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The role of functional native herbage in improving community stability: evidence from a grazing and nitrogen addition experiment in an alpine meadow of Qinghai–Xizang Plateau

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Abstract

Human activities alter the drivers of plant diversity and ecosystem stability due to intensified grazing and nutrient enrichment. Nevertheless, the interactive impacts between herbivory pressure and eutrophication on

biodiversity, productivity and ecosystem stability in grasslands remain unclear. We conducted a field experiment with four levels of nitrogen (N) addition and three rates of rotational grazing in an alpine meadow of the Qinghai–Xizang Plateau. We found that increasing N addition rates decreased plant species richness and functional native herbage (FNH) richness, while increasing stocking rates decreased community aboveground biomass (AGB) and traditional herbage (TH) AGB. Grazing tended to positively influence community AGB temporal stability due to increasing FNH richness and compositional stability, but this effect was associated with considerable uncertainty. Although N addition drove an increase in species asynchrony, the net effect of N addition on community AGB temporal stability was negative, as the destabilizing effects of reduced soil pH and FNH richness outweighed the positive contribution of enhanced species asynchrony. Furthermore, FNH richness, species asynchrony within FNH populations, and FNH–TH asynchrony were the primary mediating pathways through which community AGB temporal stability was maintained under grazing and N addition. The total biomass temporal stability was mainly mediated by belowground biomass temporal stability rather than AGB temporal stability, indicating that surveys focusing only on temporal stability of AGB provide limited evidence for the ecological consequences of grazing and nutrients. We identified an ecological threshold of 0.86 for the biomass ratio of FNH to TH in relation to community AGB temporal stability in this alpine meadow. Below the ecological threshold, community AGB temporal stability decreased

as the FNH/TH ratio increased; above the threshold, further increases in FNH proportion did not produce additional stability benefits.

Keywords: Community stability, Functional native herbage, Traditional herbage, Stocking rate, Nitrogen addition gradient, Qinghai–Xizang Plateau

1. Introduction

Human activities can substantially reshape the drivers of plant community dynamics through two key pathways, including globally increased livestock density and significantly elevated nutrient inputs[1−2]. On one hand, the restructuring of herbivore assemblages has shifted plant communities via top-down controls[3−4]. This manifests in a widespread decline of wild herbivore populations coupled with the ecological dominance of domestic megaherbivores in grazing systems[5−7]. On the other hand, anthropogenic nutrient enrichment driven by synthetic fertilizer application and atmospheric deposition has substantially modified bottom-up controls on plant productivity through increased nitrogen (N) and phosphorus (P) availability[8−9]. Grassland ecosystems epitomize these anthropogenic transformations, serving as the primary interface between global food production systems and natural biomes[10]. Remarkably, these vulnerable ecosystems sustain approximately 30% of humanity's appropriation of terrestrial net primary productivity[11]. Although numerous studies have documented both top-down and bottom-up regulation in grassland ecosystems, including analyses of their interactive effects (additive, antagonistic or synergistic) [12−14], critical knowledge gaps persist.

Specifically, the mechanistic understanding of how biodiversity, biomass allocation patterns, and ecosystem stability respond to concurrent changes in resource availability and grazing regimes in rangelands remains inadequately studied.

Anthropogenic N enrichment induces persistent alterations in both productivity patterns and biodiversity dynamics across rangeland ecosystems, fundamentally modifying their spatiotemporal stability regimes[15−16]. Community stability represents an ecosystem's ability to maintain consistent biomass production amidst environmental perturbations. It is commonly operationalized through the temporal invariability index, calculated as the ratio of mean productivity to standard deviation[17]. Empirical research consistently demonstrates that N-mediated enrichment destabilizes plant communities through biodiversity loss, with species richness reduction identified as the principal mechanistic pathway[18−19]. Nitrogen enrichment impacts species richness through four principal mechanistic pathways, including phytotoxic effects from reactive N compounds, pedogenic acidification altering soil biogeochemistry, stoichiometric disequilibrium in plant–soil nutrient relations, and competitive asymmetry favoring nitrophilous species[20−21]. In the high-altitude alpine meadows of the Qinghai–Xizang Plateau, where plant communities are highly sensitive to biogeochemical fluctuations, the soil acidification and its resulting competitive asymmetry are the most critical pathways driving biodiversity shifts. This destabilization process may result in progressive displacement of

N-sensitive taxa through niche competition, weakened compensatory population dynamics, and a subsequent decline in temporal stability across grassland biomes. These changes are driven by reduced species asynchrony, as nitrogen addition promotes the dominance of a few nitrophilous species while suppressing rare and N-sensitive counterparts. Furthermore, nitrogen enrichment synchronizes interannual population fluctuations, undermining the compensatory dynamics that normally stabilize community productivity[18, 22−23].

As the primary anthropogenic management measure in grassland ecosystems, herbivores exert profound regulatory control over biodiversity patterns, ecosystem processes, and resilience mechanisms[24−26]. Empirical investigations have yielded divergent perspectives on grazing-mediated stability dynamics, with documented cases of both enhanced stability to herbivore control[24] and aggravated instability[25−26]. This discrepancy arises because grazing influences species diversity and the abundance of dominant species in a manner dependent on stocking rate. At low to moderate stocking rates, grazing often enhances diversity by alleviating competitive exclusion, thereby promoting species asynchrony and increasing stability. Conversely, high stocking rates tend to reduce diversity through the selective removal of palatable species and can synchronize population fluctuations, ultimately leading to destabilization[27−28]. The inconsistent reactions of species diversity could drive the divergence in the impacts of grazing on the stability of the community in grasslands. Furthermore, contemporary research has

systematically examined shifts in the relative abundance of species and community assembly dynamics, underscoring the pivotal role of compositional stability within plant communities in regulating grassland ecosystem functional resilience[22, 29]. However, to date, the extent to which species richness, species asynchrony, and community compositional stability contribute to ecosystem function stabilization in grazing systems remains unclear.

Based on livestock dietary preferences, native herbage can be classified into two functional groups, i.e., functional native herbage (FNH) and the traditional herbage (TH) [30−32]. Here, TH refers to palatable native forage species that are preferentially selected and readily consumed by livestock under grazing conditions, whereas FNH includes native species that are relatively unpalatable during the growing season or throughout the year because of secondary metabolites, structural defenses, or other anti-herbivory traits[33]. As a result, FNH is often consumed only incidentally, seasonally, or under specific physiological or management conditions, and some species may become more acceptable after processing such as hay-making or silage[30−32].

Globally, approximately 3,000 FNH species, accounting for 16.8%–26.8% of grassland flora, provide critical functions such as pest regulation, pollinator support, and soil microbiome stabilization[32, 34]. The widely distributed FNH in China includes most species of *Aconitum* spp., *Astragalus* spp., *Gentiana* spp., *Ligularia* spp., *Oxytropis* spp., *Pedicularis* spp., *Stellera*

spp., etc[30−31]. The proportion of FNH in degraded grasslands worldwide and China has increased by 27%–60%, therefore some FNH species are often used as indicator species for grassland degradation[33]. Certain FNH species, such as *Oxytropis ochrocephala* and *Stellera chamaejasme*, can even ameliorate soil properties through biological nitrogen fixation[35]. Moreover, the biomass proportion of FNH in alpine meadows has been shown to have an ecological threshold (37%) for maintaining ecosystem functions and sheep production[33]. These species are not only important components of plant community structure but also play a key role in regulating ecosystem processes, including species coexistence, nutrient cycling, and belowground functional stability.

Although FNH is generally less preferred than TH by livestock, it may still be consumed under grazing and thus can influence both plant community dynamics and ecosystem functioning[30−32]. Previous studies have shown that appropriate FNH utilization can benefit livestock performance, but the ecological consequences of grazing on FNH remain poorly understood[30−32, 26]. In particular, it is still unclear how grazing and N enrichment interact to regulate FNH-mediated community stability and the associated ecological responses.

Alpine grasslands, occupying over two-thirds of the Qinghai–Xizang Plateau (QXP) and sustaining more than 40 million grazing animals, are highly vulnerable to global changes[37]. Current ecological challenges emerge from synergistic pressures of the intensified anthropogenic interventions,

particularly grazing management, fencing systems, and fertilization regimes, which may be coupled with climate-driven alterations such as the atmospheric N deposition[38−39]. Such compounded stressors have exacerbated the deterioration of grasslands on the QXP. The FNH demonstrates remarkable ecological significance in QXP's alpine meadow ecosystems, with species diversity exceeding one-third of total flora and biomass proportions ranging from 7.3% to 15.7% across various grassland types[33]. Notably, FNH in certain grassland communities contributes over 50% of biomass and represents approximately 15% of grazing livestock dietary intake by mass, serving as a fundamental component in maintaining ecosystem structure and functionality[33]. Existing literature indicates that grazing reduces TH abundance but maintains a higher FNH species richness, thus increasing the temporal stability of plant communities by increasing FNH species stability[24]. However, a sustained low-level N addition has no impact on plant community composition, and a high-level N addition can decrease the community stability by decreasing FNH species richness, TH dominance and species asynchrony [15, 23]. Meanwhile, earlier findings have revealed that herbivores effectively offset N deposition impacts on floral diversity while mitigating nitrous oxide fluxes[40-41]. However, the differing results may be due to the lack of evidence from experiments with varying stocking rates and nitrogen addition gradients to clarify the threshold for different mechanism transitions.

To address this knowledge gap regarding how grazing and N addition

modulate FNH species-mediated community stability and whether there exists an ecological threshold of FNH/TH biomass ratio for community stability, we conducted a 3-year field experiment in an alpine meadow of the QXP under four levels of N addition (0, 5, 10, and 20 g N m^{-2} yr^{-1}) and three stocking rates (0, 8, and 16 sheep ha^{-1}) to test the following hypotheses. We tested two hypotheses. In Hypothesis 1 (H1), grazing and N addition regulate community stability primarily through their effects on FNH species diversity and the FNH/TH biomass ratio, with an ecological threshold of this ratio for maintaining stability (Figure 1a–d). Specifically, we propose that: (1) the diversity of FNH species, rather than TH species, is the dominant driver of community stability under grazing and N addition (H1a, Figure 1a); (2) stocking rate and N addition have nonlinear, threshold-dependent effects on FNH diversity, i.e., moderate grazing increases FNH diversity, but overgrazing reduces it, and low N addition reduces FNH diversity, but high N addition may increase it due to intensified competition (H1b, Figure 1b); (3) grazing exerts a stronger effect on ecosystem stability than N addition, with synergistic or antagonistic interactions depending on the intensity of both factors (H1c, Figure 1c); and (4) there is an ecological threshold of the FNH/TH biomass ratio for community stability (H1d, Figure 1d). In Hypothesis 2 (H2), grazing enhances community stability by promoting FNH diversity, which generates an insurance effect (i.e., compensatory dynamics that stabilize community productivity against environmental fluctuations). This insurance effect offsets compositional instability (i.e., species turnover

or reordering) and elevates overall community stability. In contrast, nitrogen deposition suppresses these stabilizing mechanisms by reducing FNH diversity and species asynchrony (Figure 1a).

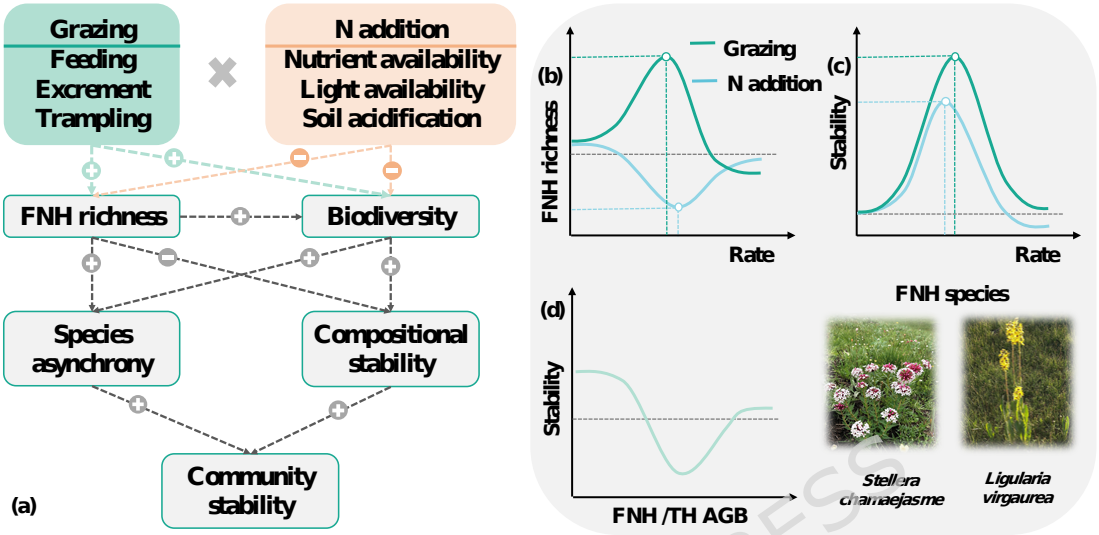

Fig. 1 Conceptual framework showing how grazing and nitrogen addition may regulate community stability in an alpine meadow through FNH-mediated pathways: (a) grazing and nitrogen addition are hypothesized to influence community stability primarily by altering FNH richness, biodiversity, species asynchrony, and compositional stability; (b) grazing and nitrogen addition may exert nonlinear effects on FNH richness, with moderate grazing increasing FNH richness and excessive grazing reducing it; nitrogen addition may alter FNH richness through changes in resource availability and interspecific competition; (c) grazing may have a stronger effect than nitrogen addition on ecosystem stability, and the two factors may interact synergistically or antagonistically depending on their intensity; and (d) community stability may respond nonlinearly to the biomass ratio of FNH

to TH, indicating an ecological threshold. Representative FNH species are shown as examples.

