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Research Article

Co-dominant species fail to compensate after 13-year of dominant species removal in a Tibetan alpine grassland

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To better understand the dynamics of community resilience, it is crucial to examine the role of dominant species in maintaining ecosystem functions. Dominant species, due to their high abundance, are considered to maintain productivity after species loss. However, it remains unclear whether the community productivity can be maintained or restored by the remaining co-dominant species after the loss of the dominant species. Therefore, we hypothesized that after the loss of dominant species, the lost productivity would be maintained by the co-dominant species in the remaining community. This study, conducted over 13 years in an alpine grassland, investigates the compensatory responses of remaining species following the removal of each of two dominant species, *Kobresia pygmaea* (sedge) and *Stipa purpurea* (grass), both individually and in combination, under two nitrogen level scenarios. We found that while partial compensation (compensation index < 1) occurred in the remaining community, neither of the remaining dominant species effectively compensated for the loss of the removed species. Leguminous plants showed the most obvious positive response to the removal of dominant species, whereas forbs and sedges showed the most marked negative responses. In addition, fertilization does not promote the recovery of community productivity following removal of the dominant species. Our findings underscore the critical role of dominant species in sustaining productivity. In the face of the accelerating crisis of biodiversity extinction, priority should be given to protecting the dominant species and key functional groups in the region.

Keywords: alpine meadow, compensation, dominant species, grassland, nitrogen, removal experiment

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Introduction

Dominant species are often regarded as keystone components of ecological communities owing to their niche advantages and disproportionate influence on community structure (Power et al. 1996, Grime 1997, Smith and Knapp 2003, O'Connor and Crowe 2005). Based on the random loss hypothesis (Suding et al. 2005), rare species are more likely to face extinction under future global changes due to their small relative abundance (Pimm et al. 1988, McKinney 1997, Genung et al. 2020). Additionally, the mass ratio hypothesis (Grime 1998, Geider et al. 2001) posits that community functions such as productivity are primarily driven by the dominant species, suggesting that the species with the highest relative abundance play a decisive role in determining functional outcomes (Grime 1998, Chapin et al. 2011). Consequently, the absence of dominant species is likely to have profound impacts on community productivity (Longo et al. 2013, Winfree et al. 2015), whereas the loss of subordinate or rare species may exert only minimal effects (Smith and Knapp 2003, Lisner et al. 2023). It is unclear how diversity changes following dominant species loss, which depends on changes in the rates of species turnover following dominant species loss. It is widely accepted that dominant species may promote the growth of subordinate species through facilitative processes, yet also inhibit them through competition (Ellison et al. 2005, Gaston 2011). However, this process is highly dependent on both biotic and abiotic factors, such as the species pool or the identity of the dominant species. For example, when tall dominant species are removed, light availability increases, allowing short-statured species to thrive due to the alleviation of light limitation (Hautier et al. 2009, Eskelinen et al. 2022). Conversely, in environments with high evaporative demand, dominant species can provide shade that acts as a refuge, thereby facilitating the growth of remaining species (Bertness and Callaway 1994, Lortie and Callaway 2006). At the same time, some studies have found no significant changes in diversity within the remaining community following the loss of dominant species (Roth et al. 2008, Li et al. 2015). Overall, it is essential to consider both the identity of the dominant species and the local environmental context when exploring changes in diversity following dominant species loss.

Previous studies examining single-species removal have shown that the loss of a dominant species can initiate cascading effects within plant communities, altering their structure, functioning, and resilience (Li et al. 2015, Chaves and Smith 2021). However, the responses of remaining species to dominant species removal differ depending on the underlying mechanism. According to the mass ratio hypothesis (Grime 1998), ecosystem functioning is primarily driven by the traits and relative abundances of dominant species, instead of emphasizing species richness by itself. Thus, after a dominant species was removed, productivity may increase for the most abundant remaining species or those better adapted to the altered microenvironment. In contrast, the niche complementarity hypothesis (Naeem et al. 1994, Loreau and Hector 2001) posits that the loss of a dominant species creates niche opportunities, facilitating resource partitioning among the remaining species. This can alter interspecific interactions and lead to a reordering of species abundances relative to the original community. Therefore, dominant species removal may not only affect overall community productivity, but also reshape community structure and abundance patterns through shifts in resource use and species interactions.

Compensatory dynamics play a critical role in sustaining ecosystem productivity following species loss (Morgan Ernest and Brown 2001, Ives and Cardinale 2004, Pan et al. 2016, Chaves and Smith 2021). Communities may exhibit partial, complete, or even negative compensation, based on the particular species removed and the characteristics of the resulting environmental changes (McLaren and Turkington 2010, Li et al. 2015, Yu et al. 2015, Pan et al. 2016, Chaves and Smith 2021). For example, in a tallgrass prairie, productivity can be partially compensated by subordinate species following the loss of dominant species (Chaves and Smith 2021). In contrast, in alpine tundra, productivity was fully compensated following dominant species loss (Suding et al. 2006). However, over the long term, dominant species loss exerted a more negative effect on productivity (Peters and Yao 2012, Avolio et al. 2019). Complete compensation may occur after increase in resource availability or following the removal of specific functional groups (Cross and Harte 2007, Bret-Harte et al. 2008, McLaren and Turkington 2011). For instance, the removal of grasses may alleviate competition for light, providing opportunities for the remaining species to compensate for losses in productivity through increased growth or recruitment (Li et al. 2015, 2020). The removal of legumes, which play a crucial role in nitrogen fixation, can disrupt nitrogen availability, leading to reduced productivity unless other nitrogen-fixing species compensate for this functional gap (van Ruijven and Berendse 2003). These scenarios illustrate the profound identity effects of dominant species, as their functional traits determine not only their contribution to ecosystem processes but also the pathways by which communities recover from their loss (Vanni et al. 2002). Thus, it remains uncertain whether the loss of dominant species is compensated by other prevailing taxa or if it results in a reshuffling of species abundances, thereby increasing the overall unpredictability of community structure. In addition, the availability of resources influences community compensation dynamics after the loss of dominant species (Hiddink and Davies 2024). According to the stress-gradient hypothesis (Bertness and Callaway 1994), in resource-rich habitats, interspecific resource competition may act as a major driver of compensation dynamics within community. By contrast, in resource-poor habitats, interspecific complementarity is the primary mechanism sustaining productivity, making it more difficult for productivity to recover after species loss. Thus, changes in resource availability may alter the compensatory effects that follow species loss.

