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Research article

Space resource utilization of dominant species integrates abundance- and functional-based processes for better predictions of plant diversity dynamics

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Sustainable ecosystem management relies on our ability to predict changes in plant diversity and to understand the underlying mechanisms. Empirical evidence demonstrates that abundance- and functional-based processes simultaneously explain the loss of plant diversity in response to human activities. Recently, a novel indicator based on percent cover ($Cover_D$) and maximum height ($Height_D$) of the dominant plant species – space resource utilization (SRU_D) – has proven to give robust and better predictions of plant diversity dynamics than community biomass. Whether the superior predictive ability of SRU_D is due to its capacity to simultaneously capture abundance- and functional-based processes remains unknown. Here, we tested this hypothesis by quantifying mechanistic links between changes in SRU_D and biodiversity in response to nutrients and herbivores. Furthermore, we assessed the relative contribution of dominant, intermediate and rare species to reduced density of individuals by combining null model analysis with field experiments. We found that SRU_D successfully captured changes in ground-level light availability and changes in the number of individuals to predict plant diversity dynamics, and each of $Cover_D$ and $Height_D$ partly and independently contributed to both processes. Comparative results from null model analysis and field experiments confirmed that individual losses of dominant, intermediate and rare species followed non-random processes. Specifically, compared with random loss process, rare species lost proportionally more individuals and thus disproportionately contributed to species loss, while dominant and intermediate species lost less. Our results demonstrate that SRU_D captures both abundance- and functional-based processes thus explaining why SRU_D provides more accurate predictions of changes in species diversity. Given that rare species can play an important role in shaping community structure, resisting against invasion, impacting higher trophic levels and providing

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multiple ecosystem functions, reducing the SRU of dominant species could alleviate the risk of exclusion of rare species by mitigating abundance- and functional-based competition processes.

Keywords: abundance-based processes, dominant species, functional-based processes, non-random loss, number of individuals, space resource utilization, species richness

Introduction

Grasslands are one of the most important ecosystems in terms of their contribution to global food production, carbon storage, climate change mitigation, pollination and scenic beauty (Hungate et al. 2017, Dass et al. 2018), and grassland plant diversity plays a critical role for the maintenance of these services (Olff and Ritchie 1998, Oba et al. 2001, Isbell et al. 2013, Hautier et al. 2015). However, human alterations of the environment are causing the loss of biodiversity from different habitats, resulting in unprecedented rate of plant species extinction worldwide (Sala et al. 2000, De Vos et al. 2015). In particular, nutrient enrichment and changes in herbivore density are known to jointly regulate local and regional plant diversity (Worm et al. 2002, Hillebrand et al. 2007, Borer et al. 2014b). Nutrient enrichment causes diversity loss in many grasslands, and herbivores can counteract diversity losses arising from nutrient enrichment by reducing the advantage of fast-growing and often more competitive species (Borer et al. 2014b). The challenge facing ecologists and decision-makers is to identify the general principles that govern the impact of human activities on plant diversity dynamics and to develop appropriate management tools and strategies. This challenge is only likely to be met if the main drivers and underlying mechanisms can be identified using robust and simple techniques.

Numerous studies investigating the processes by which nutrient enrichment and removal of herbivores jointly regulate local plant diversity as productivity increases have identified two main types of processes: abundance based and functional based. If abundance-based processes control community change (aka: density hypothesis; and trait-neutral hypothesis), loss is independent of species identity and type of perturbation and each species experiences an equal probability of loss of individuals (Stevens and Carson 1999, Suding et al. 2005, Yang et al. 2015). This leads to a reduction in the number of individuals per unit of space and the extinction of rare species is more likely because of their lower number of individuals (Luo et al. 2006). In contrast, if the community is controlled by functional-based process (aka: environmental filtering; and trait-based hypothesis), species with functional traits that are advantageous under novel conditions can competitively exclude other species (Dybzinski and Tilman 2007, Niu et al. 2008, Hautier et al. 2009). Specifically, human disturbances that favour species with fast resource acquisition and conversion into new tissue can lead to the dominance by faster growing or taller species, reducing ground-level light availability and excluding smaller, shaded species situated in the understory (Dickson and Foster 2011,

DeMalach et al. 2017). Empirical studies have shown that abundance-based process (changes in the number of individuals) and functional-based process (changes in ground-level light availability) are occurring simultaneously (Suding et al. 2005, Luo et al. 2006, Niu et al. 2008, Pan et al. 2011, Yang et al. 2015). However, indicators that can capture both processes to predict plant diversity dynamics are still lacking.

Recently, a novel indicator based on two key plant factors – percent cover and maximum height – combined into a single index representing space resource utilization (SRU), has been developed to predict diversity dynamics (Zhang et al. 2015). Evidence in grassland communities has shown that SRU measured for only a few dominant species (SRU_D) provides robust predictions of plant diversity dynamics in response to nutrient addition and altered herbivore densities (Zhang et al. 2015, 2019). This novel indicator (SRU_D) outperformed predictions based on community productivity or based on SRU of community (SRU_C), regardless of the specific plant species involved and the habitat examined (Zhang et al. 2019). This superior predictive ability of SRU_D may be attributed to the independent capacity of the two factors to represent plant competition for resources in multiple dimensions, and thus to have the potential to drive changes in ground-level light availability and the number of individuals, but evidence remains lacking. In other words, dominant species' height and cover represent these species' competitive ability for resource such as space and light in different dimensions, with height and cover representing the vertical and horizontal dimensions, respectively. When combined into a single index, SRU_D, these factors might thus represent dominant species' competitive ability in a three-dimensional volume that incorporates competition for light and space in multiple dimensions.

