RESEARCH ARTICLE

SRU_D: A simple non-destructive method for accurate quantification of plant diversity dynamics

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Abstract

1. Predicting changes in plant diversity in response to human activities represents one of the major challenges facing ecologists and land managers striving for sustainable ecosystem management. Classical field studies have emphasized the importance of community primary productivity in regulating changes in plant species richness. However, experimental studies have yielded inconsistent empirical evidence, suggesting that primary productivity is not the sole determinant of plant diversity. Recent work has shown that more accurate predictions of changes in species diversity can be achieved by combining measures of species' cover and height into an index of space resource utilization (SRU). While the SRU approach provides reliable predictions, it is time-consuming and requires extensive taxonomic expertise. Ecosystem processes and plant community structure are likely driven primarily by dominant species (mass ratio effect). Within communities, it is likely that dominant and rare species have opposite contributions to overall biodiversity trends. We, therefore, suggest that better species richness predictions can be achieved by utilizing SRU assessments of only the dominant species (SRU_D), as compared to SRU or biomass of the entire community.

2. Here, we assess the ability of these measures to predict changes in plant diversity as driven by nutrient addition and herbivore exclusion. First, we tested our hypotheses by carrying out a detailed analysis in an alpine grassland that measured all species within the community. Next, we assessed the broader applicability of our approach by measuring the first three dominant species for five additional experimental grassland sites across a wide geographic and habitat range.

3. We show that SRU_D outperforms community biomass, as well as community SRU, in predicting biodiversity dynamics in response to nutrients and herbivores in an

alpine grassland. Across our additional sites, SRU_D yielded far better predictions of changes in species richness than community biomass, demonstrating the robustness and generalizable nature of this approach.

4. *Synthesis*. The SRU_D approach provides a simple, non-destructive and more accurate means to monitor and predict the impact of global change drivers and management interventions on plant communities, thereby facilitating efforts to maintain and recover plant diversity.

1 | INTRODUCTION

Hosting up to 89 species/m^2 (Wilson, Peet, Dengler, & Partel, 2012) and covering about 40% of the land area (White, Murray, & Rohweder, 2000), grasslands represent some of the most diverse and widespread terrestrial ecosystems. Grassland plants are a major constituent of terrestrial ecosystem functioning, contributing to food production, nutrient and water cycling, carbon storage and climate mitigation (Bengtsson et al., 2019; Cardinale et al., 2012; O'Mara, 2012). However, human-induced environmental changes are threatening the plant diversity of grassland ecosystems globally (Steffen et al., 2015; Vitousek, Mooney, Lubchenco, & Melillo, 1997). For example, human alterations of the global nutrient cycles via combustion of fossil fuels, utilization of agricultural fertilizers and atmospheric deposition (Galloway et al., 2008) are well-known drivers of terrestrial plant species loss, and this trend is expected to intensify further over the course of this century (Borer, Seabloom, et al., 2014b; Hautier, Niklaus, & Hector, 2009; Payne et al., 2017; Phoenix et al., 2006; Sala et al., 2000; Stevens, Dise, Mountford, & Gowing, 2004; Suding et al., 2005; Yang, Hautier, Borer, Zhang, & Du, 2015). This loss of plant diversity often affects the functioning of ecosystems (Cardinale et al., 2012; Hautier et al., 2018; Hector et al., 1999; Isbell et al., 2011; Tilman et al., 2001), as well as the stability of ecosystem functions when exposed to perturbations (Bai, Han, Wu, Chen, & Li, 2004; Hautier et al., 2014, 2015; Isbell et al., 2015; Pfisterer & Schmid, 2002; van Ruijven & Berendse, 2010; Zhang, He, Loreau, Pan, & Han, 2018). Thus, it is critical to track and predict changes in plant diversity in response to human activities in order to improve sustainable ecosystem management.

Many studies have demonstrated that community-level changes in primary productivity following human disturbances regulate changes in grassland plant diversity, with specific disturbances having either positive or negative effects on plant diversity (Bakker, Ritchie, Olff, Milchunas, & Knops, 2006; Hillebrand et al., 2007; Olff & Ritchie, 1998; Proux & Mazumder, 1998; Worm, Lotze, Hillebrand, & Sommer, 2002). Studies to date have found that an increase in primary productivity, for example, in response to nutrient addition, usually reduces plant diversity while a decrease in standing biomass,

for example, in response to herbivory, usually maintains more diversity, especially under productive conditions unless fertility is really too low and only a few stress tolerators are found (humpback curve) (Adams, 2009; Fraser et al., 2015; Oba, Vetaas, & Stenseth, 2001; Tredennick et al., 2016). However, recent studies using data from more than 40 grasslands world-wide within the Nutrient Network (NutNet) indicate that herbivores control grassland diversity primarily through their effects on ground-level light (Borer, Seabloom, et al., 2014b) and that plant diversity is reduced even at sites where productivity is not increased by nutrient addition (Harpole et al., 2016). Moreover, a recent meta-analysis of 189 nutrient addition field experiments shows that loss of plant diversity is correlated with increased productivity, but with substantial variation (Soons et al., 2017). Thus, community-level productivity is not the sole determinant of plant community changes (Harpole et al., 2017).