To explore these issues, we conducted a 13-year removal experiment in an alpine meadow, examining compensation under various scenarios of two dominant species loss. We

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examined how the remaining community is altered after the separate removal of the dominant species *Kobresia pygmaea* (sedge) and *Stipa purpurea* (grass), as well as following their simultaneous removal. The Tibetan Plateau harbors a rich regional species pool, shaped by complex topography and long-term environmental heterogeneity (Lai et al. 2021). As the world's largest plateau, the Tibetan Plateau is dominated by alpine meadows, which cover approximately 80–90% of its surface area (Wang et al. 2023). As common and dominant species in alpine grasslands, *S. purpurea* and *K. pygmaea* support the grazing needs of local pastoralists on the Tibetan Plateau (Miehe et al. 2011, 2019). They play a crucial role in maintaining grassland productivity while contributing to regional socio-economic sustainability. Therefore, this study provides important insights for the conservation of these two key species. Specifically, we addressed two key questions: 1) does compensation occur under different dominant species loss scenarios? 2) Will the species be reordered after the dominant species are removed? We assume that when one of the dominant species is removed, compensation will occur through the remaining dominant species. When both dominant species are removed simultaneously, compensation will occur through species with the same functional group in the remaining community (Fig. 1).

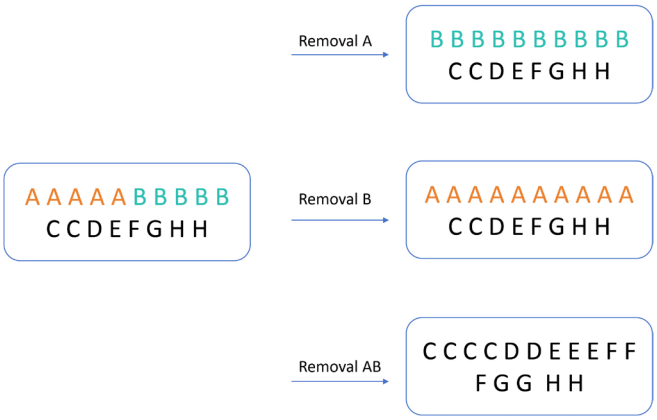


Figure 1. Schematic diagram of community composition changes under different dominant species removal treatments in an alpine grassland. The left side shows the initial community composition with dominant species A (*Kobresia pygmaea*) and B (*Stipa purpurea*), and other subordinate species (C, D, E, F, G, H). 'Removal A' refers to the treatment in which the dominant species *K. pygmaea* was removed. As a result, the community composition shifted, allowing *S. purpurea* to compensate for the loss in productivity caused by the absence of *K. pygmaea*. 'Removal B' refers to the treatment in which the dominant species *S. purpurea* was removed. As a result, the community composition shifted, allowing *K. pygmaea* to compensate for the loss in productivity caused by the absence of *S. purpurea*. 'Removal AB' denotes the treatment of removing both dominant species *K. pygmaea* and *S. purpurea*, and shows the subsequent community restructuring dominated by subordinate species (C, D, E, F, G, H).

Material and methods

Study site

The research was carried out at the Naqu Ecological and Environmental Observation and Research Station (Naqu Station), which is part of the Institute of Tibetan Plateau Research under the Chinese Academy of Sciences (Supporting information). The station is located north of the Kailas Range and Nyenchenthanglha Mountains in Tibet, China (31°16′N, 92°05′E, 4512 m a.s.l.). The area receives an average annual precipitation of about 420 mm, and its mean yearly temperature is roughly 0.29°C. It is characterized as a typical plateau sub-frigid monsoon semi-humid climate zone. The experimental area is an alpine meadow ecosystem dominated by *Kobresia pygmaea* (Kp) and *Stipa purpurea* (Sp), which accounts for over 60% of the community cover. Subordinate species (S) consist of *K. humilis*, *Aster souliei*, and *Carex moorcroftii* (see the Supporting information for details). Based on life forms and growth habits, the plants are categorized into four functional groups: sedge, grass, Leguminosae, and forbs. The soil in this region is identified as alpine meadow soil. The pH was 6.74, with soil total nitrogen, total carbon, and total phosphorus contents of 8.11, 33.12, and 0.89 g kg^{-1}, respectively. The alkali-hydrolyzable nitrogen content was 0.22 g kg^{-1}, and the available phosphorus content was 0.047 g kg^{-1}.

Experimental design

The experiment was set up in the spring of 2012 (Supporting information), utilizing a grassland area of approximately 10 000 km^2 enclosed to exclude grazing at the Naqu Station. A randomized block design was employed, consisting of four blocks, with each plot measuring 1.5 × 1.5 m. *Kobresia pygmaea* and *S. purpurea* were selected as target species for removal in the experiment. The experiment included all possible combinations of species removal, resulting in the following treatments: control (original community), Kp.re (*K. pygmaea* was removed), Sp.re (*S. purpurea* was removed), and KpSp.re (*K. pygmaea* and *S. purpurea* were removed) (Supporting information). Each treatment was paired with two nitrogen levels: N0 (ambient) and N1 (added nitrogen). This design yielded a total of 32 experimental plots (2 nitrogen levels × 4 removal treatments × 4 replicates).

Nitrogen fertilization and removal treatments

Each plot was secured at the corners with iron nails and enclosed with wire fencing. To reduce the impact of edge effects, each plot was kept at least 2 m apart. Target plants were manually removed to avoid impacts from trimming and trampling on non-removed species, soil biota, and soil structure. Selected plants were cut at ground level using scissors, and all aboveground parts, including stems, leaves, flowers, and seeds, were carefully removed. The removed plant material was cleared from the experimental plots to prevent any influence of dead biomass on the remaining plants. This process was performed carefully to minimize disturbance to other plants and preserve the original soil structure. To ensure the complete mortality of the removed plants, removal treatments were repeated over multiple years. By the end of the 2016 growing season, plot surveys confirmed that the

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removed species had not reestablished, indicating that root activity had largely ceased and validating the effectiveness of the removal treatments. To ensure experimental accuracy, removal plots were surveyed each July, and any regrowth of the removed species was promptly eliminated to maintain the reliability of the experiment.

Fertilization and species removal were initiated in the same year (2012). Urea was used as the fertilizer and was evenly applied to the plots in mid-July of each growing season. Due to the region's low-temperature constraints (Chen et al. 2016) and strong leaching effects (McGovern et al. 2014), a nitrogen addition rate of 30 g N m^{-2} yr^{-1} was initially applied to ensure that nitrogen was not a limiting factor.

During the growing season, a fixed 0.5 × 0.5 m quadrat was placed at the center of each plot to survey vegetation. This survey assessed the composition and structural responses of the plant community. In each quadrat, a 10 × 10 grid (each cell = 1 × 1 cm, total 100 cells) was used to identify every plant species. Their cover, abundance, and height were then evaluated by counting how often each species occurred within these cells. To ensure that the experiment could be sustained over a longer period without disturbance, we refrained from collecting aboveground biomass during the growing season. Additionally, conducting aboveground biomass harvesting in removal experiments would be considered a disturbance. Therefore, cover was chosen as a proxy for productivity in our study (Read et al. 2018, Arnillas and Cadotte 2019, Sundqvist et al. 2020, Rewcastle et al. 2022).