A core hypothesis for the superior predictive ability of SRU_D is that changes in both ground-level light availability and the number of individuals in the community (NI_C) can be captured and driven by a minority of dominant species that subsequently contribute to plant diversity dynamics. We tested this hypothesis by quantifying mechanistic links between changes in other variables and changes in species richness in response to nutrient addition and herbivore (vertebrate consumers) exclusion using data of one site from a project termed 'nutrient network' (NutNet) (Borer et al. 2014a). First, SRU_D, ground-level light availability and NI_C was used individually and collectively in statistical models for predicting changes in species richness. Second, we quantified the extent to which SRU_D captures changes in ground-level light availability and the number of individuals to fundamentally drive and predict plant diversity dynamics in this alpine

grassland site. Next, we assessed the relative contribution of dominant, intermediate and rare species to the reduced density of individuals (community thinning). Finally, we combined null model analysis with field experiments to test whether the losses of dominant, intermediate and rare species are random. We investigated mechanistic links by comparing bivariate relationships with multivariate partial relationships derived from a structural equation model (Grace et al. 2007).

Material and methods

Study site

The site used in our study is part of the nutrient network (NutNet; http://nutnet.org/), which is the only site that collected data of height, coverage and the number of individuals for all species in each plot (Borer et al. 2014a, Zhang et al. 2019). The experiment was carried out at the Gansu Gannan Grassland Ecosystem National Observation and Research Station of Lanzhou University (Maqu branch) in the eastern Tibetan Plateau (33°40′5″N, 101°51′44″E, altitude 3500 m a.s.l.), Gansu, China. The mean annual temperature (MAT) at this site is 1.2°C, ranging from −10°C in January to 11.7°C in July, and the mean annual precipitation (MAP) for the period from 1975 to 2012 was 620 mm, with precipitation mainly occurring during the short, cool summer. Mean richness in the untreated control plots is around 32.3 species. The area has 2580 h of sunshine and > 270 days of frost per year. The vegetation in this area, which is categorized as a typical Tibetan alpine meadow, is dominated by *Kobresia graminifolia* (Cyperaceae), *Elymus nutans* (Poaceae), *Anemone rivularis* (Ranunculaceae), *Poa poophagorum* (Poaceae) and *Carex kansuensis* (Cyperaceae), and the average above-ground dry biomass is 360–560 g m⁻². The dominant animals in the area include livestock (e.g. yaks, Tibetan sheep and horses), marmots *Marmota himalayana*, zokor *Myospalax* spp. and various ant species.

Experimental design

The field experiment was set up in April 2008 and has been described elsewhere (Zhang et al. 2019). Nutrient addition and herbivore exclusion were manipulated in a randomized block design with three replicated blocks of ten plots each (Borer et al. 2014a). There are 10 treatments – addition of nitrogen (N), phosphorus (P) and potassium (K) in a full factorial (NPK+) design and a fencing treatment crossed with NPK+. N, P and K were added annually as 10 g N m⁻² year⁻¹ of time-release urea [(NH₂)₂CO], 10 g P m⁻² year⁻¹ of triple-super phosphate [Ca(H₂PO₄)₂], 10 g K m⁻² year⁻¹ of potassium sulphate [K₂SO₄] before the beginning of the growing season. In the experimental year one only (2008), we added 100 g m⁻² of a micronutrient mix consisting of Fe (15%), S (14%), Mg (1.5%), Mn (2.5%), Cu (1%), Zn (1%), B (0.2%) and Mo (0.05%).

Measurements

In 2012, after five years of treatments, measurements were carried out at the seasonal peak in biomass (mid-August) in a fixed 0.5 × 0.5 m subplot randomly assigned within each plot for this study in 2012 (Zhang et al. 2019). The number of individuals, cover, maximum height and biomass for each species were all collected in this fixed 0.5 × 0.5 m subplot. But light availability was measured in a 1 × 1 m plot centered on the above fixed subplot because of the 1 m PAR sensor size. The number of individuals for each species (NI_{Si}) in each subplot was recorded as the total number of ramets for clonal species and the number of individuals for non-clonal species. For clonal species, it is easy to identify ramets by the location of their growth and distance from other clones. Cover was estimated independently for each species in each subplot. Total summed cover can exceed 100% due to multilayer canopies. Note that while total summed cover can exceed 100% for multilayer canopies, this does not affect the calculation of SRU as this calculation is based on species' rank. Maximum height was estimated for one to five randomly selected individuals per species in each subplot as the shortest distance between the upper boundary of the main photosynthetic tissues on a plant and the ground level. Then we calculated the average maximum height of each species in each subplot according to the height of sampled individuals. Aboveground live biomass was clipped to ground level in each subplot, dried to constant mass at 60°C, and weighed to the nearest 0.01 g. Biomass was sorted to species. The percentage of light transmitted at the ground was calculated as the ratio of the average of two light measurements at ground level (at opposite corners of the 1 × 1 m plot, diagonal to each other) and one above the canopy. Light was measured using a 1 m PAR sensor on a cloudless day as close to solar noon as possible (11:00–14:00 h).