Combining measures of cover and height for each plant species in the community and deriving a community-level volume-based indicator of plant competition for space and resources, that is, space resource utilization (SRU), may lead to better predictions of plant species richness than productivity (Zhang, Zhou, Li, Guo, & Du, 2015). Briefly, species-level SRU (SRU_{Si}) is the product of the percent cover and maximum height of each species in a given area (Figure 1a). SRU represents the competitive ability of a species for space and resources in both the horizontal and vertical dimensions, and as such, may act as a surrogate measure combining the effects of multiple factors. Individual species-level SRU's can be added together to form the community-level SRU (SRU_C). This novel approach is attractive because it provides improved predictions of plant diversity dynamics in response to perturbations compared to productivity while using non-destructive measurements. In comparison, community productivity is estimated destructively by clipping at ground level and then drying and weighing all above-ground biomass of the community. Biomass identification per species can provide detailed information on species dynamics, but is highly time-consuming and requires extensive taxonomic expertise for the identification of all the species in the community. The SRU approach suffers from similar drawbacks, as the percent cover and maximum height must be measured for each species separately (Zhang et al., 2015). The ideal method would
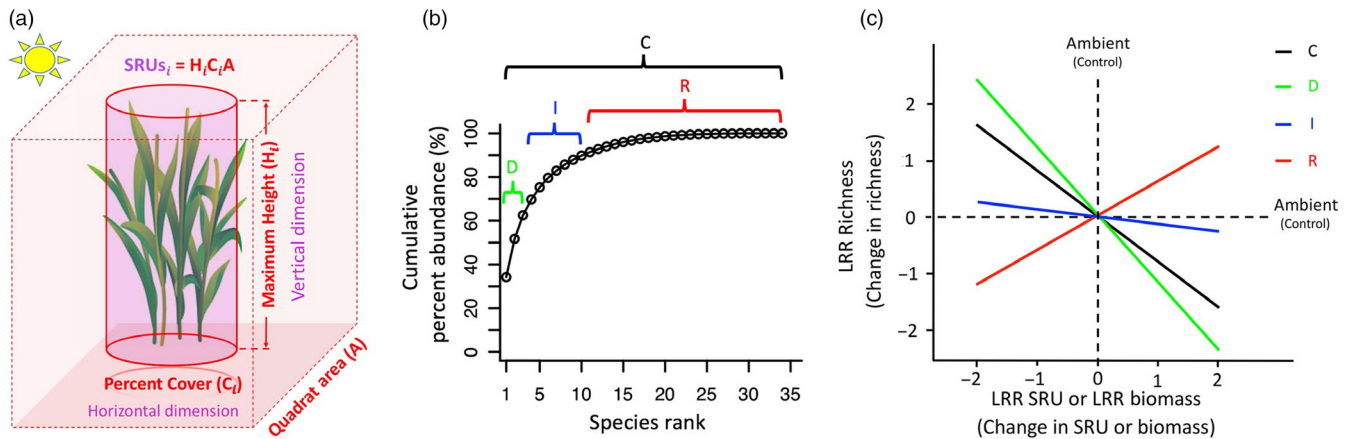
FIGURE 1 (a) Space resource utilization of species i (SRU_{Si}) is the product of the maximum height (H_i) and percent cover (C_i) of that species in a plot and the plot area (A). (b) Conceptual abundance curve (based on cover or biomass) for all species in the community and highlighting four abundance groups: C = community, D = dominant, I = intermediate and R = rare species. (c) Conceptual diagram illustrating the relationship between changes in SRU or biomass and changes in plant species richness in response to human disturbance for each of the four abundance groups. Relative changes in SRU and species richness (log response ratio or LRR) are calculated as the natural logarithm of the ratio of the variable within a treatment plot to the control plot in the same block [Colour figure can be viewed at wileyonlinelibrary.com]

provide accurate predictions of plant diversity dynamics, while using an easy, rapid, non-destructive and broadly applicable tool. The central premise of this study is that the measurement of SRU for only a few dominant species (SRU_D) provides exactly such a tool.

The relative distribution of species abundance within a local community (hereafter 'abundance curve') is characterized by a minority of locally relatively more abundant species (hereafter 'dominant species') and a vast majority of locally relatively less abundant species (hereafter 'rare species') interspersed with species of locally relatively intermediate abundance (hereafter 'intermediate species') (Matthews & Whittaker, 2015; McGill et al., 2007). It follows that the greatest contribution to the cumulative percentage of abundance (measured as biomass or cover) is represented by a few dominant species, while the intermediate and rare species contribute much less (Figure 1b). Thus, ecosystem processes and community structure and composition should be driven primarily by dominant species (those contributing most to abundance), which has been referred to as the 'mass ratio effect' (Grime, 1998) (Figure 1c). Moreover, dominant and rare species could have opposite contributions to community-level abundance. For example, the increase in community-level abundance in response to nutrient enrichment is usually the result of an increase in the abundance of some dominant species at the cost of a decrease in the abundance of some rare species (Harpole & Tilman, 2007; Zhang et al., 2015). Ultimately, the opposing effects of rare species versus dominant species on community-level abundance could weaken predictions of plant diversity dynamics made from community-level data (Figure 1c). Better predictions might thus be achieved by focusing specifically on dominant species.