2. Materials and methods

2.1. Study site

Our field experiment was conducted on the northeastern Qinghai–Xizang Plateau, Maqu County, Gansu Province, China (33°36′ N – 33◦43’ N, 101°44′ N 101°48′ E; 3520 m a.s.l.; Figure 2a). The Maqu Pratacultural Research Station of Lanzhou University has been used for the rotational grazing experiments involving Tibetan sheep and yaks in the area since 2010. The area has a typical continental plateau climate[33], characterized by 1.2 °C mean temperature, 620 mm annual precipitation and 2.2 m s^{-1} average wind velocity (Figures 2c and S1)[42]. The alpine meadow vegetation is primarily composed of perennial herbs from genera such as *Agrostis*, *Anemone*, *Carex*, *Elymus*, *Poa*, *Saussurea*, and *Stipa*.

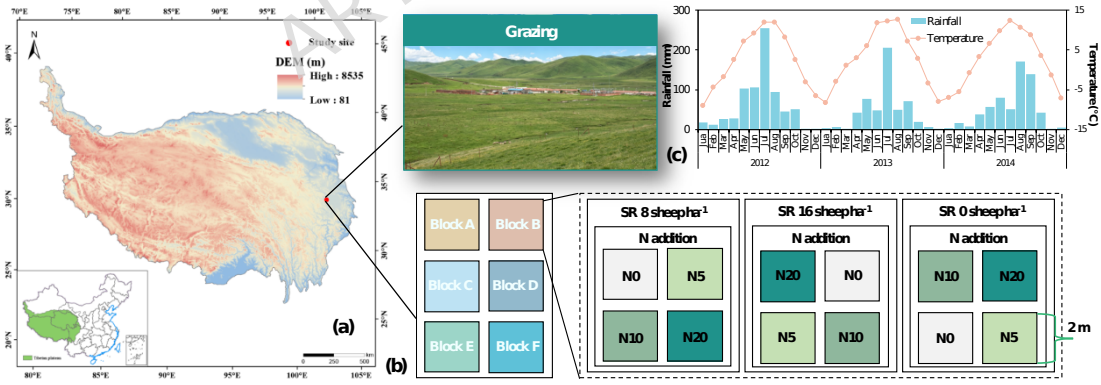

Fig. 2 Study area and experimental design: (a) geographic position of the study region; (b) schematic diagram of the randomized complete block split-plot design, including six blocks (Block A–F) established for the grazing

experiment, grazing treatments consisting of three levels of grazing at 16 sheep ha^{-1} (SR16), grazing at 8 sheep ha^{-1} (SR8), and ungrazed control (SR0), and four nitrogen addition levels [i.e., 0, 5, 10, and 20 g N m^{-2} yr^{-1} (N0, N5, N10, and N20)] assigned randomly within each block; and (c) monthly total rainfall and monthly mean temperature from 2012 to 2014.

2.2 Experimental design, sampling and measurements

The experiment was established in 2010 in an alpine meadow on the QXP. A split-plot design was employed, with stocking rate as the main plot factor and N addition rate as the subplot factor (Figure 2b). Three stocking rates were applied: no grazing (0 sheep ha^{-1}), moderate grazing (8 sheep ha^{-1}), and high grazing (16 sheep ha^{-1}). The grazing treatments were implemented in 12 paddocks established in 2010. Specifically, six paddocks (1 ha each) were assigned to 8 sheep ha^{-1}, and six paddocks (0.5 ha each) were assigned to 16 sheep ha^{-1}. In each of these 12 paddocks, a grazing exclosure (10 m × 10 m) was established as the no-grazing control (0 sheep ha^{-1}), resulting in 12 control plots. To balance the design for the N addition sub-experiment, we randomly selected three replicate paddocks from each grazing intensity (0, 8, and 16 sheep ha^{-1}). Thus, there were nine main plots (3 grazing levels × 3 replicates) for the experiment.

Within each of the nine selected main plots (each 10 m × 10 m exclosure for the 0-grazing treatment, or the entire paddock for the 8 and 16 grazing treatments), we established four 2 m × 2 m subplots spaced 0.5 m apart. The subplots were randomly assigned to four N addition levels: 0, 5, 10, and 20 g

N m^{-2} yr^{-1}. Ammonium nitrate (NH_4NO_3) dissolved in water (equivalent to 1 mm of precipitation) was applied annually in two equal splits in June and July from 2012 to 2014.

The rotational grazing regime was applied during the growing season (June–September). Each paddock was grazed for 10 days followed by a recovery period, with three grazing cycles per season. Tibetan wethers (18 months old, mean body weight 33 kg at the start) were used.

In each growing season, we randomly established a quadrat (0.5 m × 0.5 m, 0.25 m^2) in each experimental plot. The aboveground biomass (AGB) and litter biomass within the quadrat were harvested at the peak of the growing season, in August, and all collected biomass samples were sorted to species. Individual AGB was determined after washing and oven-drying at 65 °C for 72 h.

Based on livestock grazing preferences, the collected species were classified into two functional groups, FNH and TH. Following the criteria established in previous studies[30−33], TH species (mainly *Cyperaceae* and *Poaceae*) are preferentially grazed by livestock, whereas FNH species (mainly *Asteraceae*, *Fabaceae*, *Gentianaceae*, *Liliaceae*, *Ranunculaceae*, and *Scrophulariaceae*) are less palatable due to secondary metabolites but play critical ecological roles. A complete list of all species with their functional group assignments, families, photosynthetic pathways (all C3), life histories (perennial, annual, or biennial), and whether they are legumes is provided in Table S1. In summary, among the 102 recorded species, FNH comprises 68

species (including 12 legumes) and TH comprises 34 species; the vast majority are C3 perennials, with a small number of annuals/biennials (e.g., *Swertia bimaculata*, *Pedicularis* spp.). These classifications are used in all subsequent analyses of species richness, biomass, and stability. Although palatability can vary with season, livestock species, and pasture availability, the FNH/TH classification used here was based on consistent multi-year observations and literature and remained stable across all treatment-by-year combinations (Table S1).

In addition to AGB, a consistent sampling of belowground biomass (BGB) was also performed from 2012 to 2014. In early May of each year, two cylindrical holes, each 40 cm depth, were excavated in every plot using a stainless-steel coring device (inner diameter 10 cm). The extracted soil cores were segmented into four layers at a 10-cm interval. After sieving the soil through a No. 10 standard sieve (2 mm aperture) to exclude root material, the soil was refilled into the same holes, preserving the original stratification of the soil profile. In late August, roots were collected from the 0–5, 5–10, 10–20, and 20–30 cm layers at the center of the previously excavated holes by using a 7-cm-diameter soil core sampler. The harvested roots were then oven-dried at 70°C until constant weight to determine the BGB. We also measured soil pH (glass electrode pH meter) at 0–5 cm.

2.3. Diversity, asynchrony and stability evaluation

Species richness was quantified as the cumulative number of plant species recorded in each standardized 0.25 m^2 quadrat across the three sampling

years (2012–2014). Plant species were classified into FNH and TH.

To quantify temporal compensatory dynamics, we calculated four asynchrony indices by following Loreau and de Mazancourt (2013)[17]: (i) species asynchrony calculated using all species in the community, (ii) FNH–TH asynchrony calculated by treating FNH and TH as two functional-group components, (iii) FNH asynchrony calculated using all FNH species, and (iv) TH asynchrony calculated using all TH species. For each index, asynchrony was calculated as:

$$1 - \varphi = 1 - \frac{\sigma^2}{\left(\sum_{i=1}^{S} \sigma_i\right)^2}$$

where σ^2 is the variance of total biomass across years at a given subplot, σ_i is the standard (SD) deviation of biomass of component (i) across years, and S is the number of components included in the calculation (species or functional groups, depending on the index).

The biomass ratio of FNH toTH (FNH AGB / TH AGB) was calculated as FNH biomass divided by TH biomass.

Temporal stability of community AGB, FNH AGB, TH AGB, BGB, and total biomass (TB = AGB + BGB) was calculated as the ratio of the three-year temporal mean to the three-year standard deviation for each subplot following Hautier et al. (2015)[18]. Thus, for temporal stability, the unit of time was year, and (n = 3) for each subplot (2012, 2013, and 2014).

$$\text{Temporal stability} = \frac{\mu_X}{\sigma_X}$$

where μ_X is the temporal mean of X across the three years (2012–2014), and

σ_X is the temporal standard deviation of X across the same three years. Thus, for each subplot, n = 3 annual measurements were used to estimate stability.

To quantify temporal stability of plant composition[22], we calculated Bray–Curtis dissimilarity among the three annual community compositions within each subplot and converted it to a stability index as:

$$\text{Composition stability} = 1 - \overline{d}$$

where $\overline{d}$ is the mean pairwise Bray–Curtis dissimilarity across the three years for each subplot.

A complete summary of all indices, their formulas, variable definitions, and the number of temporal replicates (n=3 years) is provided in Table S2.

2.4. Statistical analysis

Prior to analysis, all data were evaluated for normality using the Shapiro–Wilk test and for homogeneity of variance using Levene's test. All statistical analyses were performed using R version 4.3.3 (R Development Core Team 2023). To account for the split-plot design (stocking rate as the main-plot factor, N addition as the subplot factor, with three replicate blocks), we fitted linear mixed-effects models (LMMs) using the lmer function from the lme4 package. For response variables measured annually (e.g., species richness, and biomass), the model included stocking rate, nitrogen addition, year, and their interactions as fixed effects, and block and main plot (paddock) as random intercepts to account for the hierarchical structure. For response variables that were not measured annually, the model included stocking rate and nitrogen addition as fixed effects, with block and main plot as random

intercepts, but without the year term. Denominator degrees of freedom were approximated using the Satterthwaite approximation method implemented in the lmerTest package. Post-hoc pairwise comparisons were conducted using Tukey's HSD test via the emmeans package. Results of these models are presented in Tables 1 and S3, and visualizations in Figures 3–7. To quantify the relative importance of each predictor (SR, NA, and their interaction) in explaining variation in plant attributes, we applied hierarchical partitioning using the glmm.hp package[43−44]. This method operates on the LMM objects described above and provides unbiased estimates of individual predictor contributions.

To investigate the relationships between soil and plant attributes and their temporal stability, we first addressed the temporal scale mismatch between annually measured variables (e.g., species richness, FNH richness, and TH richness) and single-valued stability metrics. For each experimental subplot, we calculated the temporal mean of each annually measured variable across the three-year study period (2012–2014) to represent the average condition over the same period used to compute stability and asynchrony metrics. This ensured that all variables in subsequent analyses were referenced to the identical three-year window, with each subplot contributing exactly one data point per variable.

We then performed Spearman rank correlations between soil pH (Figure S1), these temporal means and the stability metrics (community AGB stability, species asynchrony, compositional stability) across all subplots using the

"linkET" package in R. All p-values were corrected for multiple testing using the Benjamini–Hochberg false discovery rate (FDR) procedure (Benjamini & Hochberg, 1995), with correlations having FDR-adjusted $q < 0.05$ considered statistically significant (Figure 9).

To further characterize these relationships, we fitted linear and nonlinear regression models using the base R stats package (lm and nls functions) for each scatterplot involving diversity, biomass, asynchrony, and stability. Model selection was based on Akaike information criterion (AIC), R^2, and P values (Figure 10a–i). Additionally, we employed a segmented regression model to examine the relationship between the ACB ratio of FNH to TH species and community AGB temporal stability, identifying the ecological threshold using the "chngpt" package (Figure 10j).

We developed a structural equation model (SEM) to assess the direct and indirect pathways through which grazing and N addition affect community AGB temporal stability using the lavaan package (Figure 11). Model fit was evaluated using the following indices: AIC, Chi-square (χ^2), *P*, R^2, tucker–lewis index (TLI), comparative fit index (CFI) and root mean square error of approximation (RMSEA). Additionally, the standardized effects of treatment-induced variations in ecosystem stability were evaluated. For SEM analysis, data for soil pH, temporal stability of the community AGB, FNH and TH, and FNH richness underwent natural logarithm transformation prior to analysis. The model structure was specified a priori based on our conceptual framework (Figure 1) and hypotheses (H1–H2). This was a priori model

including paths from SR and N to soil pH, FNH richness, species asynchrony, and subsequently to community stability, as well as indirect pathways via FNH asynchrony and compositional stability. We also considered an alternative full model (Figure S2a). However, this full model produced inadmissible estimates after removing non-significant pathways (standardized regression coefficients with absolute values > 1, TLI > 1, CFI = 1), indicating severe multicollinearity or overfitting given our sample size (Figure S2b). Because the full model violates fundamental SEM assumptions, it was discarded and not considered further. We acknowledge that the statistical failure of the full model including TH variables does not necessarily imply that TH species are ecologically unimportant. The inadmissible estimates may have arisen from multicollinearity, overfitting, or the limited sample size relative to model complexity, rather than from a true absence of TH effects. Therefore, the exclusion of TH variables from the final SEM should not be interpreted as evidence that TH plays no role in community stability; TH may still contribute through correlated or indirect pathways not captured by the present model.

Given the brevity of the time series, we estimated the uncertainty associated with stability metrics via bootstrapping. For each subplot, we resampled the three annual biomass values with replacement (n = 1000 iterations) and recalculated the mean/SD stability for each bootstrap sample. The 2.5th and 97.5th percentiles of the bootstrap distribution were used as the 95% confidence interval for each stability estimate. This approach

provides a quantitative assessment of the uncertainty inherent in deriving stability metrics from short time series. We then re-ran the segmented regression for the FNH/TH threshold and the final SEM to evaluate the robustness of our main inferential framework against interannual anomalies (Table S4).

3. Results

3.1. Grazing and N addition effects on plant diversity

We detected a significant effect of N addition rate on plant species richness (Table 1). Specifically, increasing N addition rate significantly decreased plant species richness in 2014 ($P < 0.05$; Figure 3c). The year effect on plant species richness was significant ($P < 0.05$). Plant community diversity varied substantially across years, with temporal effects explaining the greatest variation (41.28%) (Figure 8a). Overall, plant species richness decreased over time. N addition and grazing had significant impacts on FNH richness (Table 1). Increasing N addition rate significantly decreased FNH richness in 2014 ($P < 0.05$; Figure 3f). Interestingly, increasing the stocking rate significantly increased FNH richness in 2013 ($P < 0.05$). However, it is important to contextualize this finding that this was a transient, short-term response observed only in one year of the experiment, and was primarily driven by the 16 sheep ha^{-1} treatment rather than a consistent linear effect across all grazing intensities. FNH richness varied substantially across years, with temporal effects explaining the greatest variation (30.09%) (Figure 8a). FNH richness decreased over time. Year played the main role in regulating

the change in TH richness (67.03%) (Table 1; Figure 8a), and TH richness decreased over time.