Calculations for SRU, biomass, the number of individuals (NI) and the relative number of individuals (RNI) for each of dominant, intermediate and rare groups

In this experiment, species richness, defined as the number of species per unit area (0.25 m²), ranged from 20 to 34 (rank i to j; $i = 1$, $20 \leq j \leq 34$). Firstly, we ranked species based on their cover within each plot using the 'rankabundance' function in the 'BiodiversityR' package (Kindt and Coe 2005) and divided all species into three abundance groups (dominant, intermediate and rare). These groups were defined as follows: dominant species, which represent the top ≥ 60% of total cover, included the first three species ($i = 1$, $j = 3$); rare species, which represent the bottom ≤ 10% of total cover, included the last 24 species or less ($i = 11$, $j \leq 34$); and intermediate species, which represent the mid ≈ 30% of total cover, included the remaining 7 species ($i = 4$, $j = 10$). The total community included all

three groups and species ($i = 1$, $j \leq 34$), which represent 100% of total cover. We also made a similar classification according to the proportion of total biomass. These thresholds are comparable to other studies (Soliveres et al. 2016, Zhang et al. 2019).

We calculated species-level SRU ($SRUs_i$) in each subplot as:

$$SRU_{Si} = H_i C_i A \tag{1}$$

where H_i and C_i are the average maximum height and percent cover respectively for species i in a subplot, and A is the subplot area (Zhang et al. 2015, 2019). The unit of SRU is m^3.

Secondly, based on the sets of thresholds mentioned above for each of three abundance groups, we calculated biomass and SRU for the total community, dominant, intermediate and rare species in each subplot as:

$$Biomass = \sum_i^j Biomass Si \tag{2}$$

$$SRU = \sum_i^j SRU Si \tag{3}$$

And based on the number of individuals (NI) of each species in each subplot, we also calculated the number of individuals per subplot for all community (NI_C) and each of three abundance groups: dominant (NI_D), intermediate (NI_I) and rare species (NI_R) as:

$$NI = \sum_i^j NI_{Si} \tag{4}$$

where i and j are the species' ranks mentioned above for community and each of three abundance groups.

Similarly, we calculated the relative number of individuals (RNI) within each subplot for three abundance groups: dominant (RNI_D), intermediate (RNI_I) and rare species (RNI_R) as:

$$RNI = \frac{NI}{NI_C} \tag{5}$$

where RNI_D is the ratio of NI_D to NI_C; RNI_I is the ratio of NI_I to NI_C; and RNI_R is the ratio of NI_R to NI_C.

We estimated the effects of treatments on SRU_D, light, $Biomass_D$, $Biomass_C$, the number of individuals (NI), the relative number of individuals (RNI) and species richness as changes in each variable resulting from treatments as compared to the control subplot in the same block. We quantified these changes as natural logarithm of the ratio (LRR) of the variable within a treatment subplot to the control subplot in the same block.

Statistical analyses

We performed the following analyses for testing our main hypothesis that SRU_D drives changes in ground-level light availability and the number of individuals, and thus contributes the most to predictions of changes in species richness in response to anthropogenic disturbances.

First, we use bivariate relationships to assess whether each of changes in SRU_D, changes in NI_C and changes in ground-level light availability predict changes in species richness. Abundance-based process was assessed by measuring changes in NI_C in a treated subplot as compared to the control subplot in the same block. A reduction of NI_C in response to a treatment indicates a reduction of the density of individuals (the number of individuals per unit of space). A positive relationship between changes in NI_C and changes in species richness would indicate that diversity decline is at least partly driven by abundance-based process. Functional-based process was assessed by measuring changes in ground-level light availability in a treated subplot as compared to the control subplot in the same block. A positive relationship between changes in ground-level light availability and changes in species richness would indicate that diversity decline is at least partly driven by a reduction of photosynthetically active radiation (PAR) to ground level, under which species with traits optimal for light acquisition can competitively exclude other species by functional-based process.

Next, we used structural equation models (SEM) with the 'piecewiseSEM' package (Lefcheck 2016) to assess direct and indirect effects between the predictors described above. Our model integrates theoretical expectations from competing theories. Theoretical expectations regarding what causes changes in ground-level light availability and NI_C are based on changes in biomass, cover and height. Similarly, theoretical expectations regarding what causes changes in species richness are based on changes in ground-level light availability and NI_C.

To validate the specification of this SEM and to aid in the interpretation of the SEM results, we examined the multivariate partial relationships for this model by using partial regression analysis (Grace et al. 2012, 2016). In the results we only show the partial relationships of changes in SRU_D, ground-level light availability and NI_C with changes in species richness. We also compared SEM results based on SRU_D to those based on $Biomass_D$ and $Biomass_C$. Additionally, we used another SEM (Supporting information) to assess the individual contribution of each of the two factors generating SRU_D (i.e. $Cover_D$ and $Height_D$) to changes in ground-level light availability, changes in NI_C and changes in species richness. The conceptual SEM (Supporting information) allowed us to test our hypothesis that SRU_D captures changes in ground-level light availability and NI_C to fundamentally drive and predict plant diversity dynamics. The assumption is that our hypothesis would be validated if 1) SRU_D, ground-level light availability and NI_C explain most of the variance in species richness in the bivariate relationships, 2) SRU_D explains most of the variance in ground-level light availability and NI_C in SEM and 3) ground-level light availability

and NI_C do not predict richness anymore in SEM but SRU_D does, altogether demonstrating that changes in SRU_D capture changes in ground-level light availability and NI_C to predict changes in species richness.

