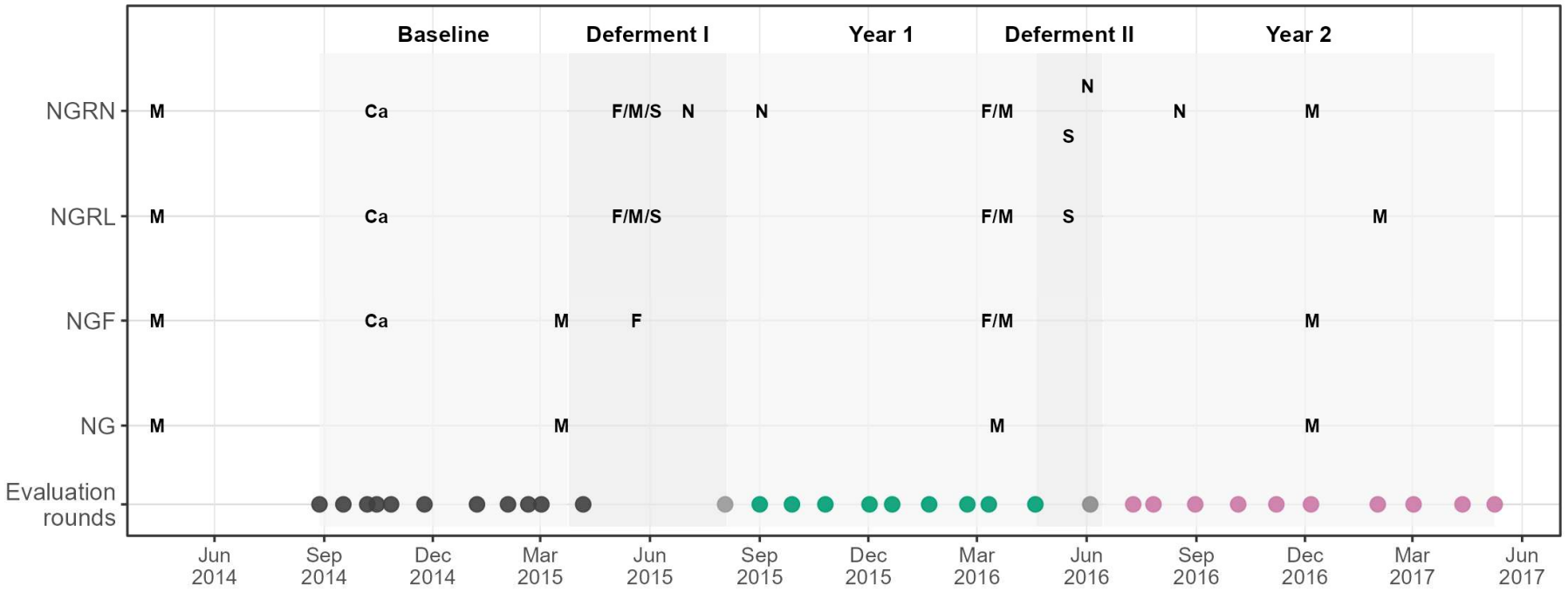


Figure S1b. Experimental chronology of intensification pathways and vegetation evaluation rounds. The strip labelled "Baseline" denotes the operational baseline used in the analyses. Shaded bands represent the operational baseline, grazing-deferment phases and post-intensification grazing-use years. Points show vegetation evaluation rounds, with point colours corresponding to the respective functional phases. Management events are shown by pathway: Ca = liming; F = fertility correction; M = mowing; S = sowing; N = additional urea-N application. In NGRL, S denotes Italian ryegrass + forage-legume sowing; in NGRN, S denotes Italian ryegrass sowing. Grazing deferment I was assigned analytically at paddock level but is displayed using the mean graphical start date of 25 March 2015. Management events are shown for chronology and were treated as components of the integrated intensification pathways rather than as isolated treatment factors.

Appendix S2. Dynamic NG-adjusted response summaries and NGRN − NGRL contrasts

Dynamic NG-adjusted responses were calculated as described in Methods 2.5. This appendix provides the derived pathway-year summaries and priority NGRN − NGRL contrasts underlying Figures 2 and 3. Values are expressed in percentage points (p.p.). Positive values indicate a greater baseline-relative increase, or a smaller decline, than the contemporaneous managed natural-grassland trajectory; negative values indicate a smaller increase or greater decline. A value of zero indicates the same baseline-relative change as NG, not absolute stability.

Table S2.1. Mean dynamic NG-adjusted responses of *Eragrostis plana* by response layer, post-intensification grazing-use year and intensification pathway. Values are means ± SE, expressed in percentage points. NGF = natural grassland with liming and basal fertility correction; NGRL = natural grassland with fertility correction, Italian ryegrass and forage legumes; NGRN = natural grassland with fertility correction, Italian ryegrass and additional urea-based mineral N.