Statistical analysis

We assessed cover compensation, which reflects the extent of productivity recovery after the removal of dominant species, using the compensation index (CI) proposed by Adler and Bradford (2002). This method can measure the impact of species loss on natural productivity under natural conditions and the resilience of natural communities in response to species loss, based on the following equation:

$$CI = \frac{\sum_{i}^{n}(O_i - E_i)}{\sum_{i}^{N} E_i - \sum_{i}^{n} E_i}$$

In this analysis, O_i denotes the measured yield of species i within the depleted (removal) community, whereas E_i represents its predicted yield, determined from the yield of species i in the intact (control) setting. Moreover, N stands for the complete group of species present in the full community, while n signifies the subset of those species that successfully persist in the depleted community.

CI = 1 indicates complete productivity compensation within the community. CI > 1 signifies overcompensation, whereas 0 < CI < 1 reflects partial recovery that does not reach full compensation. CI < 0 suggests a failure in functional recovery, with species removal exerting detrimental effects on the remaining community members. We selected data from the final two years for analysis, as partial compensation was observed in most years (Supporting information).

To evaluate the impacts of removing dominant species and adding nitrogen on cover, species richness, Shannon–Wiener diversity index, and evenness, we measured several variables in both control and removal plots. The Shannon–Wiener index reflects the overall combination of species richness and evenness within a community.

We employed linear mixed-effects models to evaluate the effects of dominant species removal and nitrogen addition on compensatory responses, species richness and diversity, and community cover. In these models, 'block' was treated as a random effect, while dominant species removal, year, and nitrogen addition were included as fixed effects. All analyses were conducted in R using the 'lme4' package (Bates et al. 2025) and the 'emmeans' package (Lenth et al. 2025).

To examine how the removal of key dominant species along with nitrogen supplementation affects community composition, we performed permutational multivariate analysis of variance (Anderson 2017), with nitrogen addition and dominant species removal included as fixed effects. To identify the species contributing most to community compositional differences following dominant species removal, we conducted a similarity percentage (SIMPER) analysis based on Bray–Curtis dissimilarities. This method is based on the Bray–Curtis distance and decomposes the community dissimilarity between two plots (e.g. the dominant-species removal and control groups) into contributions from each species. By calculating the average contribution of each species' abundance difference to the overall community difference, the species contributing most to the between-group dissimilarity are identified. All analyses were conducted using the 'vegan' package (Oksanen et al. 2015) in R. We also evaluated the log response ratios (LRR) of different species or functional groups to different nitrogen addition levels and different dominant species removal treatments. The formula is as follows:

$$LRR = \log_{10}\left(\frac{Variable_{treatment}}{Variable_{control}}\right)$$

Here, $Variable_{treatment}$ represents the response variable in the treatment group, and $Variable_{control}$ represents the response in the control group. LRR < 0 indicates a negative species response, whereas LRR > 0 indicates a positive response.

We constructed rank–abundance curves (RACs) based on species relative abundances to assess the effects of dominant species removal on changes in species relative abundance and rank. RACs were generated annually for both removal and control plots across all nitrogen addition treatments to identify temporal trends in species rank shifts. In addition, we generated ranked response ratio curves (ordered from lowest to highest) to examine the magnitude of species responses under different removal treatments and nitrogen addition levels.

Since the differences in compensatory effects and cover among years were relatively consistent across different removal treatments, subsequent analyses were mainly based on the last two years of the experiment (Supporting

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information). All statistics were conducted using R ver. 4.5.1 (www.r-project.org).

Results

Cover and compensation

Overall, after separately removing the dominant species *K. pygmaea* and *S. purpurea*, as well as removing both of these dominant species simultaneously, partial compensation occurred in the coverage of the remaining community (CI < 1; Fig. 2A, B). Nitrogen addition on average reduced the compensatory response (Fig. 2A, B; Supporting information; $p = 0.034$). Nitrogen addition had a marginally significant effect on coverage ($p = 0.061$). Moreover, there was a marginally significant interaction effect between nitrogen addition and the simultaneous removal of *K. pygmaea* and *S. purpurea* on coverage (Fig. 2C, D; $p = 0.098$). In addition, dominant species removal, fertilization treatments, and interannual variation had significant effects and interactions on community composition changes (Table 1).

Diversity changes under different dominant species removal treatments

We found that nitrogen addition significantly affected richness ($p = 0.035$) and there were interannual differences (Supporting information; $p = 0.004$). Individually removing *K. pygmaea* and *S. purpurea* significantly decreased richness and diversity (Supporting information). Removal of *S. purpurea* showed a significant interaction with year on richness (Supporting information; $p = 0.039$). There was a significant interaction effect on Shannon index when nitrogen and two dominant species were removed together (Supporting information; $p = 0.028$). There is a significant interaction effect among nitrogen, *S. purpurea* removal, and year on diversity (Supporting information; $p < 0.001$). The removal of *S. purpurea* significantly increased the community evenness (Supporting information; $p = 0.044$). There were significant interaction effects between nitrogen and the removal of *K. pygmaea* ($p = 0.011$), as well as between nitrogen and the simultaneous removal of the two dominant species, on the evenness (Supporting information; $p = 0.023$). There were significant interaction effects among nitrogen, the removal