We then tested the relative contribution of dominant, intermediate and rare species to the reduced density of individuals (community thinning), and posited that the number of individuals of all three abundance groups (dominant, intermediate and rare species) is decreasing with community thinning. To test this hypothesis, we evaluated relationships between changes in NI for each abundance group (NI_D, NI_I, NI_R) and changes in NI for the community (NI_C). A positive relationship would indicate that the reduced density of individuals of community is associated with a reduction of individuals of the abundance group investigated.

Additionally, we tested whether the losses of dominant, intermediate and rare species are random by combining null model analysis with field experiment. To assess this hypothesis, we first evaluated relationships between changes in the relative number of individuals for each of the dominant (RNI_D), intermediate (RNI_I) and rare species (RNI_R) with changes in the total number of individuals in the community (NI_C). A positive relationship would indicate that the abundance group investigated is at higher risk to be lost relatively to the other abundance group. In contrast, a negative relationship would indicate that the abundance group investigated has higher dominance in the community following the decline of NI_C. To determine whether observed changes in RNI_D, RNI_I and RNI_R were significantly different from a random expectation, we used a null model to generate 1000 random matrices using a conservative algorithm that maintained fixed sums of rows and columns total, so that each generated random matrix had the same number of species and abundance as the original matrix (Larsen and Ormerod 2014). The observed values and these random matrices were used to calculate a standardized effect size (SES) for each abundance group (dominant, intermediate and rare species) for each experimental treatment. SES is defined as follows:

$$SES = \frac{observed\ loss\ ratio - mean\ simulated\ loss\ ratio}{standard\ deviation\ of\ simulated\ loss\ ratio} \quad (6)$$

where loss ratio is equal to the relative number of individuals for each of abundance group in control minus the relative number of individuals for the same abundance group in each of other treatments divided by the relative number of individuals for the same abundance group in control. If SES > 2.0 or SES < −2.0, the individual loss in the abundance group investigated is a non-random process. Specifically, SES > 2.0 means the loss ratio of the abundance group investigated from our field experiments is significantly higher than from simulated null model; and SES < −2.0 means the loss ratio of the abundance group investigated from our field experiments is significantly lower than from simulated null model.

All relationships were modelled using the general linear models from the 'nlme' package (Pinheiro and Bates 2006). For all multivariate partial relationship analyses, we modelled the relationship by using the partial.resid function from the 'piecewiseSEM' package (Lefcheck 2016). For bivariate and multivariate partial relationship analyses, we used block as a random effect. In the text we present estimates of the slopes from the linear regression with their 95% confidence intervals (CI) and R^2 values as an indicator of the predictive power for all bivariate relationships. In SEM, we present standardized coefficients (r) as an indicator of the relative effect of changes in each of other variables on changes in species richness in the multivariate partial relationships (Grace et al. 2016). All analyses were conducted in R ver. 3.5.1 (www.r-project.org).

Results

SRU_D captures both abundance- and functional-based processes

Based on the five models with the smallest AIC from a full model in Table 1 and bivariate relationships in Fig. 1, we found that changes in NI_C and changes in ground-level light availability explained 47% and 54% of changes in species richness, respectively ($R^2 = 0.47$, AIC = −21.45; $R^2 = 0.54$, AIC = −25.07; Fig. 1b–c), and they together explained 63% of changes in species richness in response to experimental treatments ($R^2 = 0.63$, AIC = −28.64). Furthermore, changes in SRU_{D3} (three most dominant species which represent the top 60 of total cover) separately explained 72% of changes in species richness ($R^2 = 0.72$, AIC = −38.65; Fig. 1a). However, when all these three variables were present in the statistical model, they totally explained 75% of changes in species richness ($R^2 = 0.75$, AIC = −37.72) and only the

Table 1. Summary of the five models with the smallest AIC from a full model predicting changes in species richness from different predictors (NI_C, Light and SRU_D). NI_C is abbreviation of the number of individuals of community; Light is abbreviation of ground-level light availability; SRU_D is abbreviation of space resource utilization of dominant species, respectively. The model with the smallest AIC is the best. Significant values in bold: * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.