Response layer	Year	NGF	NGRL	NGRN
Frequency	Year 1	3.85 ± 6.89	−1.45 ± 5.92	7.74 ± 7.92
	Year 2	−3.71 ± 5.78	−5.75 ± 5.83	0.15 ± 10.17
Total cover	Year 1	−0.20 ± 3.37	−2.58 ± 2.64	1.21 ± 4.02
	Year 2	−0.39 ± 3.38	−1.80 ± 3.21	0.09 ± 3.57
Conditional cover where detected	Year 1	−4.15 ± 4.47	−6.65 ± 6.31	−6.17 ± 9.65
	Year 2	3.92 ± 6.59	0.92 ± 9.12	−1.62 ± 7.61

Table S2.2. Dynamic NG-adjusted NGRN − NGRL contrasts by post-intensification grazing-use year. Values are expressed in percentage points. Positive values indicate greater *Eragrostis plana* response in NGRN than in NGRL after accounting for paddock-specific operational baselines and the contemporaneous managed natural-grassland trajectory.

Response layer	Year	NGRL	NGRN	NGRN − NGRL
Frequency	Year 1	−1.45	7.74	9.19
	Year 2	−5.75	0.15	5.91
Total cover	Year 1	−2.58	1.21	3.79
	Year 2	−1.80	0.09	1.89
Conditional cover where detected	Year 1	−6.65	−6.17	0.48
	Year 2	0.92	−1.62	−2.54

Table S2.3. Overall post-intensification dynamic NG-adjusted NGRN − NGRL contrasts. Values are expressed in percentage points and summarise the two post-intensification grazing-use years combined.

Response layer	NGRL	NGRN	Overall NGRN − NGRL
Frequency	−3.71	3.75	7.46
Total cover	−2.17	0.62	2.79
Conditional cover where detected	−2.66	−3.77	−1.11

Appendix S3. Statistical model outputs, diagnostics and sensitivity analyses.

This appendix presents the model-level outputs that support the inferential statements reported in the Results section. Model structures followed the analytical workflow described in Methods 2.6. Estimates are presented on the model scale: beta-binomial logit scale for *Eragrostis plana* frequency and logit-transformed proportion scale for total cover and conditional cover where detected. For the cover responses, percentages were converted to proportions, constrained to $[\varepsilon, 1 - \varepsilon]$, with $\varepsilon = 10^{-4}$, and then logit-transformed. Therefore, model-scale estimates should not be interpreted as percentage-point differences; dynamic NG-adjusted percentage-point summaries are provided in Appendix S2.

Table S3.1. Frequency model structures used in the main and sensitivity analyses. Frequency was analysed using beta-binomial GLMMs, with the number of quadrats where *Eragrostis plana* was detected modelled relative to the number of valid quadrats evaluated within each paddock and evaluation round.

Model structure	Analytical role	Fixed-effect component	Random-effect component	Dispersion component
Pathway × post-intensification grazing-use year	Primary model for pathway-year contrasts in *E. plana* frequency	Intensification pathway, post-intensification grazing-use year, their interaction, and the centred and scaled operational frequency baseline	Random intercepts for paddock and evaluation round	Constant dispersion
Pathway × post-intensification grazing-use year × linear grazing-use time	Primary temporal model for testing whether pathway differences changed within grazing-use years	Intensification pathway, post-intensification grazing-use year, centred and scaled days since return to grazing, their interaction, and the centred and scaled operational frequency baseline	Random intercepts for paddock and evaluation round	Constant dispersion
Pathway × post-intensification grazing-use year × quadratic grazing-use time	Sensitivity model evaluating whether the temporal interpretation depended on imposing a linear grazing-use trajectory	Same fixed-effect structure as the temporal model, with the addition of a quadratic term for centred and scaled days since return to grazing and its interaction with pathway and post-intensification grazing-use year	Random intercepts for paddock and evaluation round	Constant dispersion

Table S3.2. DHARMa simulated-residual diagnostics for frequency models. Values are P-values from dispersion, uniformity and outlier tests based on 1000 simulated residuals.

Model	Dispersion test	Uniformity test	Outlier test
Pathway × post-intensification grazing-use year	0.034	0.495	1.000
Pathway × post-intensification grazing-use year × linear grazing-use time	0.044	0.367	0.520
Pathway × post-intensification grazing-use year × quadratic grazing-use time	0.046	0.213	0.520

The frequency models showed mild residual-dispersion signals, whereas uniformity and outlier diagnostics did not indicate major departures. Because the pathway-level interpretation remained stable across temporal and sensitivity structures, inference was based on the direction, magnitude and robustness of the planned contrasts rather than on a single model diagnostic.

Table S3.3. Priority pathway-year model contrasts between NGRN and NGRL. Estimates are NGRN − NGRL contrasts on the model scale. For frequency, estimates are beta-binomial logit-scale contrasts; for total cover and conditional cover, estimates are logit-transformed proportion-scale contrasts.