Available evidence suggests the general hypothesis that predictions of plant diversity dynamics based on changes in biomass or SRU depend on species abundance (Figure 1c), leading to the following hypotheses: (a) changes in SRU yield better predictions of changes in species richness than changes in biomass, (b) dominant species contribute most to community-level estimations, (c) rare species indicate opposite predictions of plant diversity as compared to dominant species and the full community, thus weakening predictions from the full community, and (d) predictions from dominant species are better than those from the full community.

We tested these hypotheses by quantifying the effect of nutrient addition and herbivore exclusion on species- and community-level plant biomass, height, cover, SRU and species richness using data from the Nutrient Network (Borer, Harpole, et al., 2014a). First, we carried out a detailed analysis in an alpine grassland that measured each species in the communities. We classified species into three groups according to their abundance rank: dominant, intermediate and rare, in addition to characterizing the communities based upon all species. We examined the extent to which species abundance impacted predictions of changes in plant diversity with the goal of providing a relatively simple, yet highly robust predictor of plant diversity dynamics. Next, we assessed the broader applicability of our approach by measuring the first three dominant species in each plot of five grassland sites with different habitat types across three continents. The performance of the SRU_D approach was compared to that of conventional use of destructive biomass and total community SRU measures.

2 | MATERIALS AND METHODS

2.1 | Study site

The five study sites are part of the Nutrient Network, a cooperative globally distributed experiment (NutNet; http://nutnet.org/) (Borer, Harpole, et al., 2014a). The sites used in our study included a tallgrass prairie (cbgb.us), a shortgrass prairie (sgs.us) and a shrub steppe (shps.us) in North America, a pasture (frue.ch) in Europe and an alpine grassland (azi.cn) in Asia (Table S1). The sites are

dominated by herbaceous vegetation and referred to as 'grassland' here. Mean species richness in the untreated control plots among these sites varied from 8 to 32 species (cbgb.us: 8; sgs.us: 8; shps. us: 15; frue.ch: 13; azi.cn: 32), and mean richness of the local species pool from 21 to 65 species (cbgb.us: 46; sgs.us: 21; shps.us: 50; frue.ch: 27; azi.cn: 65). Cover, height, species richness and biomass were sampled after 3–5 years of treatment (cbgb.us: 3; sgs. us: 4; hps.us: 4; frue.ch: 3; azi.cn:5).

2.2 | Experimental design

Each site consists of a completely randomized block design of nutrient addition and herbivore exclusion with three blocks of ten 5 × 5 m plots per block (Borer, Harpole, et al., 2014a). Nutrient addition treatments consist of a factorial combination of phosphorus (P), nitrogen (N) and potassium ($K_{+\mu}$; including a one-time addition of micronutrients) for a total of eight nutrient treatment combinations per block. Herbivore exclusion treatments consist of a fencing treatment crossed with the control and NPK treatments for a total of two treatments per block. N, P and K were applied annually, before the beginning of the growing season, using the following application rates and sources: 10 g N m^{-2} $year^{-1}$ as time-release urea or ammonium nitrate (NH_4NO_3), 10 g P m^{-2} $year^{-1}$ as triple-super phosphate ($Ca(H_2PO_4)_2$) and 10 g K m^{-2} $year^{-1}$ as potassium sulphate (K_2SO_4). In addition, 100 g/m^2 of a micronutrient mix of Fe (15%), S (14%), Mg (1.5%), Mn (2.5%), Cu (1%), Zn (1%), B (0.2%) and Mo (0.05%) was applied once with K at the start of the experiment to avoid toxicity of more immobile micronutrients (Seabloom et al., 2015).

2.3 | Measurements of plant biomass, height, cover and species richness

Measurements were carried out at the seasonal peak in biomass in a fixed 0.5 × 0.5 m subplot randomly assigned within each plot for azi.cn site and in standard 1 × 1 m subplots for the other sites (cbgb.us, sgs.us, shps.us and frue.ch). For all sites, cover was estimated independently for each species in each plot (Table S2). Note that total summed cover can exceed 100% for multilayer canopies and include two-story vegetation types (e.g. shrublands and forests), where herbaceous species play a minor role. Above-ground live biomass was estimated destructively by clipping at ground

level all above-ground biomass of individual plants rooted within two 0.1 m^2 (10 × 100 cm) strips immediately adjacent to the permanent 1 × 1 m plot, followed by drying to constant mass at 60°C and weighing to the nearest 0.01 g. Biomass was sorted to species for azi.cn and to functional group (i.e. grass, forb and legume) for the other sites. We used above-ground live biomass as a measure of primary productivity. Maximum height was estimated for one to five randomly selected individuals per species in each plot as the shortest distance between the upper boundary of a plant (flower stalk or leaf) and the ground level. Maximum height was estimated for each species for azi.cn and for the three most dominant species in each plot for the other sites.