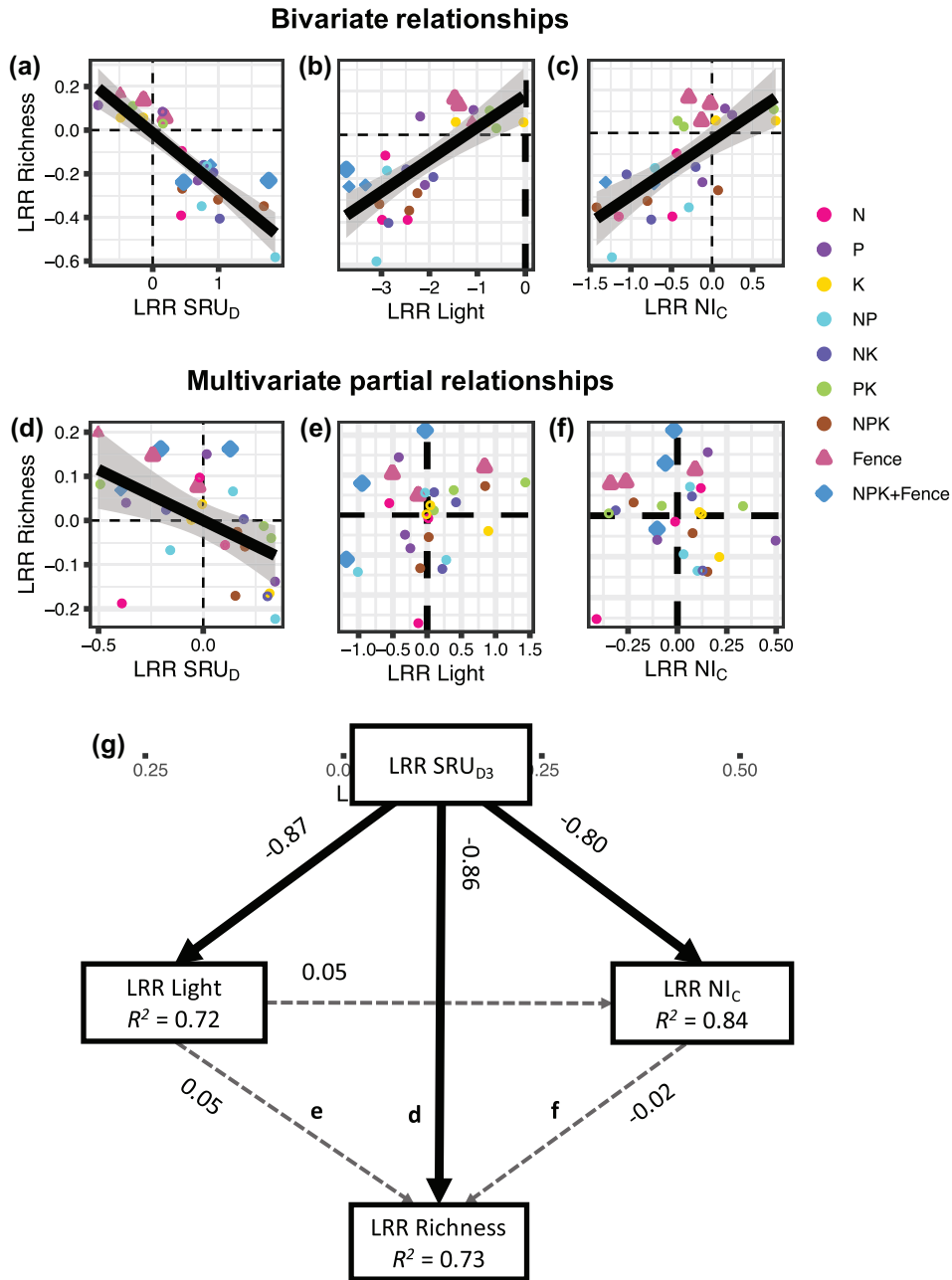| Dependent variable	Predictors in models	AIC	R^2	NI_C	Light	SRU_D
Species richness	~ NIC	−21.45	0.47	**0.26*****		
	~ Light	−25.07	0.54		**0.15*****	
	~ SRU_D	−38.65	0.72			**−0.25*****
	~ NI_C + Light	−28.64	0.63	**0.14***	**0.10****	
	~ SRU_D + NI_C + Light	−37.72	0.75	−0.03^{NS}	0.05^{NS}	**−0.21****

Figure 1. Bivariate relationships (upper row) and multivariate partial relationships (bottom row) of changes in species richness in response to experimental treatments with (a, d) changes in SRU_{D3}, (b, e) changes in light and (c, f) changes in the number of individuals in the community (NI_C). Colors indicate different treatments. The gray region indicates the 95% confidence interval around the regression. (g) Structural equation model representing connections between other variables and species richness supported by the data from azi.cn site. Letters in g correspond to partial relationships shown in d, e and f. Solid black and dashed gray arrows represent significant ($p < 0.05$) and non-significant paths ($p > 0.05$) respectively. The coefficients are standardized for each causal path. Conditional R^2 for each component model is given in the box of response variables. The model is tested using the R package piecewiseSEM (Fisher.C = 6.22, df = 6, p = 0.399). Log response ratios (LRR) are calculated as the natural logarithm of the ratio of the variable within a treatment subplot to the control subplot in the same block.

effect of changes in SRU_{D3} on the changes in species richness is significant (slope = −0.21, p < 0.01; Table 1). By comparing the five models with the smallest AIC, we also found that the optimal model was the one with only SRU_D, which could well explain the change of species richness.

Our structural equation model (SEM) further revealed that SRU_{D3} effectively drives changes in ground-level light availability and NI_C, and directly contributes the most to predictions of changes in species richness in response to anthropogenic disturbances (Fig. 1g, Supporting information). Our

model fit the data well (Fisher's C=6.22, df=6, p=0.399). Changes in SRU_{D3} explained 72% of variation in ground-level light availability (r=−0.87, p < 0.001), 84% of variation in NI_C (r=−0.80, p < 0.001) and 73% of variation in species richness (r=−0.86, p < 0.001) (Fig. 1g). As a result, the direct effect of changes in light (r=0.05, p=0.12; Fig. 1e, g) or changes in NI_C (r=−0.02, p=0.80; Fig. 1f–g) on species richness became non-significant in our multivariate analysis. Comparable results were found when SRU_D was calculated based on the first four (SRU_{D4}) and five (SRU_{D5}) most dominant species (Supporting information). However, SRU_D based on the first (SRU_{D1}) and the first two (SRU_{D2}) dominant species failed to fully capture the effects of changes in light on changes in species richness (Supporting information).