Table 1 Effects of year (Y), stocking rate (SR), nitrogen addition rate (NA), and their interactions on plant species diversity and biomass indices based on linear mixed-effects models that account for the split-plot design (block and main plot as nested random intercepts). AGB, aboveground biomass; BGB, belowground biomass; TB, total biomass; FNH, Functional native herbage; and TH, Traditional native herbage

	df	DenDF	Species richness		FNH richness		TH richness		Community AGB		FNH AGB		TH AGB		FNH AGB/TH AGB		BGB		TB	
			F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
SR	2	4	2.57	0.084	3.55	0.034	1.18	0.314	7.65	< 0.001	4.52	0.014	23.2	< 0.001	7.05	0.002	4.13	0.020	9.9	< 0.001
NA	2	12	6.76	< 0.001	7.85	< 0.001	0.307	0.821	0.766	0.520	1.29	0.283	2.67	0.054	1.22	0.309	1.33	0.273	0.9188	0.437
Y	2	24	28.1	< 0.001	17.7	< 0.001	25.1	< 0.001	25.6	< 0.001	32.1	< 0.001	5.46	0.006	3.8	0.027	6.77	0.002	4.73	0.012
SR ×Y	4	8	1.16	0.335	1.4	0.243	0.613	0.655	3.66	0.010	2.11	0.089	1.61	0.180	0.417	0.796	6.12	< 0.001	7.12	< 0.001
NA ×Y	6	24	1.33	0.254	1.69	0.137	0.2966	0.937	0.285	0.944	0.8009	0.566	0.5288	0.785	1.644	0.150	0.6444	0.6958	0.7133	0.640
SR ×NA	6	12	0.378	0.891	0.2449	0.958	0.8112	0.564	2.35	0.041	1.58	0.166	3.12	0.009	1.01	0.423	3.1667	0.008	4.47	< 0.001
SR ×NA×Y	12	24	0.664	0.780	0.654	0.789	0.817	0.632	0.647	0.800	1.25	0.269	0.597	0.8383	0.932	0.520	3.32	< 0.001	3.45	< 0.001

Denominator degrees of freedom (DenDF) vary among fixed effects because of the split-plot structure and the Satterthwaite approximation.

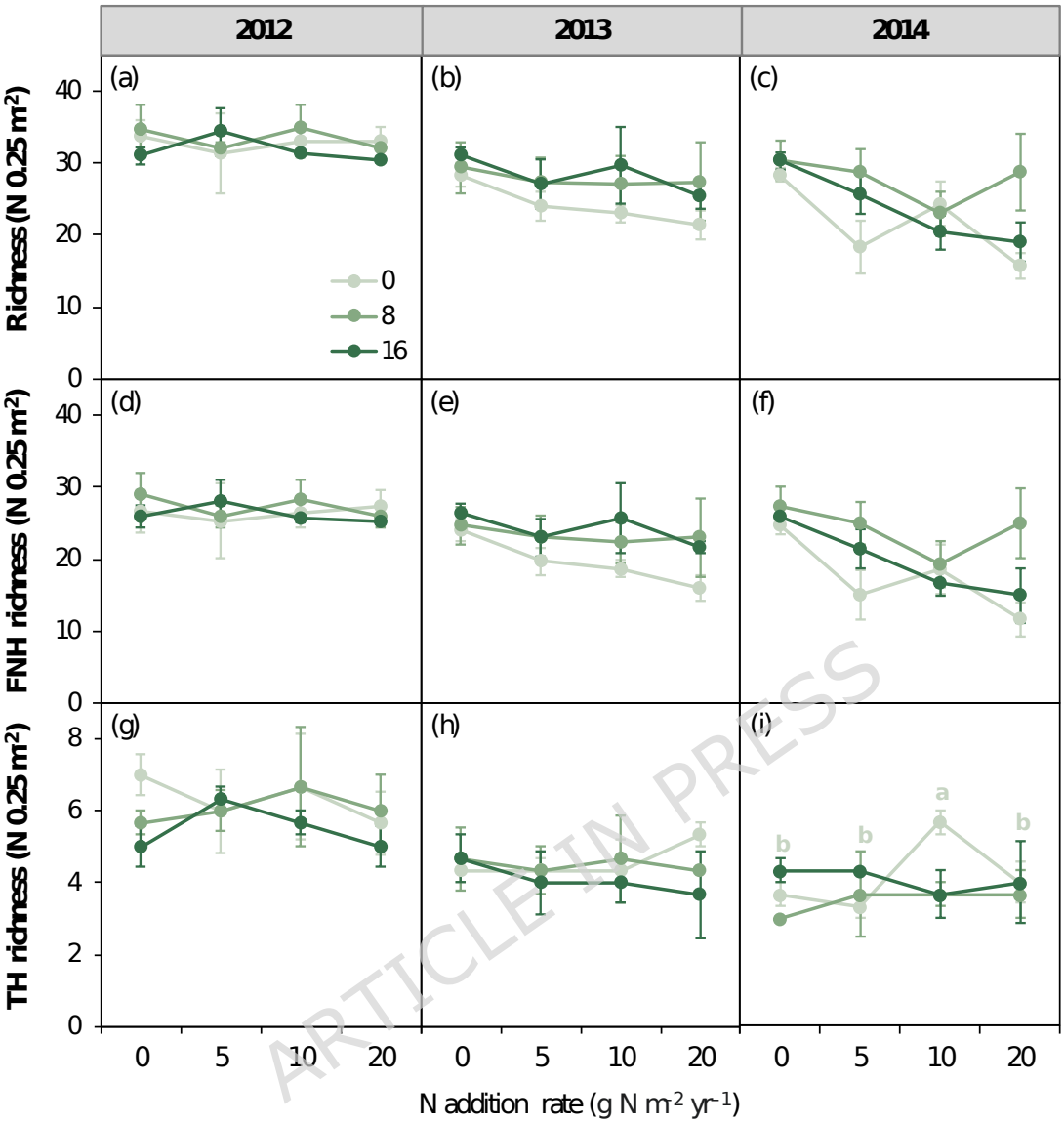

Fig. 3 Effects of stocking rate (SR), N addition rate (NA) and their interaction (SR×NA) on plant species richness (a–c), functional native herbage (FNH) richness (d–f) and traditional herbage (TH) richness (g–i) in different years. Stocking rates (SR): 0 sheep ha^{-1}, 8 sheep ha^{-1}, and 16 sheep ha^{-1}. Nitrogen addition rates (NA): 0 g N m^{-2} yr^{-1}, 5 g N m^{-2} yr^{-1}, 10 g N m^{-2} yr^{-1}, and 20 g N m^{-2} yr^{-1}. For a given stocking rate, different N addition rates with the same letter are not significantly different (Tukey's HSD test: $P < 0.05$).

3.2. Grazing and N addition effects on plant biomass

Increasing stocking rate decreased community AGB and TH AGB each year (Table 1; Figure 4a–4c). We detected significant effects of N addition rate and its interaction with stocking rate on BGB (Table 1; Figure 4d–f). Increasing stocking rate decreased the TB in 2013 and throughout three years (Figure 4g). Grazing explained the largest proportion of variance of BGB (20.90%) and TB (25.57%) (Figure 8a).

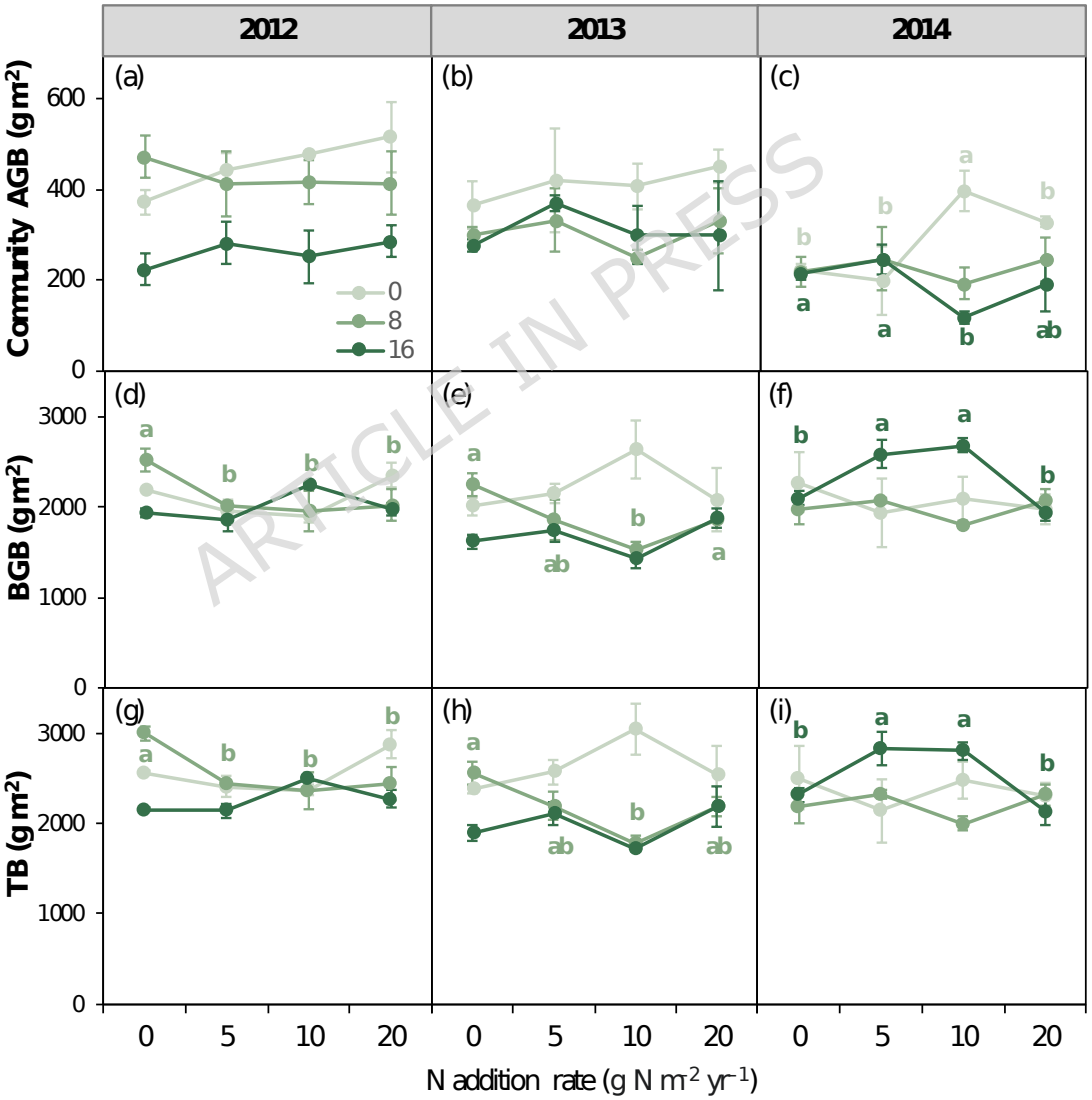

Fig. 4 Effects of stocking rate (SR), N addition rate (NA) and their interaction

(SR×NA) on aboveground biomass (AGB) of community (a–c), belowground biomass (BGB) (d–f) and total biomass (TB) (g–i) in different years. Stocking rates (SR): 0 sheep ha^{-1}, 8 sheep ha^{-1}, and 16 sheep ha^{-1}. Nitrogen addition rates (NA): 0 g N m^{-2} yr^{-1}, 5 g N m^{-2} yr^{-1}, 10 g N m^{-2} yr^{-1}, and 20 g N m^{-2} yr^{-1}. For a given stocking rate, different N addition rates with the same letter are not significantly different (Tukey's HSD test: $P < 0.05$).

In 2012, at a stocking rate of 8 sheep ha^{-1}, FNH AGB increased, but higher N addition rates reduced it under the same stocking rate (Figure 5a). Specifically, increasing N addition rate only increased the mean value of TH species AGB in no-grazed plot (Figure 5e–f). Overall, community AGB, FNH AGB, and TH AGB decreased over time. The FNH AGB / TH AGB ratio was higher at a stocking rate of 8 sheep ha^{-1} (Table 1; Figure 5g–i).