2.4 | Calculations for biomass and SRU

To test our hypothesis that predictions of plant diversity dynamics based on changes in biomass or SRU depend on species abundance, we carried out a detailed analysis in an alpine grassland (azi.cn) that measured each species in the communities. SRU for each species (SRU_{Si}) in each plot was calculated as:

$$SRU_{Si} = H_i C_i A \qquad (1)$$

where H_i is average maximum height and C_i the percent cover for species i in a plot and A is the plot area (Figure 1a). We ranked all the species based on their abundance (biomass or cover) within each plot (Figure 1b) using the 'BiodiversityR' package (Kindt & Coe, 2005) and calculated biomass and SRU per plot using Equations 2 and 3 respectively. Biomass is the sum of the individual species biomass ($Biomass_{Si}$) per plot from species i to species j within a plot and is calculated as:

$$Biomass = \sum_{i}^{j} Biomass_{Si} \qquad (2)$$

and SRU is the sum of the individual species SRU (SRU_{Si}) per plot from species i to species j within a plot and is calculated as:

$$SRU = \sum_{i}^{j} SRU_{Si} \qquad (3)$$

where i and j are the species' ranks in each plot based on species percent biomass for biomass or percent cover for SRU. Note that indices i and j can take different values depending on the approach used for modelling (see statistical analyses section hereafter and Table 1). Note also that while total summed cover can exceed 100%

TABLE 1 Cumulative percentage of abundance, species ranks and sets of thresholds explored for each of four abundance groups determined across all plots in azi.cn. Species ranks determined across all plots were used to identify the species belonging to an abundance group within each plot

Abundance groups	Relative cumulative percentage of total abundance (biomass or cover)	Species ranks for Biomass (i, j)	Species ranks for SRU (i, j)	Sets of thresholds explored (i, j)
Community (C)	100%	(1, 34)	(1, 34)	(1, 34)
Dominant (D)	≥ top 60%	(1, 3)	(1, 5)	(1, 1) (1, 3) (1, 5)
Intermediate (I)	≈ mid 30%	(4, 10)	(6, 15)	(4, 10) (6, 10) (6, 15)
Rare (R)	≤ bottom 10%	(11, 34)	(16, 34)	(11, 34) (16, 34) (21, 34)

Note: i and j are the species' ranks in each plot based on species percent biomass for biomass or percent cover for SRU.

for multilayer canopies, this does not affect the calculation of SRU as this calculation is based on species' rank.

To assess the broader applicability of our approach, we examined data for the three most dominant species in each plot across a diverse range of five grassland sites (including azi.cn) (Table S1). We ranked species based on their cover within each plot and calculated SRU for the first ($i = 1$, $j = 1$), the first two ($i = 1$, $j = 2$) and the first three ($i = 1$, $j = 3$) dominant species in each plot using Equation 3.

We calculated biomass, SRU and species richness responses to treatments (log response ratio or LRR) as the natural logarithm of the ratio of the variable within a treatment plot to the control plot in the same block.

2.5 | Statistical analyses

We began by a detailed analysis of an alpine grassland (azi.cn). We modelled the relationships between changes in above-ground biomass or SRU and changes in plant species richness in response to human disturbance with linear mixed effects models using two approaches: the cumulative abundance approach and the abundance groups approach. Sites and blocks nested within sites were treated as random effect in all models.

For the cumulative abundance approach, we examined the impact of adding plant species based on their abundance ranks on the slope and predictive power of the relationships. Biomass and SRU were calculated within each plot for each set of cumulative abundance ranks. Sets were specified by starting with the first most abundant species in each plot and adding the next most abundant species until all the species were included (maximum of 34 species in azi.cn site). Thus, for both biomass and SRU, 34 slopes and R^2 values were generated, one for each species cumulative rank from 1 ($i = 1$, $j = 1$) to 34 species ($i = 1$, $j = 34$).