Examining the individual contribution of each of the two factors ($Height_D$ and $Cover_D$) generating SRU_D revealed that each of changes in $Height_D$ and $Cover_D$ partly and independently contributed to explain changes in ground-level light availability (r=−0.60, p < 0.001; r=−0.36, p < 0.001; respectively; Fig. 2, Supporting information), changes in NI_C (r=−0.53, p < 0.001; r=−0.32, p < 0.001; respectively; Fig. 2, Supporting information) and changes in species richness (r=−0.36, p < 0.001; r=−0.59, p < 0.001; respectively; Fig. 2, Supporting information). In other words,
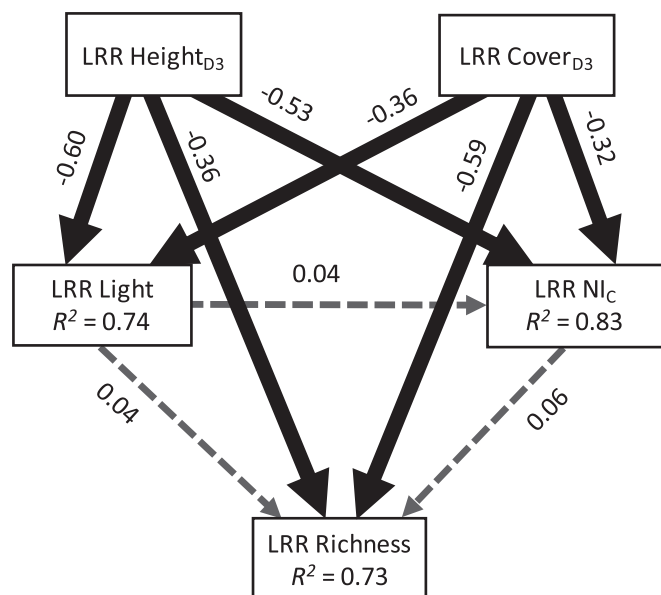

Figure 2. Structural equation model representing connections between each of variables ($height_{D3}$, $cover_{D3}$, light and NI_C) and species richness supported by the data with height and cover of three most dominant species from azi.cn site. Solid black and dashed gray arrows represent significant (p < 0.05) and non-significant paths (p > 0.05) respectively. The coefficients are standardized for each causal path. Conditional R^2 for each component model is given in the box of response variables. The model is tested using the R package piecewiseSEM (Fisher.C = 5.444, df=6, p=0.488). Log response ratios (LRR) are calculated as the natural logarithm of the ratio of the variable within a treatment subplot to the control subplot in the same block.

the increase of height and cover of the dominant species in response to nutrient addition and altered herbivore densities directly led to the decrease of ground-level light availability, NI_C and the number of plant species.

In contrast to SRU_{D3}, SEMs based on either community biomass ($Biomass_C$) or biomass of dominant species ($Biomass_{D3}$) revealed that these measures were not consistently able to directly capture and explain changes in ground-level light availability, NI_C and species richness (Supporting information). Thus, SRU_D is better at capturing both abundance- and functional-based processes compared to $Biomass_C$ or $Biomass_{D3}$ and explains why SRU_D is a better predictor of plant diversity dynamics than biomass.

Contributions and non-random losses of dominant, intermediate and rare species to the reduced density of individuals (community thinning)

Our study further revealed the different contributions of dominant, intermediate and rare species to the reduced density of individuals of community. We found that the decrease in the number of individuals in the community (i.e. community thinning) was the result of a reduction of the number of individuals from each of the dominant (slope with 95% CI=0.82 (0.41–1.22), R^2=0.38; Fig. 3a), intermediate (0.75 (0.55–0.94), R^2=0.71; Fig. 3b) and rare species (0.61 (0.48–0.73), R^2=0.78; Fig. 3c). However, in terms of the relative number of individuals, we found that the dominant species increased (−0.82 (−1.22 to −0.41), R^2=0.39; Fig. 3d), the intermediate species were not affected (−0.10 (−0.78 to 0.58), R^2=0.00; Fig. 3e) and the rare species decreased (0.56 (0.06–1.07), R^2=0.14; Fig. 3f) with community thinning.

Furthermore, we conducted a null model analysis with field experiments where we asked whether the individual losses in dominant, intermediate and rare species followed non-random processes. We found that the individual losses of rare species in all treatments except K addition followed non-random processes, and the loss ratios of rare species from our field experiments were significantly higher than from simulated null model (SES > 2.0; Fig. 4). For dominant and intermediate species, the individual losses in all treatments were also non-random processes, but the loss ratios of these two abundance groups from our field experiments were significantly lower than from simulated null model (SES < −2.0; Fig. 4).