Response layer	Year	Estimate	SE	Test statistic	P
Frequency	Year 1	0.420	0.128	z = 3.271	0.0011
	Year 2	0.262	0.129	z = 2.027	0.0427
Total cover	Year 1	0.360	0.230	t = 1.562	0.1239
	Year 2	0.113	0.223	t = 0.505	0.6156
Conditional cover where detected	Year 1	−0.009	0.256	t = −0.034	0.9732
	Year 2	−0.138	0.252	t = −0.546	0.5876

Table S3.4. Sensitivity of the priority NGRN − NGRL frequency contrast to block adjustment and baseline definition. Estimates are NGRN − NGRL contrasts on the beta-binomial logit scale. Because only two blocks were available, block was included as a fixed effect in the sensitivity model. The common truncated-baseline sensitivity recalculated operational paddock baselines using a common window ending on 12 March 2015, the earliest first-deferment date.

Sensitivity structure	Year	Estimate	P
Main frequency model	Year 1	0.420	0.0011
	Year 2	0.262	0.0427
Block included as fixed effect	Year 1	0.463	0.0005
	Year 2	0.306	0.0230
Common truncated baseline	Year 1	0.471	0.0003
	Year 2	0.313	0.0163

Table S3.5. Pathway-specific temporal slopes for *Eragrostis plana* frequency within each post-intensification grazing-use year from the primary linear temporal frequency model. Estimates are slopes for centred and scaled days since return to grazing, on the beta-binomial logit scale. CL = confidence limit. NG = managed natural grassland under grazing control; NGF = natural grassland with liming and basal fertility correction; NGRL = natural grassland with fertility correction, Italian ryegrass and forage legumes; NGRN = natural grassland with fertility correction, Italian ryegrass and additional urea-based mineral N.

Year	Pathway	Slope estimate	SE	95% lower CL	95% upper CL
Year 1	NG	0.147	0.137	−0.120	0.415
	NGF	0.119	0.134	−0.144	0.382
	NGRL	0.357	0.138	0.086	0.628
	NGRN	0.403	0.137	0.134	0.672
Year 2	NG	0.063	0.096	−0.124	0.250
	NGF	−0.008	0.095	−0.194	0.178
	NGRL	−0.020	0.096	−0.208	0.167
	NGRN	0.252	0.096	0.063	0.441

Table S3.6. Priority temporal slope contrasts between NGRN and NGRL within each post-intensification grazing-use year. Estimates are NGRN − NGRL differences in pathway-specific slopes for centred and scaled days since return to grazing. Frequency contrasts are on the beta-binomial logit scale; total-cover and conditional-cover contrasts are on the logit-transformed proportion scale.

Response layer	Year	Estimate	SE	Test statistic	P
Frequency	Year 1	0.046	0.153	z = 0.298	0.7658
	Year 2	0.272	0.108	z = 2.518	0.0118
Total cover	Year 1	0.092	0.197	t = 0.468	0.6405
	Year 2	0.165	0.135	t = 1.224	0.2228
Conditional cover where detected	Year 1	0.085	0.171	t = 0.497	0.6196
	Year 2	−0.046	0.117	t = −0.394	0.6944

Table S3.7. Sensitivity of the priority NGRN − NGRL frequency slope contrast to linear versus quadratic temporal specification. Estimates represent NGRN − NGRL differences in pathway-specific temporal slopes for centred and scaled days since return to grazing, on the beta-binomial logit scale.

Time structure	Year	Estimate	SE	z-ratio	P
Linear time	Year 1	0.046	0.153	0.298	0.7658
	Year 2	0.272	0.108	2.518	0.0118
Linear + quadratic time	Year 1	0.098	0.157	0.625	0.5322
	Year 2	0.344	0.116	2.980	0.0029

The quadratic-time sensitivity analysis supported the same qualitative interpretation as the preferred linear-time model. In Year 1, the NGRN − NGRL frequency slope contrast remained weak. In Year 2, the contrast remained positive and statistically supported, indicating that the temporal

divergence between the Italian ryegrass + additional urea-N pathway (NGRN) and the Italian ryegrass + legume pathway (NGRL) was not an artefact of imposing a linear temporal structure.

Overall, the model-level outputs support the interpretation adopted in the Main Text: the clearest pathway-dependent signal occurred in *E. plana* frequency. Total cover showed the same NGRN − NGRL contrast direction but with weaker statistical support, whereas conditional cover where detected showed no corresponding statistically supported difference. The priority NGRN − NGRL frequency contrast remained positive and statistically supported in the block-adjusted and common truncated-baseline sensitivity models, indicating that the main pathway-level inference did not depend materially on excluding block from the primary model or on the use of paddock-specific operational baseline windows. Likewise, the Year 2 temporal divergence in frequency remained supported under the quadratic-time sensitivity specification, indicating that this temporal result was not an artefact of imposing a linear within-year trajectory.