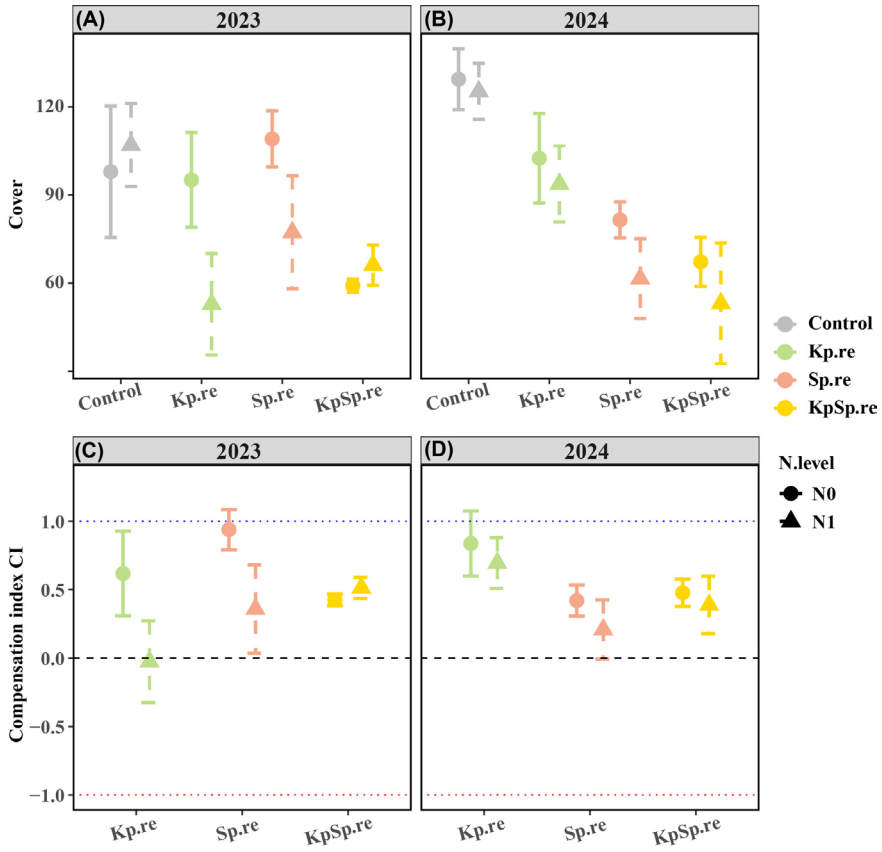


Figure 2. (A) and (B) The model-based average cover (%) represents the results obtained following the removal of the dominant species *Kobresia pygmaea* and *Stipa purpurea* in an alpine meadow community. (C) and (D) The model-based average cover compensation index (CI) ± 1 SE. The experiment was conducted under two nitrogen treatments: no nitrogen addition (N0) and nitrogen addition (N1, 30 g m^{-2} per year). The black dashed line indicates CI = 0, representing the threshold for functional recovery, while the blue dashed line represents CI = 1, the point of complete cover compensation. Kp.re represents the treatment where *K. pygmaea* was removed. Sp.re represents the treatment where *S. purpurea* was removed. KpSp.re represents the treatment where both *K. pygmaea* and *S. purpurea* were removed simultaneously.

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Table 1. PERMANOVA results of the effects of removal of the dominant species *Kobresia pygmaea, Stipa purpurea* and nitrogen addition on community composition of an alpine meadow plant community for 2023 and 2024. Significance $\alpha = 0.05$. Kp.re represents the treatment where *K. pygmaea* was removed. Sp.re represents the treatment where *S. purpurea* was removed. KpSp.re represents the treatment where both *K. pygmaea* and *S. purpurea* were removed simultaneously. Significant ($\alpha \leq 0.05$) p-values are bolded.

	df	SS%	R^2	F	p
N	1	6122	0.05	4.94	**0.001**
Kp.re	1	13620	0.12	10.98	**0.001**
Sp.re	1	18068	0.16	14.57	**0.001**
Year	1	3958	0.04	3.19	**0.003**
N:Kp.re	3	22484	0.20	4.84	**0.001**
N:Sp.re	3	25188	0.22	5.59	**0.001**
KpSp.re	3	33027	0.29	8.06	**0.001**
N:Year	2	9876	0.09	2.85	**0.003**
Kp.re:Year	2	17399	0.15	5.41	**0.001**
Sp.re:Year	2	21850	0.19	7.13	**0.001**
N:KpSp.re	7	44249	0.39	5.02	**0.001**
N:Kp.re:Year	4	26087	0.23	4.31	**0.001**
N:Sp.re:Year	4	29293	0.26	5.03	**0.001**
KpSp.re:Year	4	36956	0.33	6.99	**0.001**
N:KpSp.re:Year	8	48177	0.43	4.98	**0.001**
Residuals	46	54016	0.48		
Total	61	112281	1.00		

of *S. purpurea*, and interannual variations on the evenness (Supporting information; $p = 0.002$).

Species and functional group responses after dominant species were removed

Nitrogen addition decreased the coverage of sedge and forbs. Without nitrogen addition, the removal of *K. pygmaea* and the simultaneous removal of *K. pygmaea* and *S. purpurea* significantly decreased the sedge coverage. Under nitrogen addition, the removal of *S. purpurea* and the simultaneous removal of *K. pygmaea* and *S. purpurea* significantly decreased the grass coverage in 2024. The removal of *K. pygmaea* significantly increased the Leguminosae coverage in 2024 (Supporting information). We found that when *K. pygmaea* and *S. purpurea* were removed simultaneously and separately, compared with the control, sedge and forbs decreased, while Leguminosae increased. Grass decreased, except when *K. pygmaea* was removed without nitrogen addition in 2024, in which case it increased (Supporting information).

Nitrogen addition and the removal of *K. pygmaea* led to the reordering of species in the remaining community. After the removal of *S. purpurea, K. pygmaea* became the species with the highest abundance. When both *K. pygmaea* and *S. purpurea* were removed simultaneously, the forbs became the species with the highest abundance (Fig. 3). In order to understand the response degree of different species under different removal treatments, we sorted the response ratios of the coverage of all species under different treatments to the control. We found that leguminous plants exhibited the strongest positive responses, while forbs and sedges showed the most pronounced negative responses (Fig. 4, 5). In addition, there is an interaction among the removal of two dominant species, nitrogen addition, and year, which affects the changes in community composition (Supporting information).

Discussion

Inconsistent with our hypothesis, after removing the dominant species *K. pygmaea*, no obvious compensatory effect of the remaining dominant species *S. purpurea* was observed. Similarly, after removing the dominant species *S. purpurea*, no significant compensation effect of the remaining dominant species *K. pygmaea* was observed. We found that the response of *Hedysarum tibeticum* (Leguminosae) was the greatest among all the treatments of removing dominant species. In addition, nitrogen addition reduced the compensatory response, and the compensation responses to nitrogen under different removal treatments were different. Our results emphasize the functional independence among different dominant species and the crucial role of key functional groups (such as leguminous plants) in the restoration of grassland productivity. In the context of biodiversity extinction, they should be protected according to their unique functions and ecological niches.

The co-dominant species did not exhibit dominant compensation after dominant species were removed

Consistent with the short-term removal experiments (Wardle et al. 1999, Li et al. 2020, Chaves and Smith 2021), in the 13-year removal experiment of this study, the productivity lost due to the removal of dominant species has still not been fully restored. As the mass ratio hypothesis (Grime 1998, Geider et al. 2001) suggests, dominant species, which are the most abundant components in a community, play a decisive role in the functioning of the ecosystem. Although our removal experiment has been carried out for 13 years, it is likely that a 13-year recovery period is still insufficient to account for the impacts of the loss of dominant species. Secondly, although the remaining community exhibited a compensatory response, it did not fully recover to the initial level after dominant species were removed. This indicates that even if there are functionally similar species compensating for the productivity lost due to the absence of the dominant species, the initial abundance of the species also affects the productivity recovery after species loss. Our results also show that after dominant species were removed, there is a significant gap between the initial abundances of most of the species with high abundance rankings and the initial abundance of the dominant species.