These results indicate that community thinning was the result of a faster decrease in the number of individuals of rare species and a slower decrease in the number of individuals of dominant and intermediate specie compared with random loss process, and individual loss in all abundance groups are non-random processes. This implies that changes in the number of species resulted from disproportionate loss of rare species, rather than from random loss of all individuals and species. Exploring different thresholds to classify species ranks into abundance groups revealed consistent results (Supporting information).
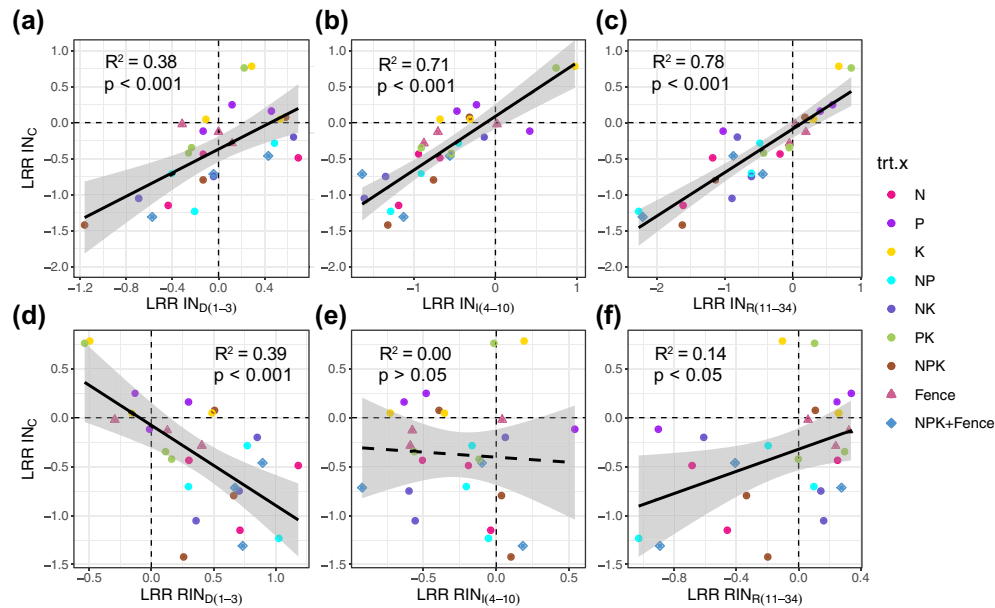
Figure 3. Bivariate relationships of changes in the number of individuals in the community (NI_C) in response to experimental treatments with (a) changes in the number of individuals of three most dominant species ($NI_{D(1-3)}$), (b) changes in the number of individuals of seven intermediate species ($NI_{I(4-10)}$), (c) changes in the number of individuals of 24 rare species ($NI_{R(11-34)}$), (d) changes in the relative number of individuals of three most dominant species ($RNI_{D(1-3)}$), (e) changes in the relative number of individuals of seven intermediate species ($RNI_{I(4-10)}$) and (f) changes in the relative number of individuals of 24 rare species ($RNI_{R(11-34)}$). Colors indicate different treatments. The gray region indicates the 95% confidence interval around the regression. Log response ratios (LRR) are calculated as the natural logarithm of the ratio of the variable within a treatment subplot to the control subplot in the same block.

Discussion

Investigations in our field experiments demonstrate that SRU_D is a superior predictor and fundamental driver of plant diversity dynamics because it captures both changes in ground-level light availability and changes in NI_C. The contributions of different abundance groups to the reduced density of individuals of community are different, although the number of individuals from all abundance groups decreased in response to experimental treatments, rare species contribute the most. In addition, our null model analysis indicates that the losses of individual in dominant, intermediate and rare species are all non-random processes. Below we elaborate on the mechanistic basis of the experimental and simulated results.

Developing an appropriate methodology to predict diversity dynamics is crucial for empirical studies of community ecology and the development of appropriate management strategies to prevent diversity decline, and its importance goes much beyond the response of plant communities to nutrient addition and altered herbivore densities (Suding et al. 2005, DeMalach et al. 2016). SRU_D has been shown to outperform both community biomass ($Biomass_C$) and biomass of dominant species ($Biomass_D$) in predicting plant diversity dynamics (Zhang et al. 2019). Here, we explored the mechanisms behind this and found that much of the effects of changes in ground-level light availability (functional-based process) and of changes in NI_C (abundance-based process) on changes in plant species richness were captured and thus explained

directly by changes in SRU_D rather than by changes in community biomass or biomass of dominant species. In other words, the increase (or decrease) of SRU of dominant species, which decreased (or increased) ground-level light availability and NI_C, was the fundamental driver of decreased (or increased) plant species richness in response to experimental treatments. While the significant pathway of influence on changes in species richness in SEMs was also direct from changes in $Biomass_C$ or $Biomass_{D3}$ (Supporting information), neither of them explained changes in ground-level light availability, NI_C and species richness as well as SRU_D did. These results show that more superior predictions are obtained by SRU_D because it consistently captures both changes in ground-level light availability and NI_C compared to community biomass and biomass of dominant species.

Our study further demonstrates that better predictions of SRU_D are due to the inclusion of two key factors (height$_D$ and cover$_D$) that independently capture changes in ground-level light availability and NI_C, and thus contribute to asymmetric competition for light and the reduced density of individuals of community (Suding et al. 2005, Hautier et al. 2009, Yang et al. 2015, Kaarlejärvi et al. 2017). Our results extend previous evidence linking increased height and/or cover of dominant species with increased light asymmetry (Borer et al. 2014b, DeMalach et al. 2016, Xiao et al. 2021), emphasizing competition for light as a major mechanism of species loss with nutrient addition and altered herbivore densities.