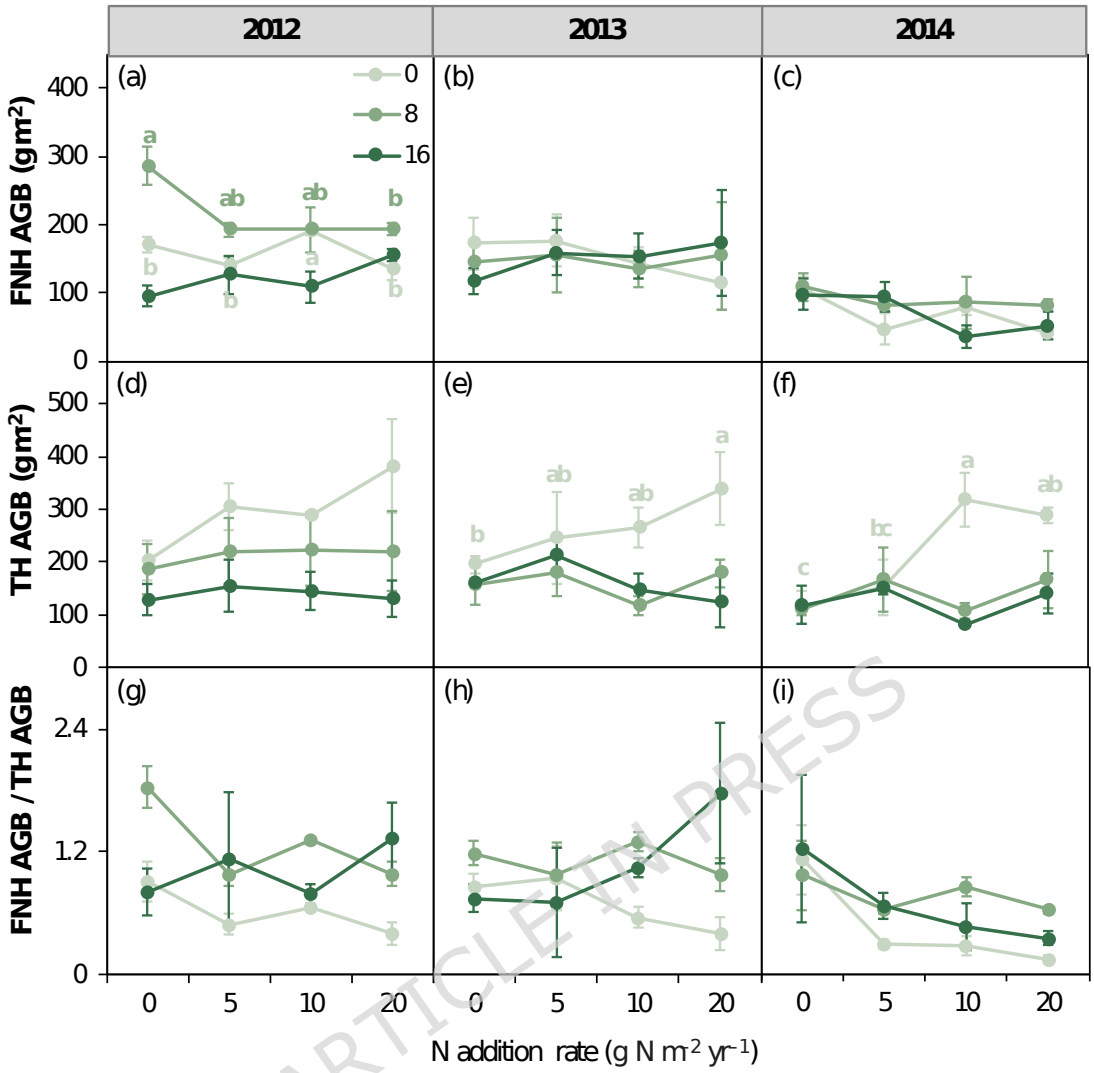

Fig. 5 Effects of stocking rate (SR), N addition rate (NA) and their interaction (SR×NA) on the aboveground biomass (AGB) of functional native herbage (FNH) (a–c), aboveground biomass (AGB) of traditional herbage (TH) (d–f), and aboveground biomass (AGB) of functional native herbage (FNH) to aboveground biomass (AGB) of traditional herbage (TH) ratio (g–i) in different years. Stocking rates (SR): 0 sheep ha^{-1}, 8 sheep ha^{-1}, and 16 sheep ha^{-1}. Nitrogen addition rates (NA): 0 g N m^{-2} yr^{-1}, 5 g N m^{-2} yr^{-1}, 10 g N m^{-2} yr^{-1}, and 20 g N m^{-2} yr^{-1}. For a given stocking rate, different N addition rates with

the same letter are not significantly different (Tukey's HSD test: $P < 0.05$).

3.3. Grazing and N addition effects on plant asynchrony and stability

No statistically significant main effects of grazing, N addition, year, or their interactions were detected on the temporal stability of community AGB, BGB, TB, FNH, TH, or on species asynchrony, FNH asynchrony, TH asynchrony, or FNH-TH asynchrony (Table S3; Figures 6 and 7). Grazing accounted for the highest proportion of variance in FNH temporal stability and asynchrony, while N addition explained the largest proportion of variance in compositional temporal stability and TB temporal stability (Figure 8b). The combined effects of grazing and N addition explained the greatest variation in community AGB temporal stability, species asynchrony, and TH asynchrony (Figure 8b).

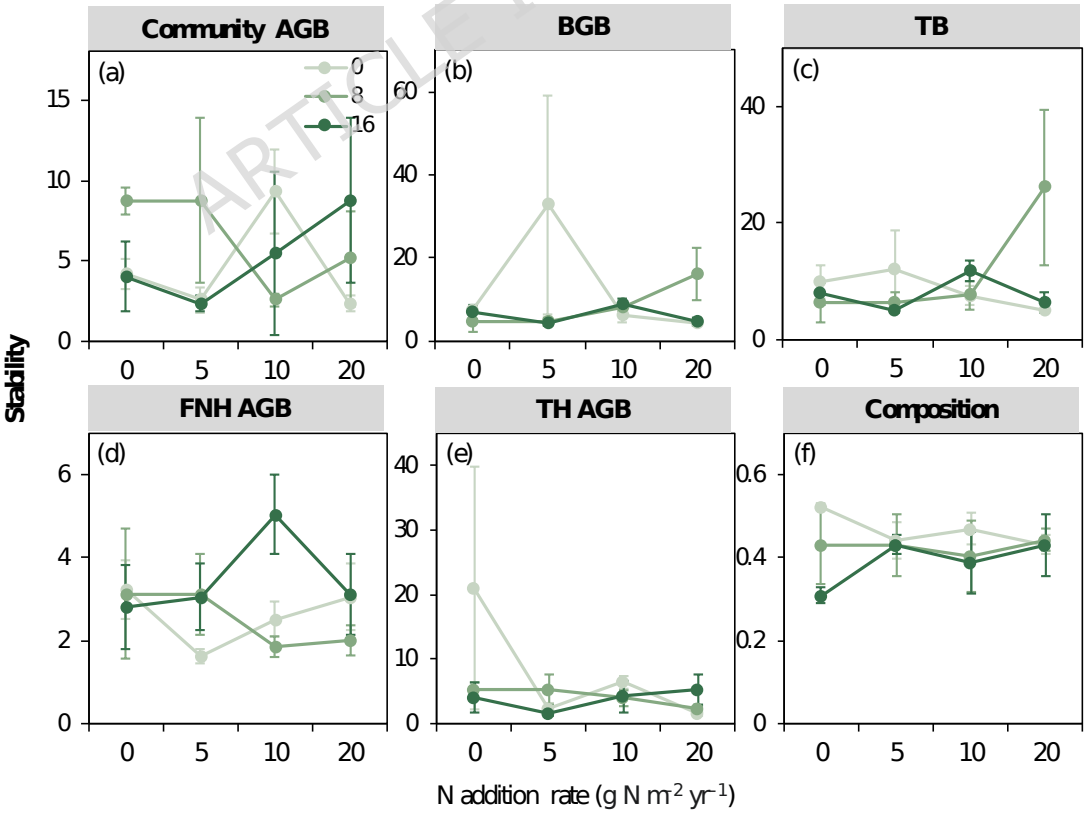

Fig. 6 Effects of stocking rate (SR), N addition rate (NA), and their interaction (SR×NA) on temporal stability of aboveground biomass (AGB) (a), belowground biomass (BGB) (b), total biomass (TB) (c), functional native herbage (FNH) AGB (d), traditional herbage (TH) AGB (e), and composition (f) in different years. Stocking rates (SR): 0 sheep ha^{-1}, 8 sheep ha^{-1}, and 16 sheep ha^{-1}. Nitrogen addition rates (NA): 0 g N m^{-2} yr^{-1}, 5 g N m^{-2} yr^{-1}, 10 g N m^{-2} yr^{-1}, and 20 g N m^{-2} yr^{-1}.

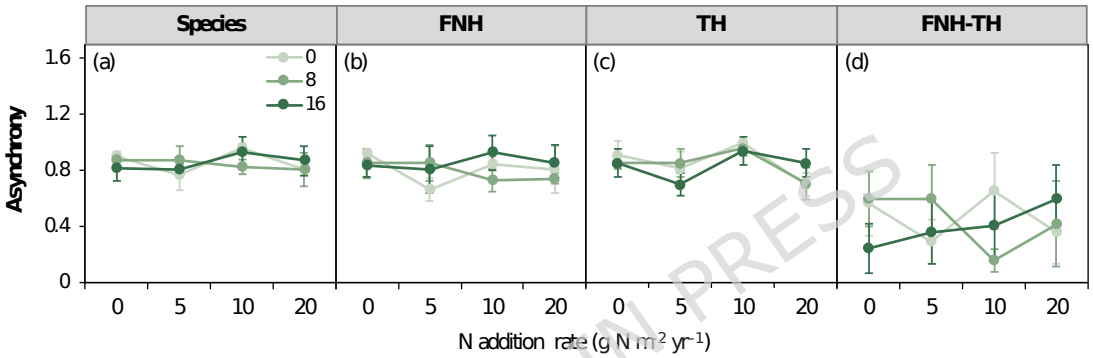

Fig. 7 Effects of stocking rate (SR), N addition rate (NA), and their interaction (SR×NA) on asynchrony of species (a), FNH (b), TH (c), and FNH–TH (d). Stocking rates (SR): 0 sheep ha^{-1}, 8 sheep ha^{-1}, and 16 sheep ha^{-1}. Nitrogen addition rates (NA): 0 g N m^{-2} yr^{-1}, 5 g N m^{-2} yr^{-1}, 10 g N m^{-2} yr^{-1}, and 20 g N m^{-2} yr^{-1}.

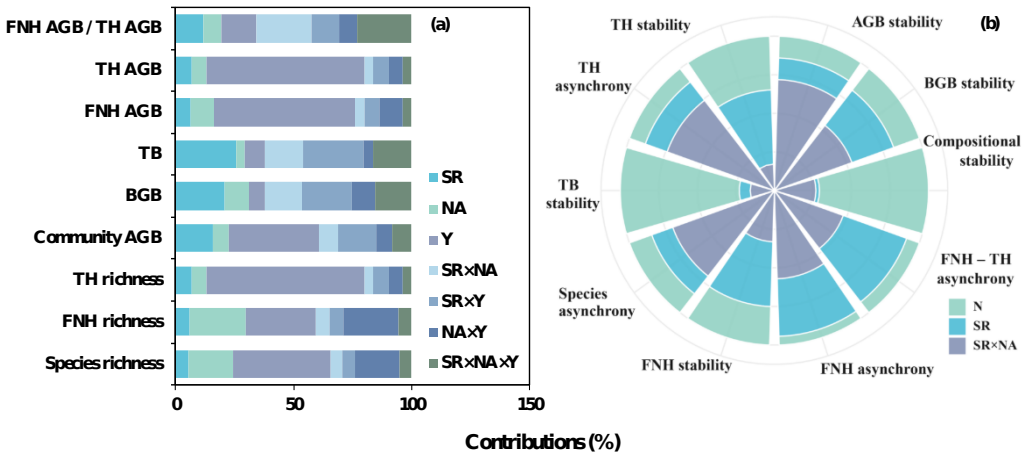

Fig. 8 Relative importance of stocking rate (SR), N addition rate (NA), and their interaction (SR×NA) explaining the variation of plant diversity and biomass (a), and temporal stability and asynchrony (b) based on the hierarchical partitioning analysis.

3.4. Diversity–asynchrony–stability relationships under grazing and N addition

Temporal stability of community AGB exhibited strong positive correlations with species richness and asynchrony, FNH richness, asynchrony and temporal stability, TH asynchrony and temporal stability, and FNH–TH asynchrony (Figures 9, 10a–10b, and 10d–10i). The relationship between BGB temporal stability and TB temporal stability was positive (Figure 9). As the species richness or FNH richness increased, compositional temporal stability, FNH species temporal stability, and asynchrony significantly increased (Figure 9). Compositional temporal stability showed strong positive associations with FNH species temporal stability. FNH asynchrony was closely linked to species asynchrony and positively correlated with FNH

temporal stability. FNH–TH asynchrony had significantly positive correlations with compositional temporal stability and species asynchrony. We identified an ecological threshold at an FNH/TH biomass ratio of 0.86 (95% bootstrap CI: 0.72–0.98, based on 1,000 resamples) in the response of community AGB temporal stability (Figure 10j). Among 36 data points, 22 fell below the threshold (ratio < 0.86) and 14 fell above (ratio ≥ 0.86).

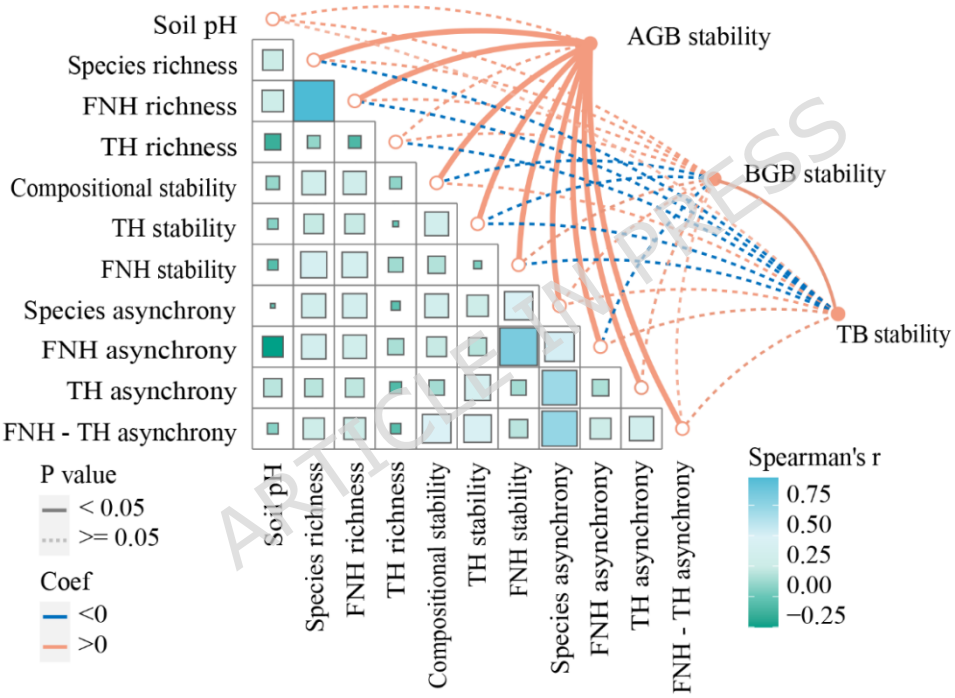

Fig. 9 Heatmap of correlation between soil pH, diversity, asynchrony and stability. AGB, aboveground biomass; BGB, belowground biomass; TB, total biomass; FNH, functional native herbage; and TH, traditional native herbage. Only correlations with FDR-adjusted q < 0.05 are shown. Blue indicates positive correlation, red indicates negative correlation.