We anticipate that after the dominant species are removed, competitive release will exert a positive influence on the remaining dominant species in the community, stimulating their growth and ultimately giving rise to a compensatory effect (Grime 1973, Wardle et al. 1999). However, we found that after the removal of the dominant species *K. pygmaea* and when both *K. pygmaea* and *S. purpurea* were removed simultaneously, the remaining dominant species *S. purpurea*

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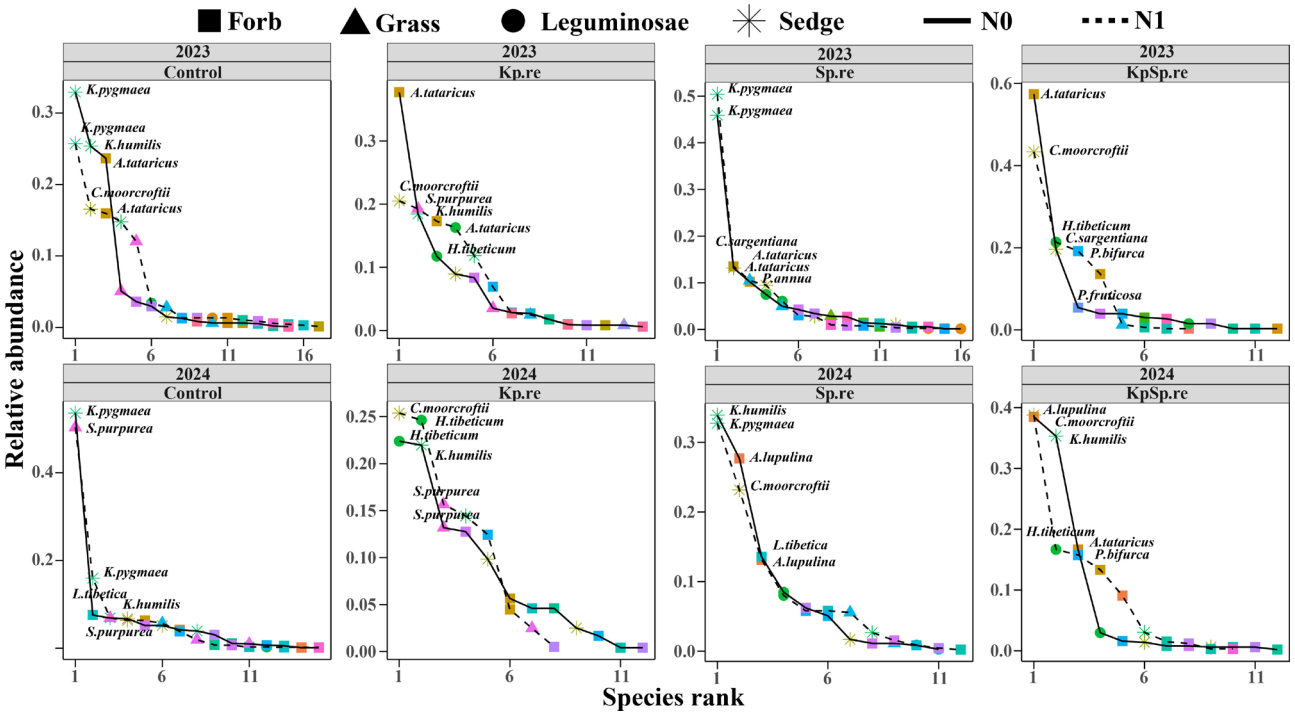


Figure 3. Relative abundance curves under different treatments, showing the top three ranked species. The experiment was conducted under two nitrogen treatments: no nitrogen addition (N0) and nitrogen addition (N1, 30 g m^{-2} per year). Kp.re represents the treatment where *Kobresia pygmaea* was removed. Sp.re represents the treatment where *Stipa purpurea* was removed. KpSp.re represents the treatment where both *K. pygmaea* and *S. purpurea* were removed simultaneously. The data is presented by year, with different shapes representing different functional groups. Species code: *Kobresia pygmaea* (*K. pygmaea*, sedge), *Stipa purpurea* (*S. purpurea*, grass), *Kobresia humilis* (*K. humilis*, sedge), *Carex moorcroftii* (*C. moorcroftii*, sedge), *Aster tataricus* (*A. tataricus*, forb), *Carex sargentiana* (*C. sargentiana*, sedge), *Poa annua* (*P. annua*, grass), *Hedysarum tibeticum* (*H. tibeticum*, Leguminosae), *Potentilla bifurca* (*P. bifurca*, forb), *Potentilla fruticosa* (*P. fruticose*, forb), *Lancea tibetica* (*L. tibetica*, forb), *Ajuga lupulina* (*A. lupulina*, forb).

did not become the most abundant species. In contrast, when the dominant species *S. purpurea* was removed, the remaining dominant species *K. pygmaea* became the most abundant species as we had anticipated. One possible explanation lies in the morphological and physiological differences between the two dominant species. We found that after the removal of the dominant sedge plant *K. pygmaea*, the abundance of forbs in the community or sedge plants within the same functional group became the highest. This might be related to their more similar ecological niches and functions. For example, they are all shallow-rooted plants, capable of quickly absorbing nutrients from the soil surface (Miehe et al. 2019). When the grass plant *S. purpurea* was removed, due to the small number of grasses remaining in the community and the fact that the remaining species were all shorter plants, there was an obvious differentiation in ecological niches compared with *S. purpurea*. It is generally believed that grasses have a stronger ability to compete for light (Namuhan et al. 2024, Baird et al. 2025).

Generally, after the removal of a dominant species, compensation tends to occur through three types of species: 1) co-dominant species within the remaining community (Akhmetzhanova 2010, Pan et al. 2016), 2) subordinate species from the same functional group (Joner et al. 2011, Souza et al. 2011, Chaves and Smith 2021), and 3) species from a different functional group (Bret-Harte et al. 2004, Suding et al. 2006, Cross and Harte 2007, Pan et al. 2016). Similarly, in our study, whether the dominant species *K. pygmaea* and *S. purpurea* were removed individually or both of these dominant species were removed simultaneously, the species that showed the greatest response was *H. tibeticum*, a common leguminous plant in the alpine meadow. However, because its plants are inherently short and it belongs to the colonizing species, its response to compensation is also limited.