Biomass and SRU were calculated within each plot for each of four abundance groups (dominant, intermediate, rare and all), which were defined as follows: dominant species representing the top 60% of total abundance, rare species representing the bottom 10%, intermediate species representing the mid 30% and the total community representing 100%. These thresholds are comparable to other studies (Clark & Tilman, 2008; Soliveres et al., 2016). For each of these abundance groups, we assessed whether the direction of predictions changed depending on species abundance group (Figure 1c). Thus, for each biomass and SRU, four slopes and R^2 values were generated, one for each abundance group. Note that different numbers of species between biomass and SRU are observed for a given abundance group (Table 1). For example, dominant species are represented by the three most dominant species for biomass and by the five most dominant species for SRU. Biomass$_D$ was therefore calculated from the first through the third most abundant species ($i = 1$, $j = 3$) and SRU$_D$ was calculated from the first through the fifth most abundant species ($i = 1$, $j = 5$). Note that ranking the species within each plot can lead to a given rank being occupied by a different species when comparing between plots. Thus, our method focuses on relationships based

upon changes for a particular abundance group as opposed to for a particular species or group of species. Our method is, therefore, also applicable for sites with two distinct canopy layers (i.e. shps. us), where herbaceous species play a minor role as compared to other vegetation types (e.g. forests and shrublands). Additionally, we modelled the relationship between changes of each of the individual factors generating SRU$_D$ (i.e. Cover$_D$ and Height$_D$) on changes in plant species richness by using linear mixed effects models with block as a random effect.

Next, to assess the generality of our results across five disparate grassland sites, we used the cumulative abundance approach described above to examine the impact of adding plant species from the most dominant to the third most dominant species within each plot on the slope and predictive power of the relationships and compared our results based on SRU$_D$ to total community biomass. We modelled the relationships between changes in above-ground biomass or SRU$_D$ and changes in plant species richness in response to human disturbance using linear mixed effects models with block nested within site as a random effect. We calculated conditional R^2 using the 'piecewiseSEM' package (Lefcheck, 2016). We allowed both the intercepts and slopes of regressions to vary between sites if supported by model selection approach based on minimization of BIC (Pinheiro & Bates, 2000).

For each regression, we extracted the slopes with 95% confidence intervals (CI) and extracted the percentage of variation explained by each of the relationships using R^2 values as an indicator of the predictive power for both approaches (higher R^2 values represent better predictive power). In the text, we present estimates of the slopes from the linear regression with their 95% confidence intervals (95% CI). Slopes were considered significant if the intervals did not overlap zero. All analyses were conducted in R 3.4.2 (R Development Core Team, 2014).

3 | RESULTS

### 3.1 | Single study site—alpine grassland (azi.cn)

The abundance curves across all plots show that more than 60% of total abundance was accounted for by a small number of abundant species (hereafter 'dominant species'); while less than 10% of total abundance was represented by the vast majority of much less abundant species (hereafter 'rare species') (Figure 2, Table 1). Across all plots, dominant species consisted of the first three most dominant species for biomass (ranks 1–3) and of the first five most dominant species for cover (ranks 1–5). Rare species were comprised of the least dominant 24 species for biomass (ranks 11–34) and the least dominant 19 species for cover (ranks 16–34). The remaining 30% of total abundance (hereafter 'intermediate species') consisted of seven species for biomass (ranks 4–10) and 10 species for cover (ranks 6–15).