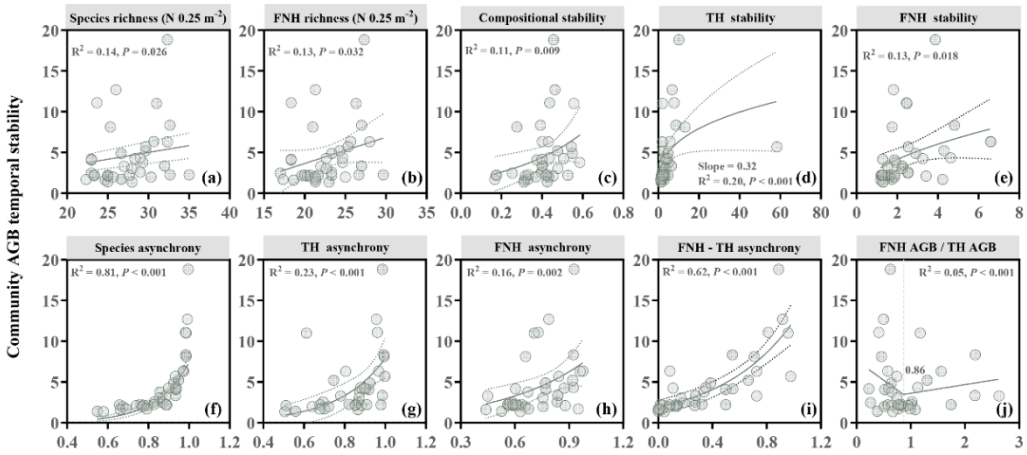

Fig. 10 Aboveground biomass (AGB) temporal stability in relation to species richness (a), functional native herbage (FNH) richness (b), compositional temporal stability (c), aboveground biomass (AGB) of traditional herbage (TH) temporal stability (d), aboveground biomass (AGB) of functional native herbage (FNH) temporal stability (e), species asynchrony (f), traditional herbage (TH) asynchrony (g), functional native herbage (FNH) asynchrony (h), functional native herbage (FNH)–traditional herbage (TH) asynchrony (i), and aboveground biomass (AGB) of functional native herbage (FNH) species to traditional herbage (TH) species ratio (j).

3.5. Pathways through which grazing and N addition affected community stability

The SEM revealed a potential positive total effect of grazing on community AGB temporal stability (standardized effect = 0.13), which was primarily mediated by increased FNH richness, compositional stability, FNH asynchrony, and species asynchrony (Figure 11a). However, this effect was associated with substantial uncertainty, as the bootstrap confidence interval overlapped zero.Although N addition drove an increase in species asynchrony,

the net effect of N addition on community AGB temporal stability was negative, as the destabilizing effects of reduced soil pH and FNH richness outweighed the positive contribution of enhanced species asynchrony. Furthermore, FNH richness, species asynchrony within FNH populations, and FNH–TH asynchrony were the primary mediating pathways through which community AGB temporal stability was maintained under grazing and N addition (Figure 11b). Community AGB stability improved with higher FNH richness (total effect size = 0.51, Figure 10b) through increases in compositional stability, FNH asynchrony, and species asynchrony (Figure 11a).

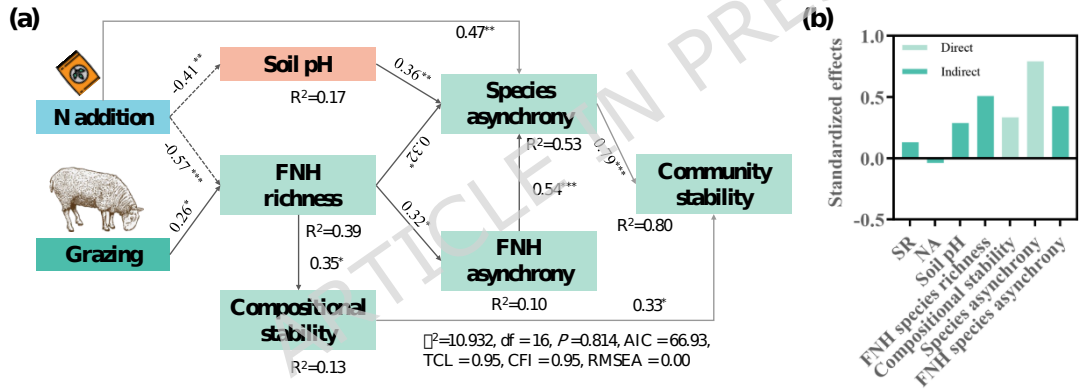

Fig. 11 Structural equation model (SEM) showing the direct and indirect effects of stocking rate and N addition on soil pH, diversity, and stability. Solid and dashed black arrows indicate the significant positive and negative pathways, respectively. Numbers at arrows are standardized path coefficients. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. The proportion of variance explained (R^2) appears alongside the response variable in the model. Standardized direct and indirect effects of stocking rate (grazing intensity)

on community AGB temporal stability derived from the structural equation model (SEM).

4. Discussion

Grassland plants are commonly classified by livestock palatability into traditional forage (TH) and functional native herbage (FNH). Our decision to utilize this palatability-based classification, rather than conventional functional traits (e.g., C3/C4 photosynthesis, growth form, or nitrogen fixation capacity), was motivated by the central role of selective herbivory in structuring grassland communities. Grassland plants have evolved various physical (e.g., spines, trichomes) and chemical (e.g., secondary metabolites, odors) defenses against herbivory, prompting livestock to instinctively avoid or limit the consumption of such species. This behavioral response creates a fundamental ecological dichotomy: species that are preferentially consumed TH experience direct biomass removal and competitive suppression, whereas those that are avoided FNH are relatively released from grazing pressure and can exert indirect effects on community dynamics through competition and facilitation. Compared with traditional functional classifications, which often fail to capture this differential vulnerability to herbivory, the FNH–TH framework directly links the primary grazing mechanism to the community response. Although FNH species are often less preferred due to secondary metabolites, they play critical ecological roles when maintained within appropriate thresholds[30−31,33]. For example, an appropriate FNH proportion (20%–50%) can enhance ecosystem multifunctionality in alpine meadows[33],

and certain FNH species improve soil properties[35]. In this study, we reveal that increasing stocking rate tended to increase, whereas increasing N addition decreased community AGB temporal stability, primarily through changes in FNH richness. The FNH/TH biomass ratio of 0.86 represented a critical threshold for maintaining grassland community stability.

4.1. Grazing tended to positively influence community AGB temporal stability, but this effect was associated with considerable uncertainty

Increased FNH diversity under grazing mainly resulted from selective foraging, that grazers prefer palatable TH species, releasing FNH from competition. This FNH richness-driven enhancement of community AGB temporal stability supports the biodiversity insurance effect[17, 25]. Higher species richness increases temporal stability through compensatory dynamics among species. Our SEM analysis confirms that grazing-mediated increases in FNH richness and asynchrony collectively drove community-level species asynchrony, aligning with studies showing that anthropogenic drivers affect stability via biodiversity pathways[18].

Our analyses also show that grazing enhanced compositional stability and reduced interannual species turnover, which further contributed to community AGB temporal stability. This result was consistent with the hypothesis that grazing increases insurance effects by promoting FNH diversity and compositional stability, thereby stabilizing community productivity.

The full model, including TH variables, was statistically inadmissible, which prevented us from directly comparing TH and FNH pathways. This failure may reflect collinearity or overfitting rather than a true lack of TH effects. Consequently, our finding that FNH dominates stability pathways should not be taken to exclude the possibility that TH species also contribute to stability via correlated or indirect mechanisms. Future studies with larger sample sizes and longer time series are needed to disentangle the relative contributions of FNH and TH.

4.2. N addition decreased community AGB temporal stability

N addition decreased community AGB temporal stability through multiple interconnected mechanisms, despite simultaneously enhancing species asynchrony. Substantial evidence indicates that N enrichment drives biodiversity loss and destabilizes community productivity[18, 22]. In our study, this instability was primarily mediated through the decline of FNH species richness, which diminished compensatory dynamics among plant populations[19]. Species asynchrony emerged as the dominant predictor of community stability across N addition gradients, supporting the biodiversity insurance hypothesis[17]. The decline of subordinate FNH species populations significantly modified community species synchrony. While we did not measure root architecture in this study, one plausible hypothesis drawn from similar ecosystems is that forbs (which constitute a large portion of FNH) with well-developed taproots may possess a stronger capacity to stabilize plant communities compared with grasses having shallow fibrous roots[15].

Future studies incorporating belowground trait measurements are required to explicitly test this mechanism.

Notably, our SEM analysis reveals that N addition exerted a direct positive effect on species asynchrony, which partially compensated for the decreased stability caused by FNH richness loss. This finding aligns with previous research demonstrating that N enrichment can enhance grassland stabilization through a selection effect that increases dominant species abundance[45]. However, the negative impact of FNH species loss outweighed this compensatory effect, resulting in net destabilization. Furthermore, N-induced soil acidification may have contributed to these patterns by increasing the dominance of perennial grasses while reducing FNH species prevalence[20, 21]. Such compositional shifts toward homogenized plant communities can further compromise ecosystem stability.

4.3. Regulation of total biomass stability

Herbivore grazing has shown a positive effect on AGB and BGB in grasslands[46], while N enrichment could enhance AGB, unaffected or even inhibit BGB[14, 47]. This study revealed an asymmetric response, as grazing decreased AGB but did not significantly influence BGB. The observed AGB reduction directly reflects the mechanical removal of forage by grazing livestock. Contrary to expectations, N enrichment exhibited no significant effects on AGB or BGB pools. Collectively, these results demonstrate transient ecosystem resilience to short-term grazing and N enrichment.

Mechanistic analyses reveal that total biomass stabilization was predominantly mediated through BGB rather than AGB dynamics, which exposed the critical limitations of only applying AGB stability to predict the BGB stability responses. These findings demonstrate that BGB destabilization may result in the reduction of total biomass stability, resolving a critical knowledge gap in ecological forecasting where historical overemphasis on AGB dynamics masked system-level vulnerabilities. Monitoring frameworks restricted to AGB stability systematically underestimate grazing and nutrient deposition effects on ecosystem processes.

4.4. Ecological significance and management strategies of FNH species in grassland ecosystems

Two competing hypotheses have been proposed to explain biodiversity-stability relationships: the insurance hypothesis, which posits that diverse communities exhibit greater stability through species asynchrony[48], and the mass ratio hypothesis, which emphasizes the functional importance of dominant species[49]. Our findings provide experimental support for the insurance hypothesis by demonstrating that community-wide species asynchrony and population stability were strongly driven by subordinate FNH species, including FNH richness, asynchrony, and FNH–TH asynchrony. These results identify FNH species as keystone taxa that underpin critical ecological processes in alpine meadows.

Our quantification of the FNH-to-TH biomass ratio revealed a segmented (piecewise) relationship with a breakpoint at 0.86. Below the ecological

threshold (FNH/TH = 0.86), community AGB temporal stability decreased as the FNH/TH ratio increased; above the threshold, further increases in FNH proportion did not produce additional stability benefits. A plausible explanation is that, at low FNH/TH ratios, TH-dominated communities (*Poaceae*/*Cyperaceae*) exhibit inherently higher biomass stability due to clonal architecture and phenological synchrony, whereas intermediate FNH ratios introduce compositional flux without yet delivering the full diversity insurance benefit, which only emerges above the 0.86 threshold. While our SEM demonstrates that FNH richness was the fundamental mechanistic driver of ecosystem stability, quantifying species richness in the field can be operationally challenging for local herders and land managers. Therefore, we conducted a parallel analysis using the FNH-to-TH biomass ratio as an easily observable, macroscopic proxy for management purposes. Although this biomass ratio was naturally correlated with FNH richness (r = 0.55), analyzing it independently allowed us to identify practical management targets without confounding our mechanistic models. FNH species exhibit distinct ecological advantages, including stress tolerance, adaptability to nutrient-poor soils, and high resource-use efficiency, making them ideal pioneer species for grassland restoration (Wang et al., 2022). Additionally, certain FNH species possess ornamental value and enhance pollination networks that benefit TH species[50].

Practical management strategies can be informed by these findings. For instance, adaptive grazing management in Qilian Mountain grasslands has

demonstrated differential response thresholds between FNH species (e.g., *Achnatherum inebrians*) and TH species (e.g., *Stipa purpurea*), enabling targeted control through grazing intensity modulation[51]. Rotational grazing combined with fertilization and reseeding has proven more effective than free grazing for controlling FNH species expansion[52, 53]. Therefore, strategic FNH management balancing ecological preservation with socioeconomic demands presents a viable pathway toward sustainable grassland utilization.

4.5. Limitation

Our findings demonstrate that FNH species significantly enhance community stability under grazing and N addition conditions. However, the current investigation focused exclusively on alpine meadow ecosystems grazed by Tibetan sheep, and caution should be exercised when extrapolating these results to other herbivores due to interspecific differences in foraging strategies and nutritional ecology. Methodological constraints, including limited spatial replication and the absence of precise herbivory quantification, may have yielded conservative estimates of AGB stability responses. Meanwhile, each FNH plant has unique characteristics, and grazing experiments within the fence are necessary to establish optimal supplementation thresholds for different FNH species. Developing adaptive threshold-based management frameworks for FNH species represents a critical pathway toward sustainable grassland utilization.