Compensation can occur through increasing the utilization rate of organism functions, increasing the number of individuals of species in the remaining community, and promoting the colonization of new species (Hiddink and Davies 2024). However, there are some limitations in using cover to substitute for productivity compensation, such as the species compensation effect calculated by cover more reflecting the abundance effect of the community. Nevertheless, we still obtained some interesting results. This study found that the leguminous plant *H. tibeticum* is the species that shows the greatest response among all the treatments of dominant species removal, and this plant is absent in the control treatment. The removal of dominant species may lead to a large number of ecological niche vacancies and the release of resource competition, and this process may be more favorable to nitrogen-fixing plants than non-nitrogen-fixing plants, especially

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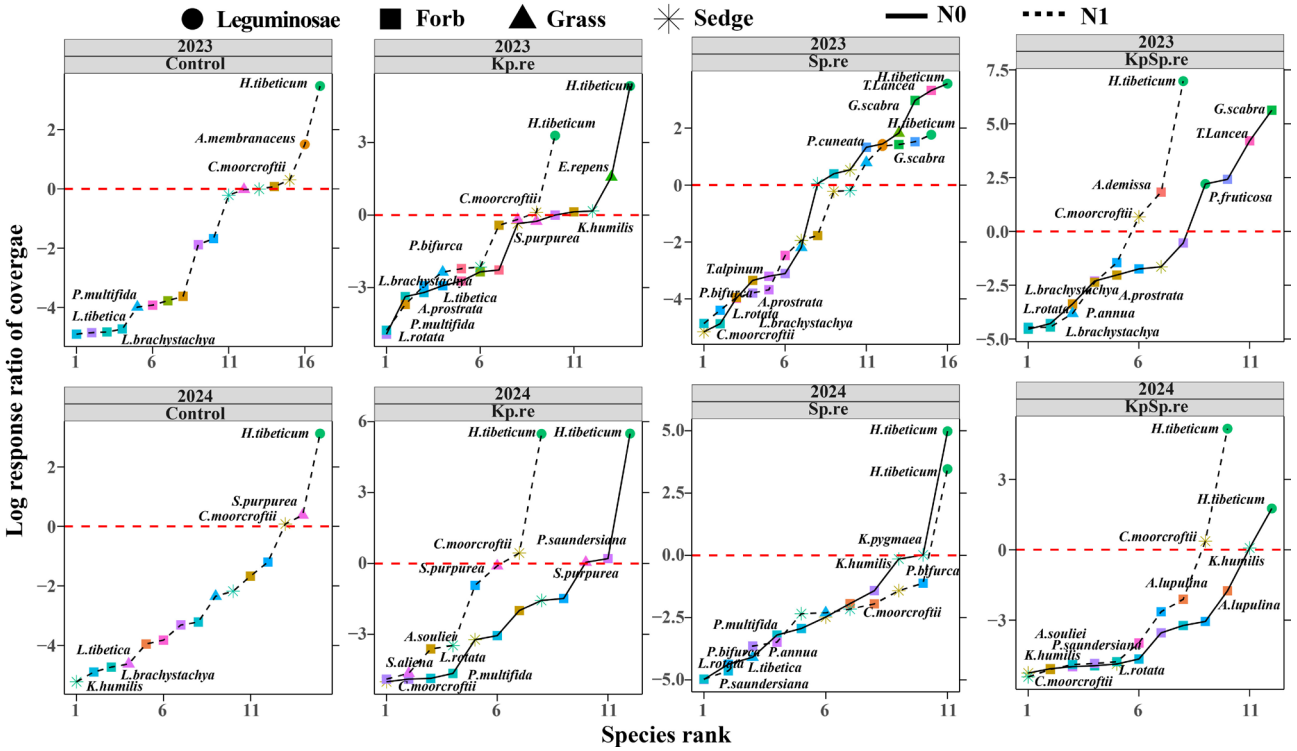


Figure 4. Species ranked by their cover response ratios under different treatments, showing the top three and the bottom three species. The experiment was conducted under two nitrogen treatments: no nitrogen addition (N0) and nitrogen addition (N1, 30 g m^{-2} per year). Kp.re represents the treatment where *Kobresia pygmaea* was removed. Sp.re represents the treatment where *Stipa purpurea* was removed. KpSp.re represents the treatment where both *K. pygmaea* and *S. purpurea* were removed simultaneously. The data is presented by year, with different shapes representing different functional groups. The red dashed line indicates a response ratio of 0, meaning no significant change in cover compared to the control. Values greater than 0 indicate an increase in cover relative to the control, while values less than 0 indicate a decrease. Species code: *Kobresia pygmaea* (*K. pygmaea*, sedge), *Stipa purpurea* (*S. purpurea*, grass), *Kobresia humilis* (*K. humilis*, sedge), *Carex moorcroftii* (*C. moorcroftii*, sedge), *Aster tataricus* (*A. tataricus*, forb), *Poa annua* (*P. annua*, grass), *Hedysarum tibeticum* (*H. tibeticum*, Leguminosae), *Potentilla bifurca* (*P. bifurca*, forb), *Potentilla fruticosa* (*P. fruticose*, forb), *Lancea tibetica* (*L. tibetica*, forb), *Ajuga lupulina* (*A. lupulina*, forb), *Astragalus membranaceus* (*A. membranaceus*, Leguminosae), *Elytrigia repens* (*E. repens*, grass), *Lagotis brachystachya* (*L. brachystachya*, forb), *Lamiophlomis rotata* (*L. rotata*, forb), *Axyris prostrata* (*A. prostrata*, forb), *Gentiana scabra* (*G. scabra*, forb), *Potentilla cuneata* (*P. cuneata*, forb), *Artemisia demissa*, (*A. demissa*, forb), *Stipa aliena* (*S. aliena*, grass), *Potentilla saundersiana* (*P. saundersiana*, forb).

in ecosystems that are limited by nutrients (McKey 1994). Leguminous plants have stronger competitive advantages compared with forbs and grass plants. In addition, due to their biological nitrogen-fixing ability, leguminous plants are less affected by the priority effect, enabling them to adapt to nutrient-poor environments (van Steijn et al. 2025). Leguminous plants can convert nitrogen gas in the atmosphere into forms that can be utilized by plants. This function plays a crucial role in maintaining the balance of the nitrogen cycle in ecosystems. The nitrogen fixed by leguminous plants increases the nitrogen content in the soil, providing more nitrogen sources for other plants and promoting their growth and development (McKey 1994, Vitousek et al. 2010). Secondly, leguminous plants provide crucial genetic resources for the genetic improvement of protein-rich crop and forage species. In sustainable livestock production, leguminous plants, as high-quality forage, contribute to improving the nutritional level and production performance of livestock. This is of vital importance for ensuring food security and the sustainable development of agriculture (Vitousek et al. 2010). However, at the same time, atmospheric nitrogen deposition and other anthropogenic nitrogen supply pathways are expected to significantly reduce their competitive advantages in plant communities (Suding et al. 2005, Storkey et al. 2015). Therefore, in situations where the soil nitrogen content is high, they will be at a disadvantage due to the high energy cost of nitrogen fixation (Houlton et al. 2008). This may explain why the positive response of leguminous plants is weakened after nitrogen addition when the dominant species are removed individually. We expect that when one of the dominant species is removed, the lost productivity will be compensated mainly by the remaining dominant species. However, this result was not observed, which indicates that there is an obvious niche differentiation between *K. pygmaea* and *S. purpurea*. Due to their different life histories and strategies for coping with the environment, the two dominant species did not compensate for each other after one of them was removed (Wang et al. 2023, Niu et al. 2025). Our results emphasize the importance of leguminous plants as grass species for restoration in alpine regions.