We examined the extent to which changes in biomass or changes in SRU could explain changes in plant species richness in response to nutrient addition or herbivore exclusion (Figure 3). Our cumulative
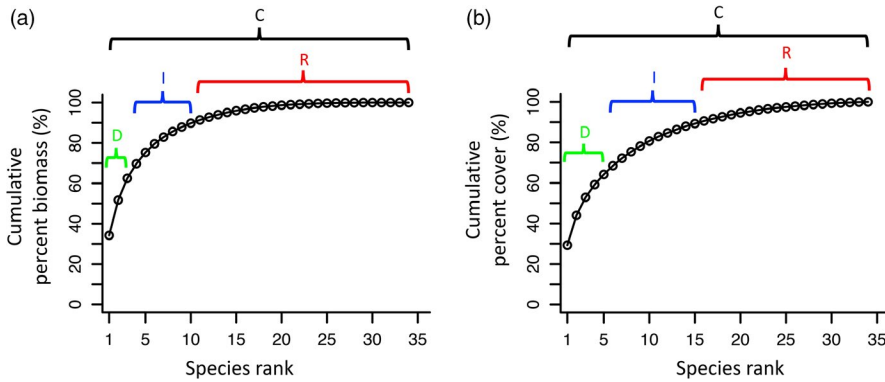
FIGURE 2 Abundance curve for (a) above-ground biomass and (b) cover across all experimental plots of the alpine grassland in Asia (azi.cn). Abbreviations and colours are as in Figure 1b and c [Colour figure can be viewed at wileyonlinelibrary.com]
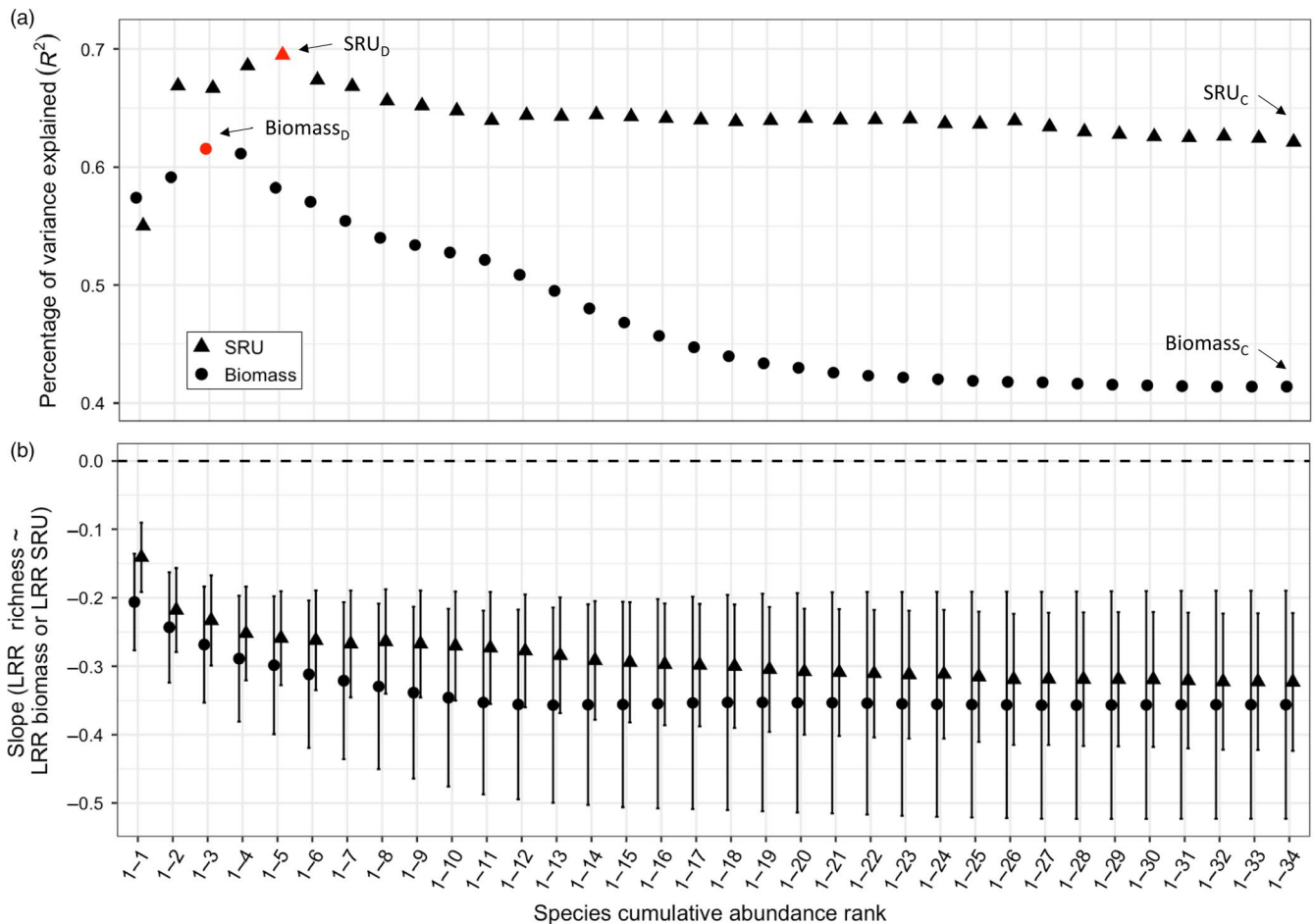
FIGURE 3 Results of the cumulative abundance approach for the alpine grassland in Asia (azi.cn). Percentage of variance explained (R^2) (a) and slopes with 95% CI (b) of the relationship between changes in species richness and changes in biomass or SRU in response to human disturbance, for different sets of increasing species cumulative abundance rank. Log response ratios (LRR) are calculated as in Figure 1c. Highlighted in red are the set of species with the highest percentage of variance explained. Biomass$_C$, SRU$_C$, Biomass$_D$ and SRU$_D$ correspond to Figure 4a–d respectively [Colour figure can be viewed at wileyonlinelibrary.com]