It is crucial to acknowledge the inherent statistical constraints associated with our large-scale split-plot design. Given the logistical challenges of

manipulating stocking rates across extensive alpine paddocks, our experiment was limited to three replicates at the main-plot level. Consequently, the effective denominator degrees of freedom for testing the overarching effects of stocking rate in our LMMs are inherently low. Therefore, the non-significant main effects of grazing on variables such as species richness and overall community stability must be interpreted with caution; they likely reflect insufficient statistical power to detect a direct signal against the substantial background environmental heterogeneity of the Qinghai–Xizang Plateau, rather than a true absence of ecological impact. This limitation provides critical context for reconciling the apparent divergence between our LMM and SEM results. While the conservative LMMs detected no significant direct effect of grazing on community stability, the SEM revealed a significant total positive effect. This discrepancy is not contradictory but rather ecologically informative. LMMs evaluate discrete, direct treatment comparisons heavily penalized by low main-plot replication. In contrast, SEM operates as a system-level network, aggregating continuous, indirect cascading pathways. Our SEM results demonstrate that the stabilizing effect of grazing does not manifest as a massive direct impact, but rather operates subtly through indirect functional shifts, specifically by preserving FNH richness, which subsequently enhances species asynchrony. We acknowledge the risk of confirmatory bias when excluding variables based on fit. However, our approach followed a theory-driven model comparison framework, i.e., the full model (including TH) was specified a

priori as an alternative hypothesis, and its poor fit together with non-significant TH paths justified retaining the more parsimonious FNH-focused model. We have reported all fit statistics for both models and provided the full model in the Supplementary Materials. Future studies with larger sample sizes and longer time series may improve the evaluation of the potential role of TH in stability regulation.

While our findings highlight the critical role of FNH species, a fundamental constraint of this study is the brevity of the time series. The temporal stability and asynchrony metrics were calculated from three annual measurements (2012–2014). As demonstrated in recent biodiversity-stability syntheses[54], robust estimation of long-term equilibrium stability typically requires longer time series (e.g., 5–8 years). The ratio of the mean to standard deviation derived from small samples (n = 3 in this study) is highly sensitive to interannual climatic anomalies, meaning a single unusual year can disproportionately inflate or deflate point estimates of stability. Consequently, the stability metrics, the exact FNH/TH ecological threshold (0.86), and the SEM pathways reported here should be strictly interpreted as short-term transient compensatory dynamics in response to the immediate implementation of grazing and N enrichment, rather than long-term asymptotic stability. Future long-term monitoring is imperative to validate the temporal persistence of these FNH-mediated insurance effects and to refine the exact management thresholds for alpine meadows.

5. Conclusions

Our study highlights the critical, yet historically overlooked, role of FNH in maintaining ecosystem stability under concurrent anthropogenic pressures in alpine meadows. Grazing tended to positively influence community AGB temporal stability due to increasing FNH richness and compositional stability, but this effect was associated with considerable uncertainty, as the bootstrap confidence interval overlapped zero. Conversely, although N addition increases species asynchrony, its net effect on AGB stability is fundamentally negative. This destabilization is driven by the overriding negative impacts of soil acidification and the suppression of FNH richness. The asynchronous dynamics within FNH populations act as a critical buffer, sustaining community AGB stability under both grazing and N addition. Furthermore, TB temporal stability is predominantly mediated by BGB stability rather than AGB. This strongly indicates that ecological assessments relying solely on aboveground metrics provide limited evidence and may fundamentally underestimate the consequences of grazing and nutrient enrichment. We identified a critical ecological threshold based on the FNH to TH biomass ratio (0.86). Given that these estimates are based on only three years of data, the proposed threshold and the inferred stabilizing pathways should be validated with longer-term datasets (≥5 years). While the short-term (3-year) nature of our experiment and the statistical constraints inherent to large-scale field designs (e.g., LMM vs. SEM divergence) necessitate future validation through long-term monitoring, our findings prompt a paradigm shift in grassland management. Nevertheless, integrating moderate grazing

with other grassland management practices can transform functionally important native herbage from a perceived constraint into an ecological asset, contributing to sustainable grassland management on the Qinghai–Xizang Plateau.

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Author contribution

Fujiang Hou, Lan Li, Yi Sun, Tianhao Xiao, Yang Liu contributed to the conceptualization and design of this study. Lan Li, Yi Sun, Tianhao Xiao, Yang Liu and Wuchen Du prepared experimental materials, collected and measured samples, and organized data. Lan Li, Mingshan Xu, Fujiang Hou, Xiong Zhao He and Adilbek Nogayev conducted data analysis, authored the preliminary draft, and participated in subsequent revisions. All co-authors critically evaluated and formally endorsed the finalized document.

Declarations

Conflict of interest

The authors declare that they have no known competing financial interests

or personal relationships that could have appeared to influence the work reported in this paper.

Ethical statement

The authors declare that the research work described in this manuscript was conducted in accordance with the ethical standards of academic research and integrity. The study did not involve human participants or experimental animals.

Consent for publication

Not applicable.

Data availability

Data will be made available on request.

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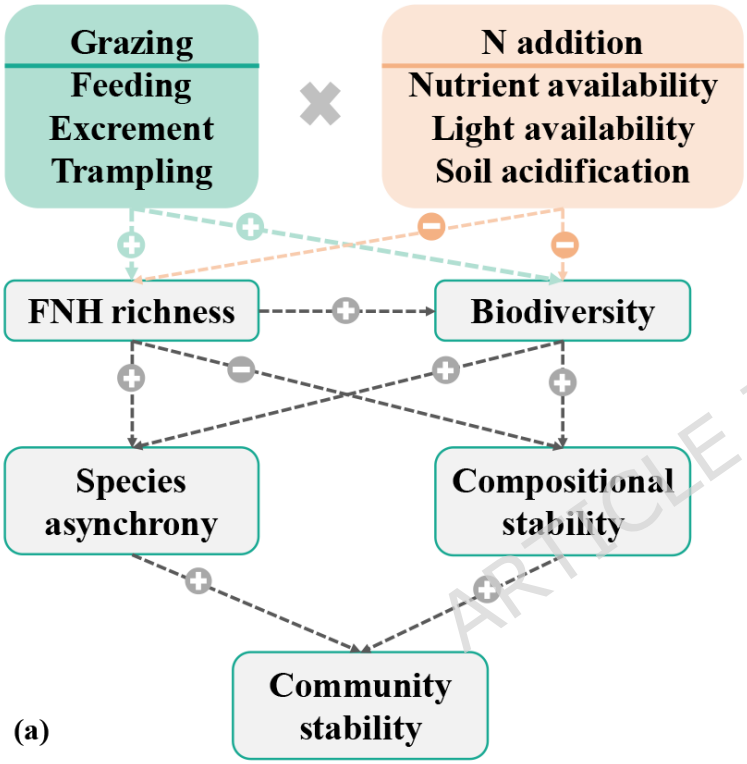