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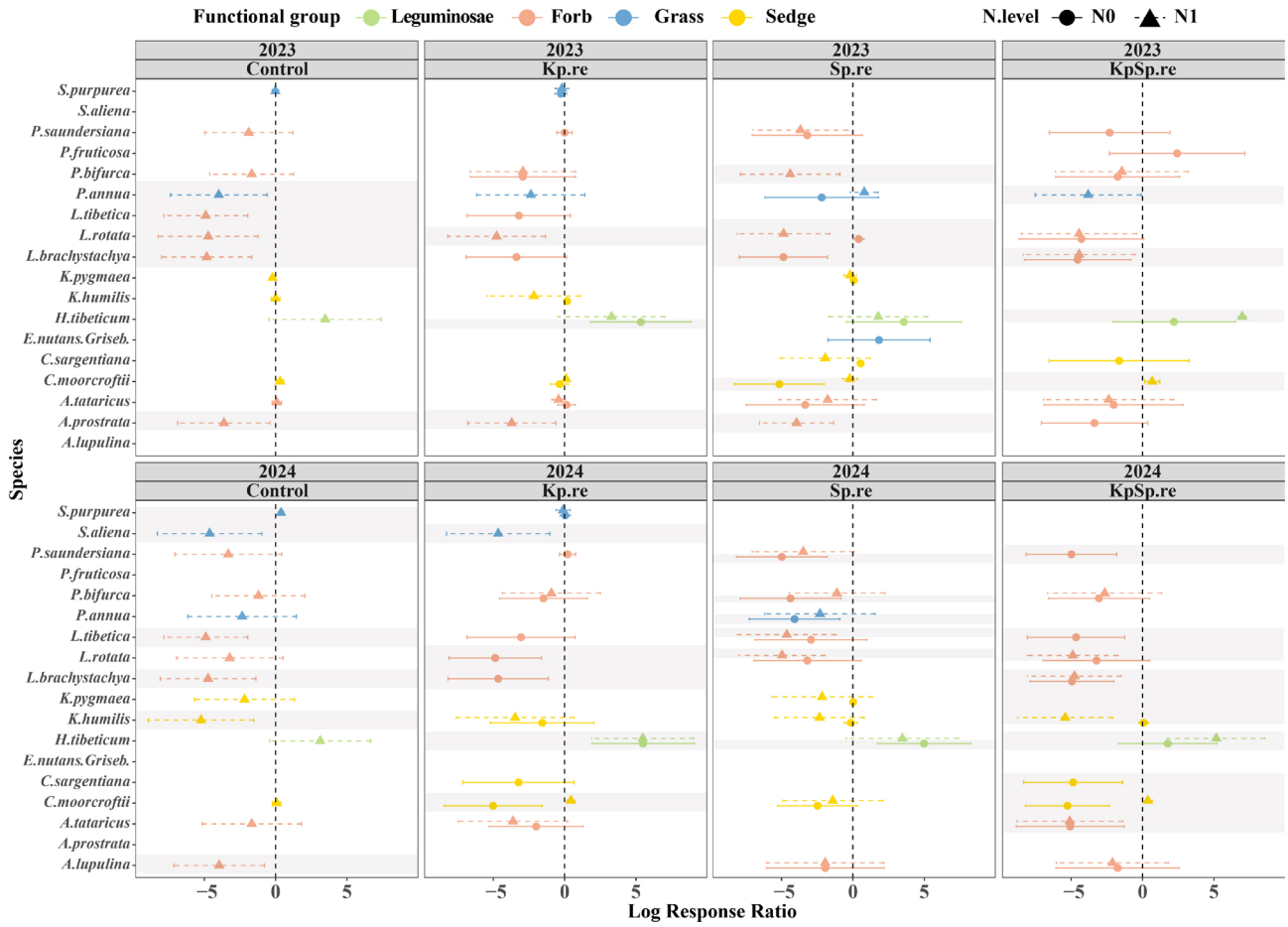


Figure 5. Based on SIMPER analysis, the figure shows the log response ratios of coverage for the ten species contributing most to community compositional changes under different removal treatments in an alpine meadow, following the exclusion of *Kobresia pygmaea* and *Stipa purpurea*. The data are presented by year, with different shapes representing different nitrogen levels and different colors representing different functional groups. The experiment was conducted under two nitrogen treatments: no nitrogen addition (N0) and nitrogen addition (N1, 30 g m^{-2} per year). Kp.re represents the treatment where *Kobresia pygmaea* was removed. Sp.re represents the treatment where *Stipa purpurea* was removed. KpSp.re represents the treatment where both *K. pygmaea* and *S. purpurea* were removed simultaneously. Error bars that intersect with $x=0$ indicate that the species' response is not statistically significant. Therefore, species with non-significant coverage responses are shown with black lines. Species code: *Stipa purpurea* (*S. purpurea*, grass), *Stipa aliena* (*S. aliena*, grass), *Potentilla saundersiana* (*P. saundersiana*, forb), *Potentilla fruticosa* (*P. fruticose*, forb), *Potentilla bifurca* (*P. bifurca*, forb), *Poa annua* (*P. annua*, grass), *Lancea tibetica* (*L. tibetica*, forb), *Lamiophlomis rotata* (*L. rotata*, forb), *Lagotis brachystachya* (*L. brachystachya*, forb), *Kobresia pygmaea* (*K. pygmaea*, sedge), *Kobresia humilis* (*K. humilis*, sedge), *Hedysarum tibeticum* (*H. tibeticum*, Leguminosae), *Elymus nutans*, (E. nutans, grass), *Carex sargentiana* (*C. sargentiana*, sedge), *Carex moorcroftii* (*C. moorcroftii*, sedge), *Aster tataricus* (*A. tataricus*, forb), *Axyris prostrata* (*A. prostrata*, forb), *Ajuga lupulina* (*A. lupulina*, forb). Species with significant cover responses are highlighted with shading in the figure.