abundance approach revealed that a sizable portion of the total variance was explained by the biomass or SRU of only the single most dominant plant species (R^2 = 0.57 and 0.55, respectively, rank 1–1 in Figure 3a). The percentage of variance explained increased by the inclusion of the biomass or SRU data from other dominant species. This explanatory power soon reached a maximum when including the three dominant species for biomass and the five dominant species for SRU (R^2 = 0.62 and 0.70 respectively; highlighted in red in Figure 3a). Inclusion of additional species led to a decline in explanatory power, reaching rather stable levels of R^2 until all species were included (R^2 = 0.41 and 0.62 for biomass and SRU respectively; Figure 3a). Changes in the biomass or SRU measured for a few
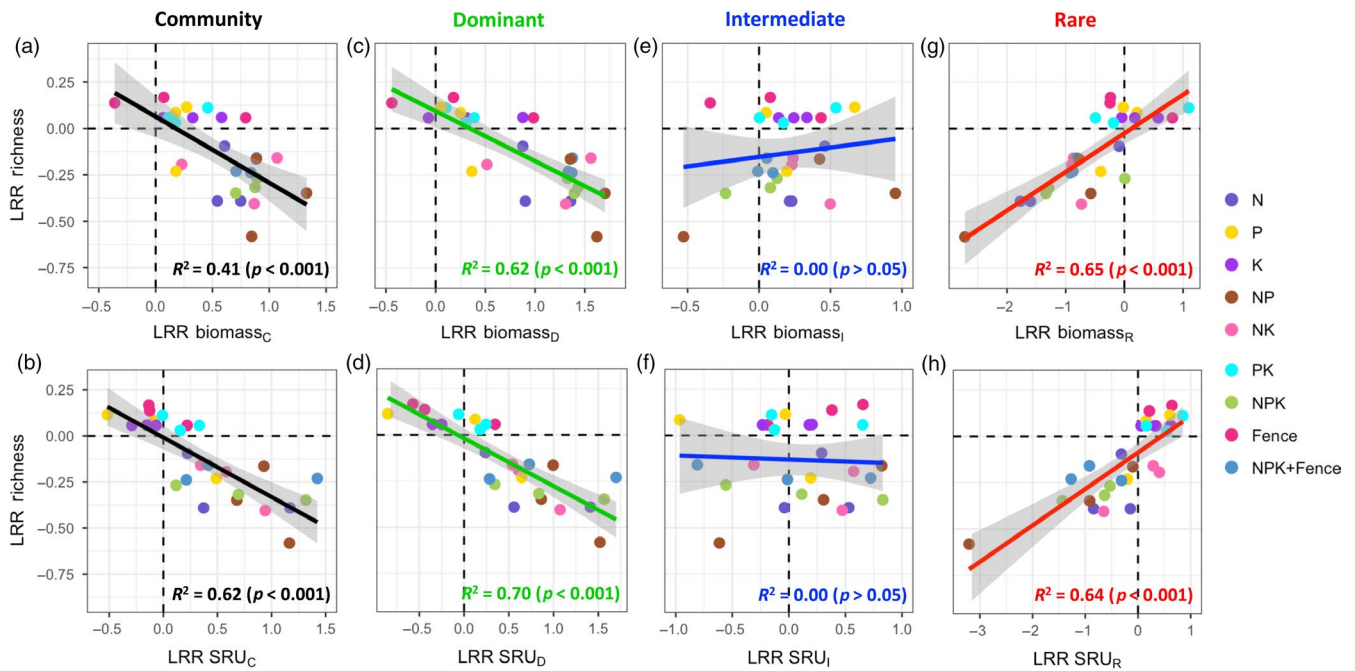
FIGURE 4 Results of the abundance groups approach for the alpine grassland in Asia (azi.cn). Relationships of changes in biomass (upper row) and changes in SRU (lower row) with changes in plant species richness in response to human disturbance for different species abundance groups (Table 1): (a, b) Community representing 100% of total abundance ($i = 1$, $j = 34$); (c, d) dominant species representing the top 60% of total abundance ($i = 1$, $j = 3$ for $biomass_D$; $i = 1$, $j = 5$ for SRU_D); (e, f) intermediate species representing the mid 30% of total abundance ($i = 4$, $j = 10$ for $biomass_I$; $i = 6$, $j = 15$ for SRU_I); and (g, h) rare species representing the bottom 10% of total abundance ($i = 11$, $j = 34$ for $biomass_R$; $i = 16$, $j = 34$ for SRU_R). Line colours as in Figure 1c. Dot colours indicate different treatments. Log response ratios (LRR) are calculated as in Figure 1c. The grey region indicates the 95% confidence interval around the regression [Colour figure can be viewed at wileyonlinelibrary.com]

dominant species (referred to as $Biomass_D$ and SRU_D respectively; Figure 3a) were thus better predictors of changes in plant species richness than changes in biomass or SRU measured for the full community (referred to as $Biomass_C$ and SRU_C respectively; Figure 3a). Furthermore, except for predictions based on only the most dominant species, the percentage of variance explained by the relationship with SRU was always higher than that derived from biomass (Figure 3a, higher R^2 values), leading to narrower 95% confidence intervals around the slope for SRU as compared to biomass (Figure 3b). Changes in SRU thus provide a better predictor of changes in plant species richness in response to human disturbance than changes in biomass.