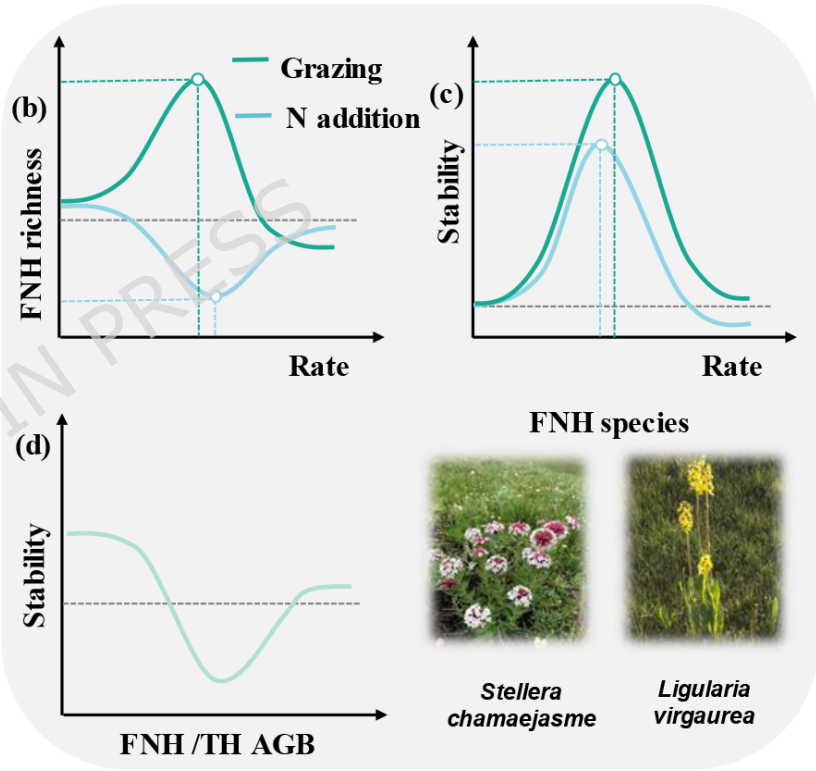

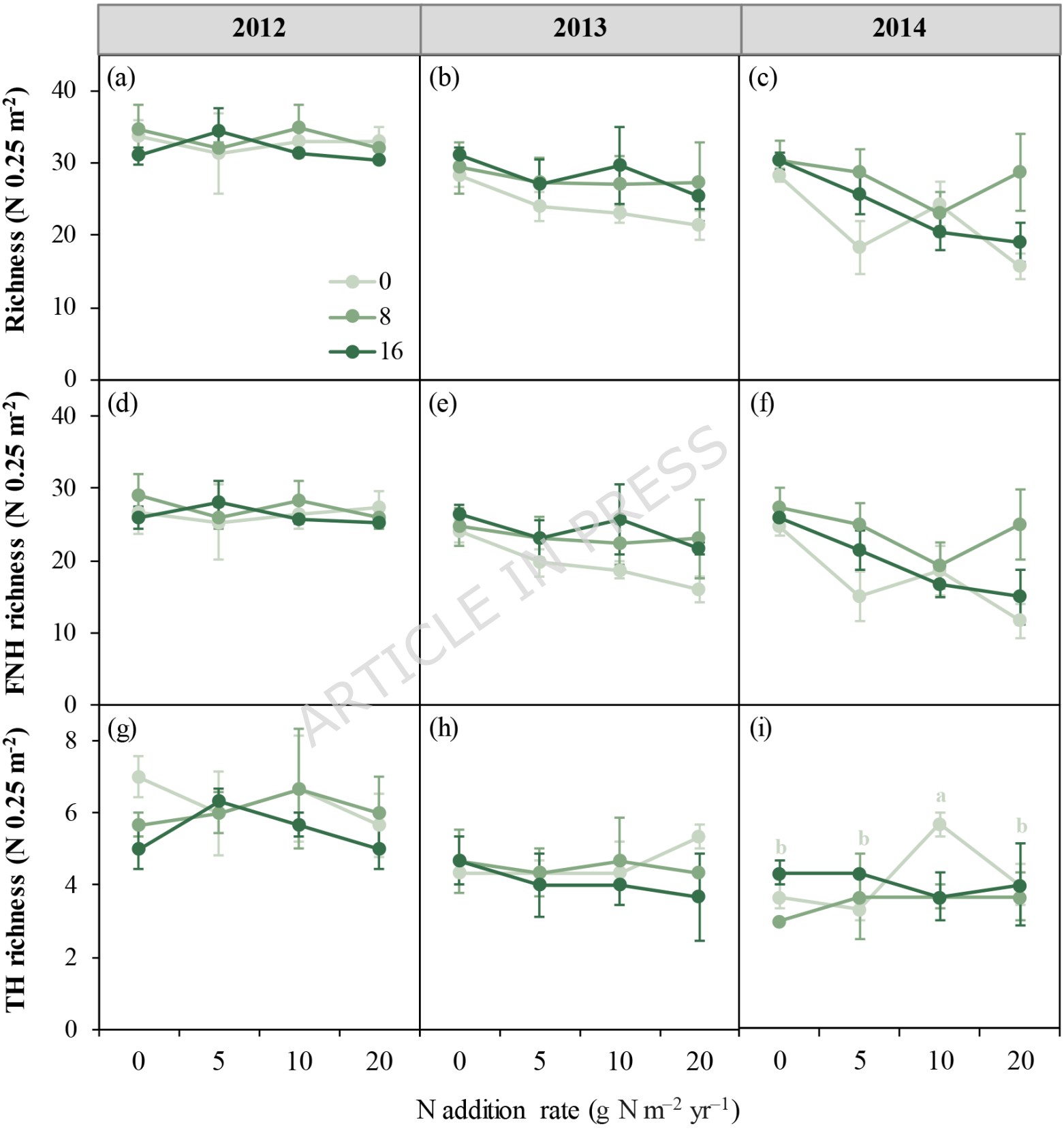

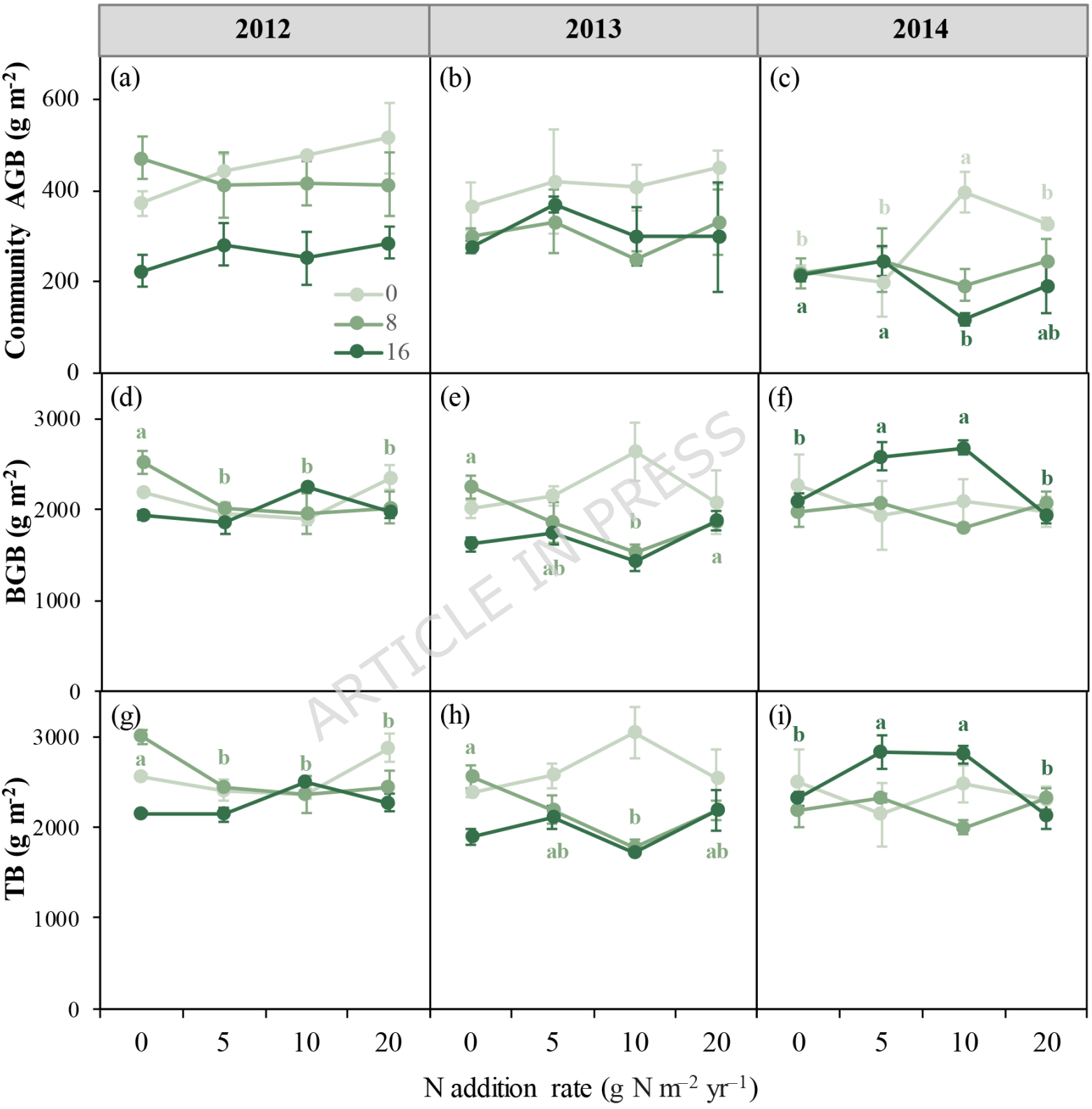

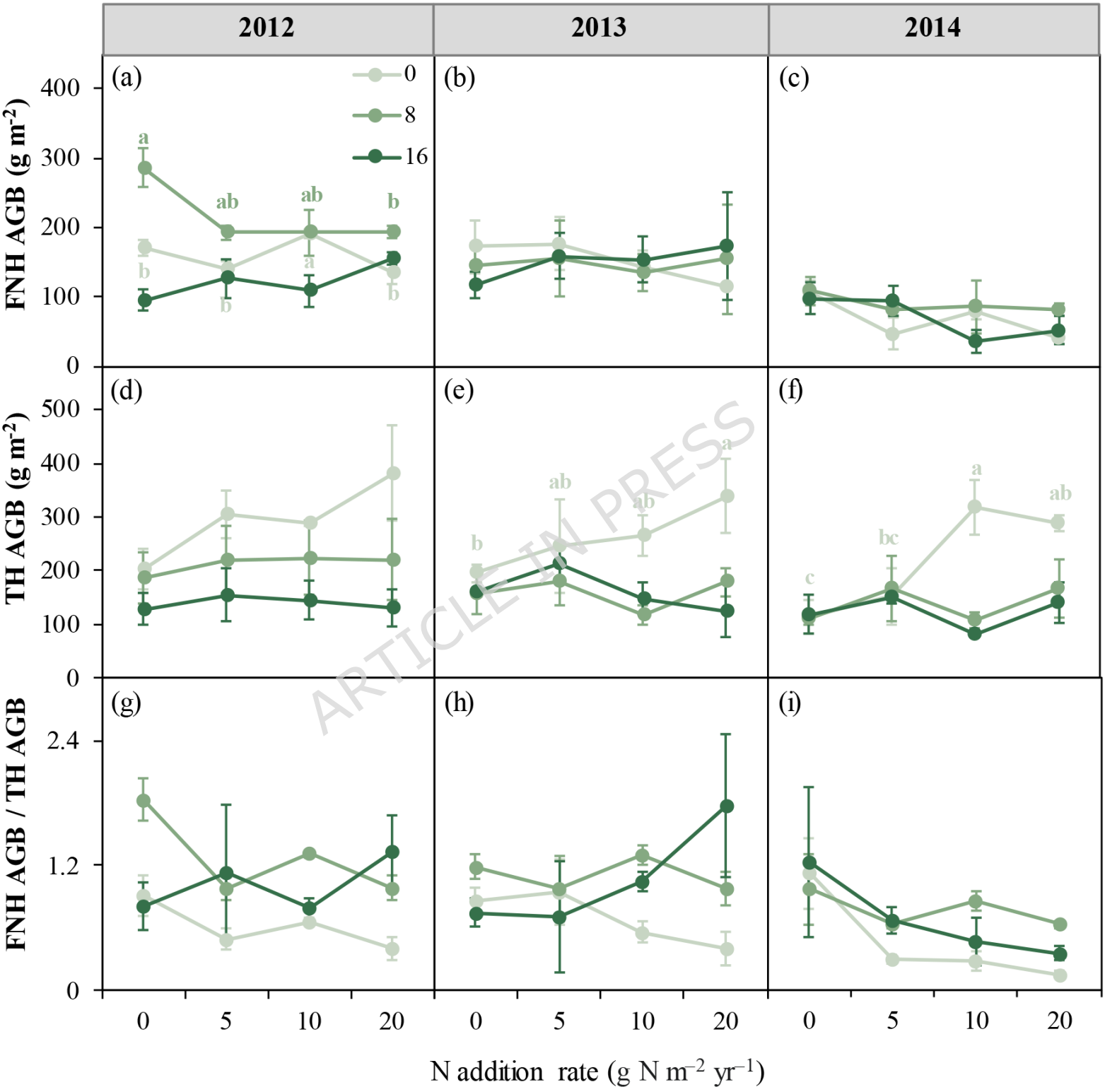

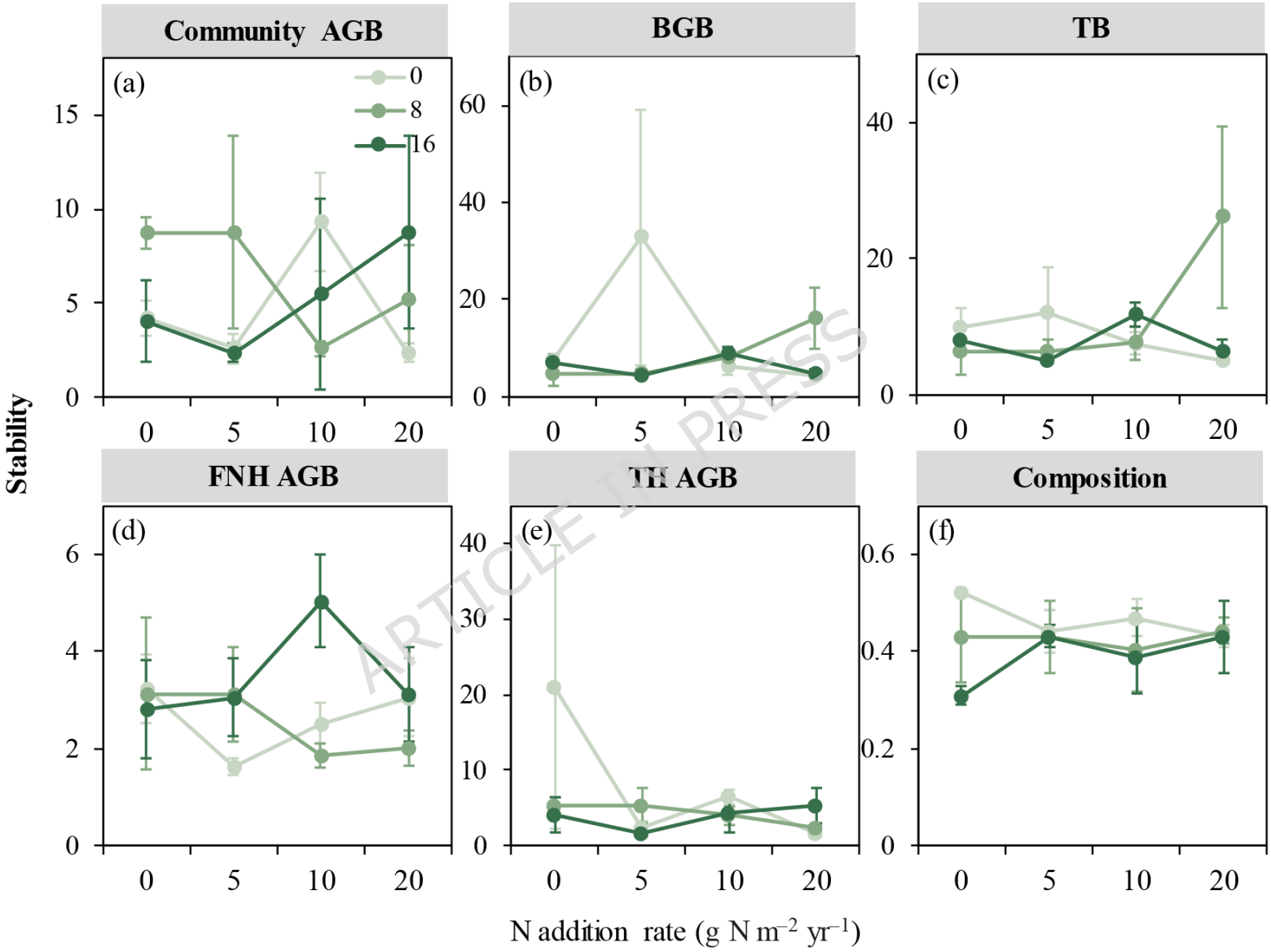

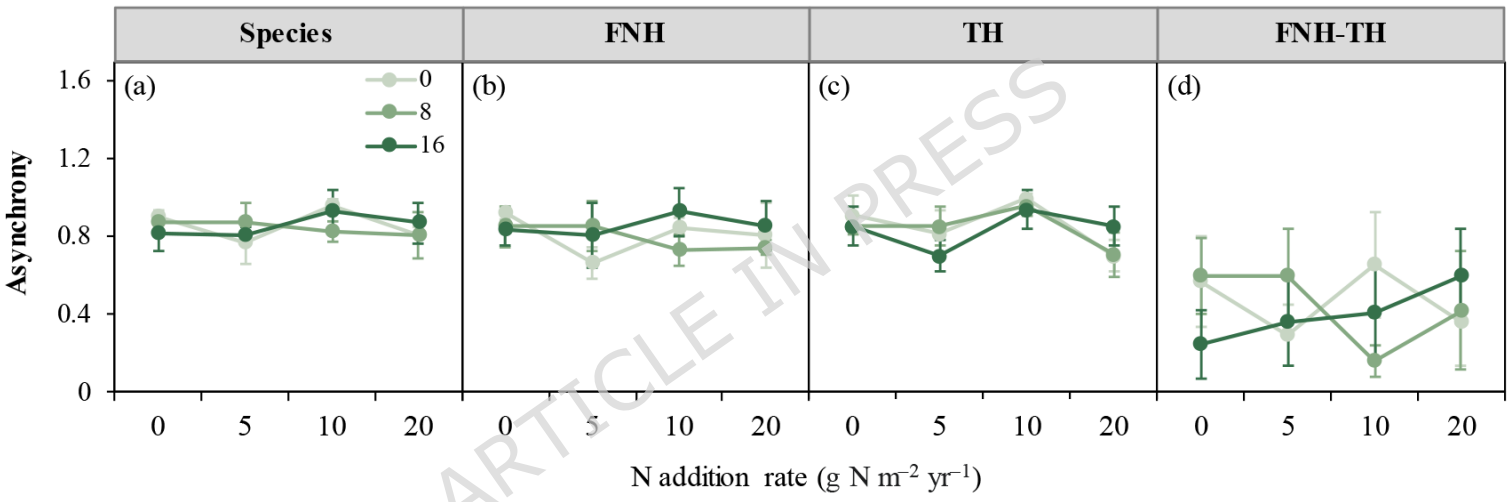

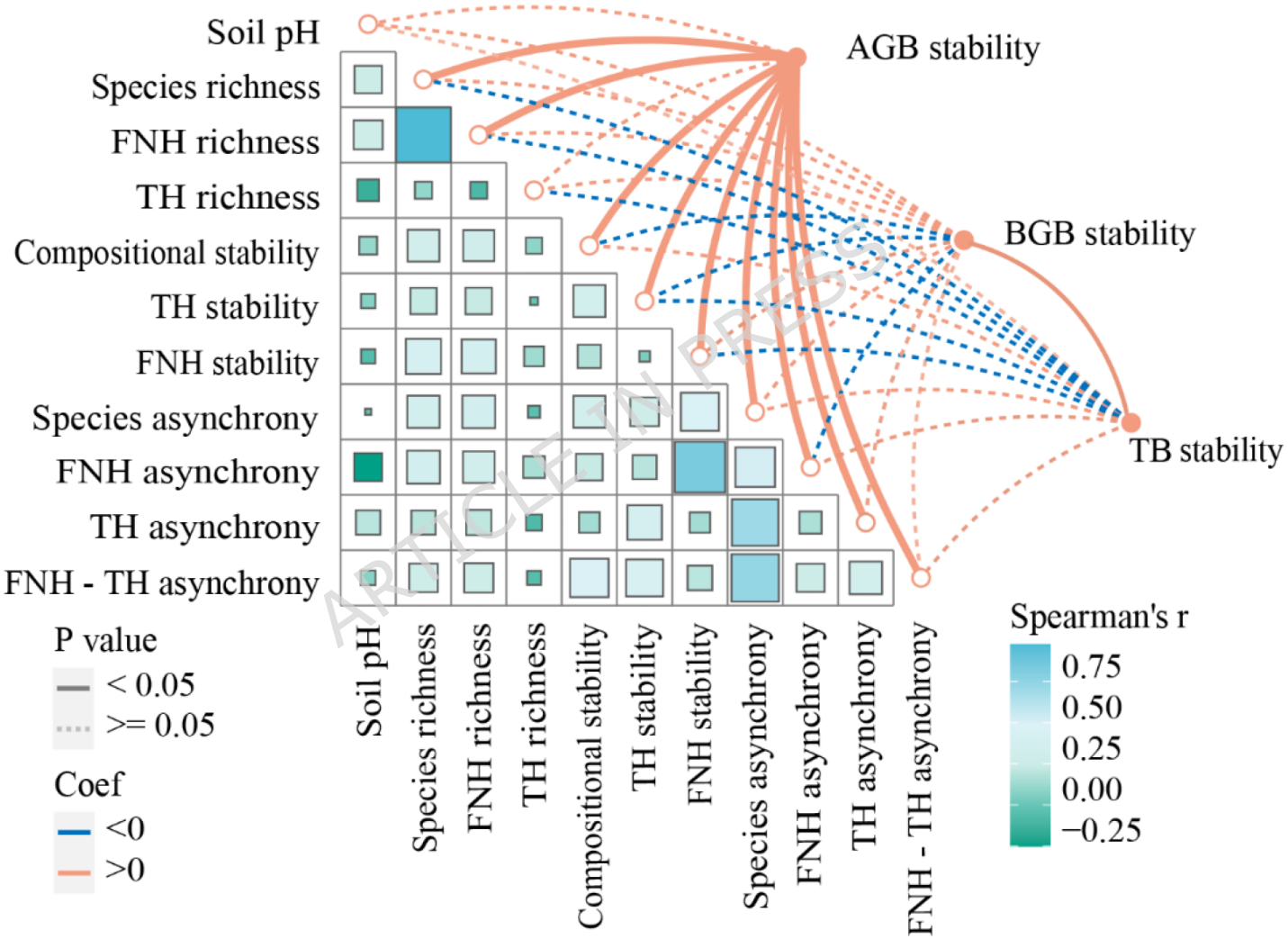

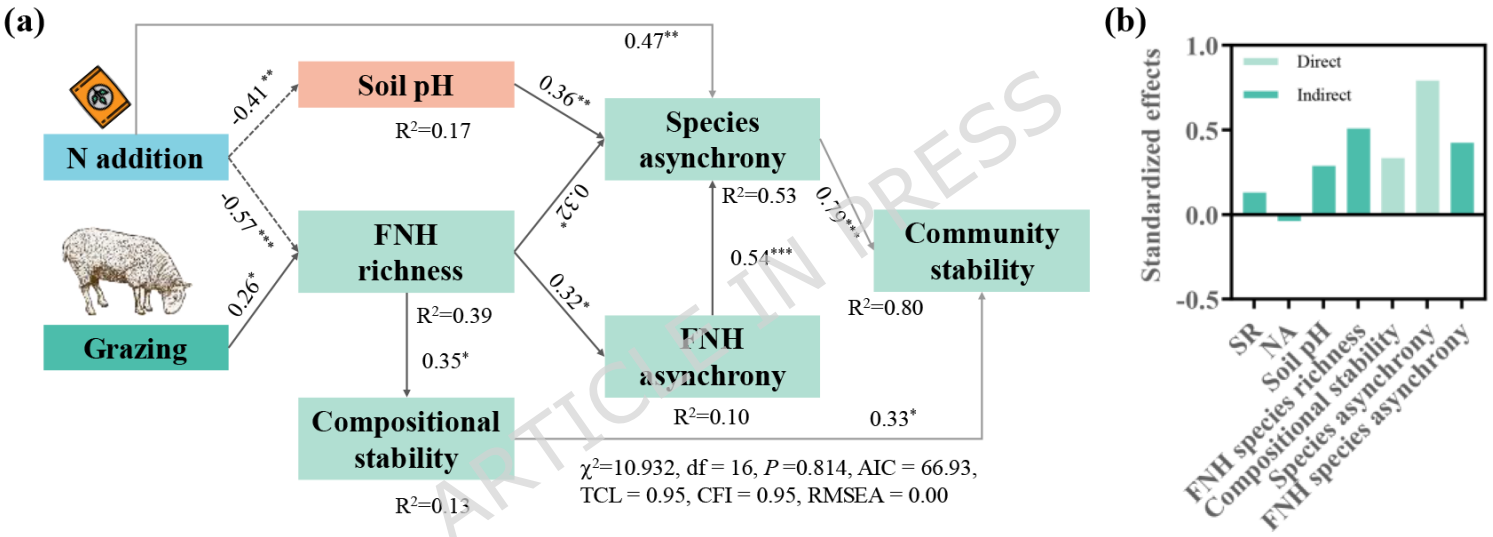

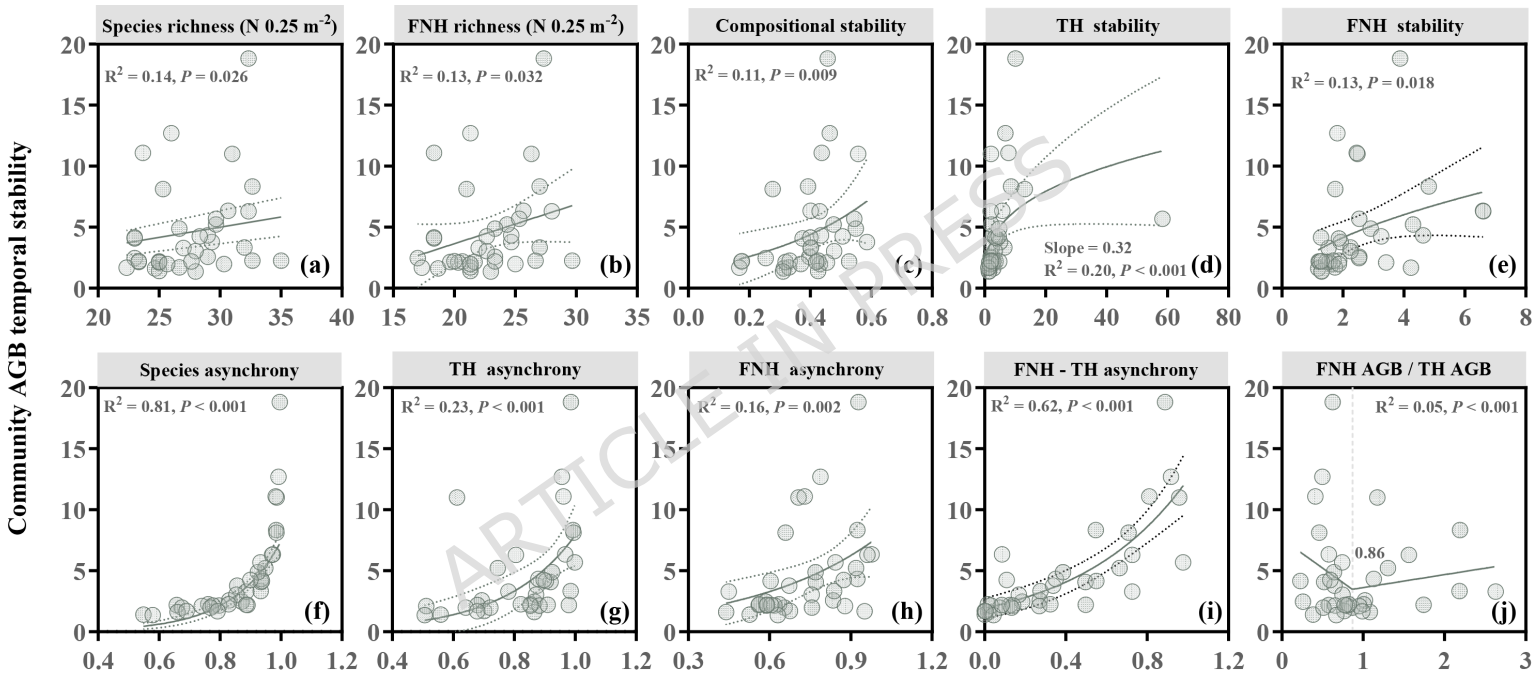

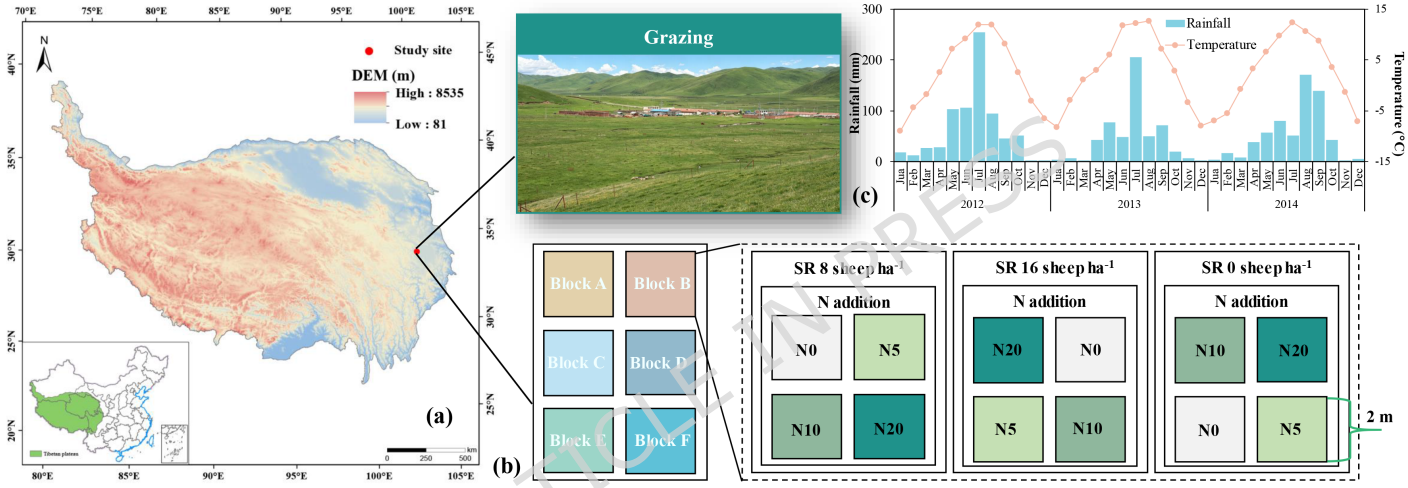

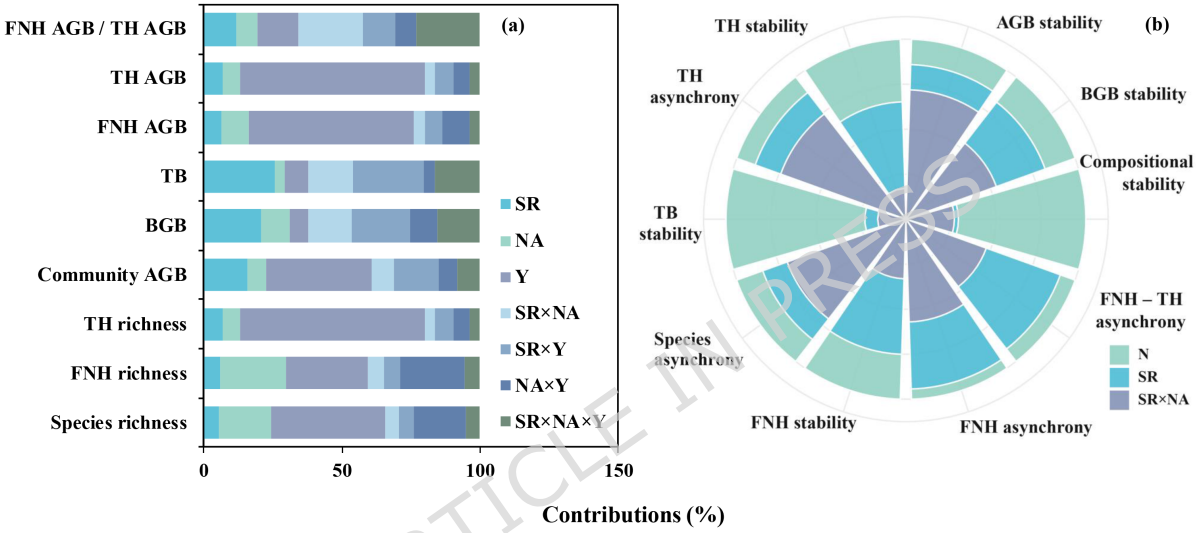

Table 1 Effects of year (Y), stocking rate (SR), nitrogen addition rate (NA), and their interactions on plant species diversity and biomass indices based on linear mixed-effects models that account for the split-plot design (block and main plot as nested random intercepts). AGB, aboveground biomass; BGB, belowground biomass; TB, total biomass; FNH, Functional native herbage; and TH, Traditional native herbage

	df	DenDF	Species richness		FNH richness		TH richness		Community AGB		FNH AGB		TH AGB		FNH AGB/TH AGB		BGB		TB	