Nitrogen addition resulted in a reduction of the compensation effect

Surprisingly, nitrogen, which is a commonly limiting resource for grassland productivity, did not promote the compensatory effect after being added. Instead, it led to a decrease in the compensatory effect after the individual removal of *K. pygmaea* and *S. purpurea*. This is inconsistent with some studies (Pan et al. 2016, Read et al. 2018, Hiddink and Davies 2024). The ecosystem in this study is an alpine meadow, and recent research increasingly indicates that this ecosystem is co-limited by nitrogen and phosphorus (Zhu et al. 2023, Li et al. 2024). Thus, the input of high levels of nitrogen alone may lead to negative effects such as stoichiometric imbalance, acidification, and metal ion toxicity (Li et al. 2021, Namuhan et al. 2024). According to resource competition theory, a species' ability to endure environments with minimal essential resources is fundamental to its competitive success (Tognetti et al. 2021). Consequently, plant functional groups that employ specialized nutrient uptake strategies are likely to outperform others in nutrient-poor environments, yet they tend to be especially sensitive to conditions of nutrient surplus (Suding et al. 2005, Tilman 2020). We found that after the removal of *K. pygmaea*, the addition of nitrogen caused the positive response of the grass to turn negative. A possible reason is that after the nitrogen addition, we found that *Carex moorcroftii* (*C. moorcroftii*, sedge) increased significantly.

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Due to its more similar functions to *K. pygmaea*, both are the main dominant plants in alpine meadow communities (Wang et al. 2023), it led to stronger competitive exclusion of other species. Eventually, the degree of decline of other species exceeded the degree of its own increase, ultimately resulting in a decrease in the compensatory effect. However, after the removal of *S. purpurea*, nitrogen addition mainly reduced the positive response of leguminous plants and increased the negative response to forbs. This indicates that nitrogen addition is unfriendly to leguminous plants (Tognetti et al. 2021). A possible explanation is that the removal of grass plants has altered the microenvironment of aboveground plants, such as the light conditions. After the addition of nitrogen, it has led to stronger environmental filtering, resulting in the elimination of more species (Zhang et al. 2022). Therefore, our results emphasize that for grasslands under nutrient co-limitation, the input of a single resource is detrimental to the restoration after biodiversity loss.

The loss of dominant species is more often considered to lead to a decline in productivity. However, its impacts on species richness and diversity can be either positive (McCain et al. 2010, Avolio et al. 2019), or neutral (Roth et al. 2008). In this study, however, we found that both richness and diversity decreased after removing *K. pygmaea* and *S. purpurea* individually, as well as after removing both dominant species simultaneously. We speculate that the removal increased the dominance of the remaining dominant species, either *K. pygmaea* or forbs, which in turn had a negative impact on diversity. Secondly, we speculate that the removal of the dominant grass *S. purpurea* may have altered the local microenvironment, resulting in stronger radiation and drier soil (Chaves and Smith 2021). Additionally, fertilization is generally thought to reduce diversity due to environmental filtering (Gough et al. 2000, Suding et al. 2005, Bowman et al. 2006, Harpole et al. 2016, Zhu et al. 2023). In this study, the impact of fertilization on biodiversity varied among different treatments and across different years. Therefore, fertilization adds more uncertainties to the prediction of biodiversity changes following species loss. Thirdly, we emphasize that the removal of dominant species does not increase biodiversity. On the contrary, the removal of dominant species may change the interaction relationships among the remaining species, leading to the loss of more species. This suggests that although the loss of dominant species can release more resources and create niche vacancies, it may also alter the interspecific relationships and microenvironment of the remaining community, a process that could be detrimental to the remaining species.

Conclusions

This 13-year experiment reveals that alpine grassland communities exhibit limited compensation for productivity loss following dominant species removal. This is due to the negative response of forbs and sedges following the loss of dominant species. Although legumes exhibit a strong positive response, their abundance is insufficient to compensate for the negative effects caused by the loss of the dominant species. Partial compensation (CI < 1) across all removal treatments indicates that, even after over a decade, productivity has not recovered to the initial levels prior to the loss of dominant species. These results highlight that dominant species play a dual role: they sustain productivity while also occupying unique ecological niches in the community. However, nitrogen addition attenuated legume responses, possibly due to reduced competitive advantage under elevated nitrogen or stoichiometric imbalances in this co-limited system, emphasizing the context-dependent nature of compensation.

Species reordering was evident: forb dominance emerged under dual removal, while *K. pygmaea* regained top abundance after *S. purpurea* removal. These shifts reflect niche differentiation and competitive release, with functional group turnover mediating community restructuring. The decline in richness and diversity post-removal challenges the notion that dominant species loss enhances biodiversity, instead suggesting that intensified competition or microenvironmental changes (e.g. light availability) drive homogenization.

Our study underscores the importance of preserving both dominant species and functional groups (e.g. legumes) in alpine ecosystems. Under global change, nitrogen deposition may erode the compensatory capacity of nitrogen-fixing species, exacerbating vulnerabilities in nutrient-constrained grasslands. The study contributes valuable insights into the complex interactions that govern species loss and recovery, particularly in alpine regions vulnerable to environmental changes.

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Author contributions

Wenyu Li: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Methodology (lead); Software (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Quzong Ciren**: Data curation (supporting); Writing – review and editing (supporting). **Xianzhou Zhang**: Conceptualization (supporting); Writing – review and editing (supporting). **Shiping Wang**: Conceptualization (supporting); Data curation (supporting). **Yangjian Zhang**: Conceptualization (supporting); Writing – review and editing (supporting). **Xine**

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Li: Conceptualization (lead); Data curation (supporting). **Yunlong He**: Writing – review and editing (supporting). **Ge Hou**: Data curation (supporting), Formal analysis (supporting). **Rina Wendu**: Data curation (equal); Formal analysis (equal). **Wenchao Wu**: Data curation (supporting); Formal analysis (supporting). **Dorji Tsechoe**: Conceptualization (equal); Funding acquisition (equal); Writing – review and editing (equal). **Lin Jiang**: Conceptualization (supporting); Writing – review and editing (equal). **Josep Peñuelas**: Conceptualization (supporting); Writing – review and editing (equal). **Yann Hautier**: Conceptualization (supporting); Writing – review and editing (equal). **Juntao Zhu**: Conceptualization (equal); Funding acquisition (lead); Writing – review and editing (equal).

Data availability statement

All data and code are available from the Figshare Digital Repository: https://doi.org/10.6084/m9.figshare.29356511 (Li et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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