Our study is, to our knowledge, the first to directly test the contributions and loss patterns of three abundance groups
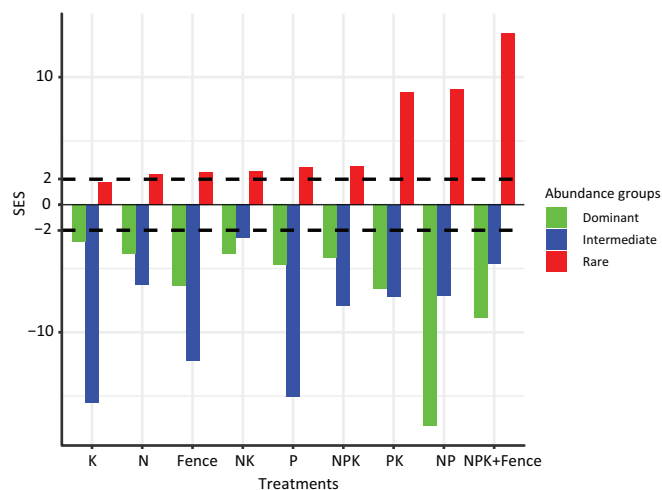
Figure 4. Standardized effect size (SES) from null-model analysis of species loss patterns of three abundance groups in response to experimental treatments. Colors indicate different abundance groups (green: dominant species group; blue: intermediate species group; red: rare species group). Values above the dashed line at SES = 2.0 or below the dashed line at SES = −2.0 indicate non-random species loss. Specifically, SES > 2.0 means the loss ratio of the abundance group investigated from our field experiments is significantly higher than from random loss process; and SES < −2.0 means the loss ratio of the abundance group investigated from our field experiments is significantly lower than from random loss process.

(dominant, intermediate and rare species) to the reduced density of individuals of community in response to nutrient addition and altered herbivore densities (Goldberg and Miller 1990). Here, we used a direct measure of community thinning, the change in the number of individuals of each abundance group between the treated and control subplots to test whether species loss is due to equal chance of losing individuals of all species. Our results show that while each abundance group suffer from thinning, rare species lose more individuals compared to dominant and intermediate species, and thus disproportionately contribute to species loss. Our null model analysis further demonstrate that the loss ratios of rare species are significantly higher than from simulated null model (i.e. random loss process), in contrast, the loss ratios of dominant and intermediate species are significantly lower than from simulated null model (Suding et al. 2005, Larsen and Ormerod 2014, Kaarlejärvi et al. 2017). Thus, the decline in diversity is driven by non-random losses of all three abundance groups and primarily by the disproportionately loss of rare species. Again, because extinctions also occurred in some abundant species, this demonstrates that abundance-based process is one but not the sole process at play (Suding et al. 2005).

Indeed, our observed and simulated results strongly suggest that non-random loss of species is an important process of plant diversity dynamics following experimental treatments. Specifically, species that grew faster and taller had a functional competitive advantage as they were able to increase their height and cover and reduce ground-level

light availability to subordinate species leading to their exclusion (Xiao et al. 2021). In other words, the combination of changes in height and cover of dominant species leads to the disproportional loss of rare species with functional competitive disadvantage. This result emphasizes that rare species are particularly susceptible to anthropogenic environmental changes (Smith and Knapp 2003). Given that rare species can also play an important role in shaping community structure, resisting invasion, impacting higher trophic levels and providing multiple ecosystem functions, management strategies tailored to conserving rare species and/or reducing the SRU of dominant species could help protecting ecosystems from degradation (Lyons and Schwartz 2001, Lyons et al. 2005, Bracken and Low 2012, Mouillot et al. 2013, Soliveres et al. 2016, Dee et al. 2019) but see Smith and Knapp (2003).

Although changes in ground-level light availability and changes in NI_C are often invoked to explain changes in community diversity following experimental treatments, our results suggest that these changes arise through both effects simultaneously owing to the influence of disturbance on community composition, especially on changes in height and cover of some dominant species (i.e. space resource utilization of dominant species; SRU_D). Comparative studies of bivariate and multivariate partial relationships provide important insights into the plant diversity dynamics that happened when disturbance drives the common occurrence of abundance- and functional-based processes in human-modified communities (Grace et al. 2014, 2016). The extent to which our findings can be generalized to other ecosystems (e.g. forests, shrublands and seagrass meadows) is currently unknown. However, given that plant competitive ability of in these ecosystems is also driven by resources such as space and light, it is likely that SRU_D generally integrates the driving factors of diversity dynamics in these plant communities.

Conflicts of interest – We declare no conflicts of interest.

Author contributions

Pengfei Zhang: Conceptualization (lead); Data curation (equal); Formal analysis (lead); Funding acquisition (lead); Investigation (equal); Methodology (lead); Project administration (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Elizabeth T. Borer**: Conceptualization (equal); Formal analysis (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Eric W. Seabloom**: Conceptualization (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Merel B. Soons**:

Conceptualization (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Mariet M. Hefting**: Conceptualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **George A. Kowalchuk**: Supervision (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Peter B. Adler**: Writing – original draft (supporting); Writing – review and editing (supporting). **Chengjin Chu**: Writing – original draft (supporting); Writing – review and editing (supporting). **Xiaolong Zhou**: Data curation (equal); Writing – original draft (supporting). **Cynthia S. Brown**: Writing – original draft (supporting); Writing – review and editing (supporting). **Zhi Guo**: Data curation (equal); Writing – original draft (supporting). **Xianhui Zhou**: Investigation (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Zhigang Zhao**: Writing – original draft (supporting); Writing – review and editing (supporting). **Guozhen Du**: Supervision (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Yann Hautier**: Formal analysis (supporting); Methodology (supporting); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (equal).

Data availability statement

All code and data associated with this manuscript will be archived and publicly accessible from the Dryad Digital Repository: https://doi.org/10.5061/dryad.tqjq2bw3k (Zhang et al. 2022).

Supporting information

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

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