			F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
SR	2	4	2.57	0.084	3.555	0.034	1.118	0.314	7.65	< 0.001	4.52	0.014	23.2	< 0.001	7.05	0.002	4.13	0.020	9.9	< 0.001
NA	2	12	6.76	< 0.001	7.85	< 0.001	0.307	0.821	0.766	0.520	1.29	0.283	2.67	0.054	1.22	0.309	1.33	0.273	0.918	0.437
Y	2	24	28.1	< 0.001	17.7	< 0.001	25.1	< 0.001	25.6	< 0.001	32.1	< 0.001	5.46	0.006	3.8	0.027	6.77	0.002	4.73	0.012
SR ×Y	4	8	1.16	0.335	1.4	0.243	0.613	0.655	3.66	0.010	2.11	0.089	1.61	0.180	0.417	0.796	6.12	< 0.001	7.12	< 0.001
NA ×Y	6	24	1.33	0.254	1.69	0.137	0.296	0.937	0.285	0.944	0.809	0.566	0.528	0.785	1.644	0.150	0.6444	0.69578	0.7133	0.640
SR ×NA	6	12	0.378	0.891	0.249	0.958	0.812	0.564	2.35	0.041	1.58	0.166	3.12	0.009	1.01	0.423	3.167	0.008	4.47	< 0.001
SR ×NA×Y	12	24	0.664	0.780	0.654	0.789	0.817	0.632	0.647	0.800	1.25	0.269	0.597	0.8383	0.932	0.520	3.32	< 0.001	3.45	< 0.001

Denominator degrees of freedom (DenDF) vary among fixed effects because of the split-plot structure and the Satterthwaite approximation.