Our abundance group approach further revealed that changes in biomass and SRU indicate the same direction for predictions of changes in plant species richness, but the direction of predictions differed depending on the particular species abundance groups examined (Figure 4). Changes in plant species richness were negatively associated with changes in biomass or SRU measured for both the whole community (Figure 4a,b; slope and 95% CI for $Biomass_C = -0.36$ (−0.52 to −0.19) and $SRU_C = -0.32$ (−0.42 to −0.22)) and the dominant species in each plot (Figure 4c,d; $Biomass_D = -0.27$ (−0.35 to −0.18) and $SRU_D = -0.26$ (−0.33 to −0.19)). In contrast, changes in plant species richness were positively associated with changes in biomass or SRU measured for the rare species (Figure 4g,h; $Biomass_R = 0.21$ (0.15–0.27) and $SRU_R = 0.20$ (0.14–0.26)). We found no association between changes in species richness and changes in biomass or SRU

measured for the intermediate species (Figure 4e,f; $Biomass_I = 0.10$ (−0.18 to 0.38) and $SRU_I = -0.02$ (−0.20 to 0.15)). Our results show that an increase in biomass or SRU at the community level or for a minority of dominant species in a community leads to a decrease in plant species richness regardless of the identity of the dominant species. At the same time, this decrease in plant species is accompanied by a decrease in the biomass and SRU for the majority of rare species. Note that while the analysis of the relationships of rare and intermediate species is of less practical relevance and can partly be derived from the difference in slope between whole community versus dominant species measures, it uncovers the finding that intermediate species dilute the predictive power offered by the dominant species, while rare species actually oppose the signal.

Examining the individual factors generating SRU_D ($Cover_D$ and $Height_D$) reveals that while changes in each factor partly and independently contribute to explaining changes in species richness (Figure S1), their aggregation into SRU_D leads to much better predictions of diversity dynamics as compared to each of $Biomass_D$ (Figures 3 and 4), $Cover_D$ and $Height_D$ (Figure S1).

Because the choice of the thresholds used to classify species ranks into abundance groups is arbitrary to some extent, we explored the effects of selecting a range of different sets of thresholds (Table 1). We found that our results were independent of the thresholds used to classify species into different abundance groups (Figure S2; Figure S3). Taken together, these results indicate that the opposite direction of predictions derived from rare species (Figure 4g,h;

Figures S2 and S3) weakens predictions from the full community (Figure 4a,b; Figures S2 and S3) and explains why better predictions are achieved by only including dominant species regardless of which species are dominant (Figures 3 and 4c,d; Figures S2 and S3).

3.2 | Multiple study sites

The abundance curves for cover across all plots within each of the five study sites confirms that rare species are numerous while dominant species are few (Figure S4) (McGill et al., 2007). Similar to results of our alpine grassland, changes in plant species richness were negatively associated with changes in community biomass or SRU measured for the dominant species (black lines in Figure 5). Moreover, whether measured for the most (Figure 5b; SRU_{D1} = −0.09 (−0.14 to −0.05)), the two most (Figure 5c; SRU_{D2} = −0.14 (−0.20 to −0.09)), or the three most (Figure 5d; SRU_{D3} = −0.15 (−0.21 to −0.09)) dominant species, the percentage of variance explained by the relationship with SRU_D was always higher than that derived from community biomass (Figure 5a; $Biomass_C$ = −0.09 (−0.15 to −0.02)). These associations were generally consistent across sites (coloured lines in Figure 5). These results clearly show, across multiple and disparate study sites, that SRU measured for the two most dominant species in each plot gives better predictions of changes in species richness than community biomass (compare Figure 5a,c). Predictions under either nutrient addition (Figure S5) or herbivore exclusion (Figure S6) show similar trends as when analysed together, but with weaker predictive power due to reduction in sample size, especially under herbivore exclusion.

4 | DISCUSSION

We investigate a new method for measuring plant diversity dynamics aimed at tracking plant community responses to environmental change including human disturbances. Specifically, we assessed how well changes in SRU predict changes in plant species richness and compared this approach to the use of conventional destructive biomass measures. We found that SRU provides stronger predictive power than biomass measurements, while also being non-destructive and easier to perform. We also found that species richness predictions are best achieved by utilizing biomass or SRU assessments of only the dominant species as compared to the entire community.

Based on a single-site level analysis of an alpine grassland, we found that changes in community-level SRU (SRU_C) and biomass ($Biomass_C$) are strong predictors of changes in plant species richness in response to human disturbances. Disturbances that increased SRU_C or $Biomass_C$ relative to the undisturbed conditions led to a decrease in plant species richness. Several previous observational and experimental studies have reported such an inverse relationship between community plant productivity and species richness upon human disturbance (Borer, Seabloom, et al., 2014b; Clark et al., 2007; Harpole & Tilman, 2007; Hautier et al., 2009). Here, we extend these findings by showing that human disturbances that increase plant competition for space and resources lead to a reduction in plant species richness.

We hypothesized that changes in SRU in response to human disturbances would better predict changes in species richness than changes in biomass. Our results indeed show that changes in SRU have higher predictive power as compared to changes in biomass, regardless of the species abundance investigated (Figure 3). This result reinforces the earlier finding that SRU_C is a better predictor of species richness than biomass (Zhang et al., 2015) and extends it to predictions of changes in species richness across dominance groups and in response to multiple human disturbances (nutrient enrichment and herbivore exclusion).

We also hypothesized that dominant species would contribute the most to community-level predictions. Our results show that, although the reduction in species richness can be predicted from
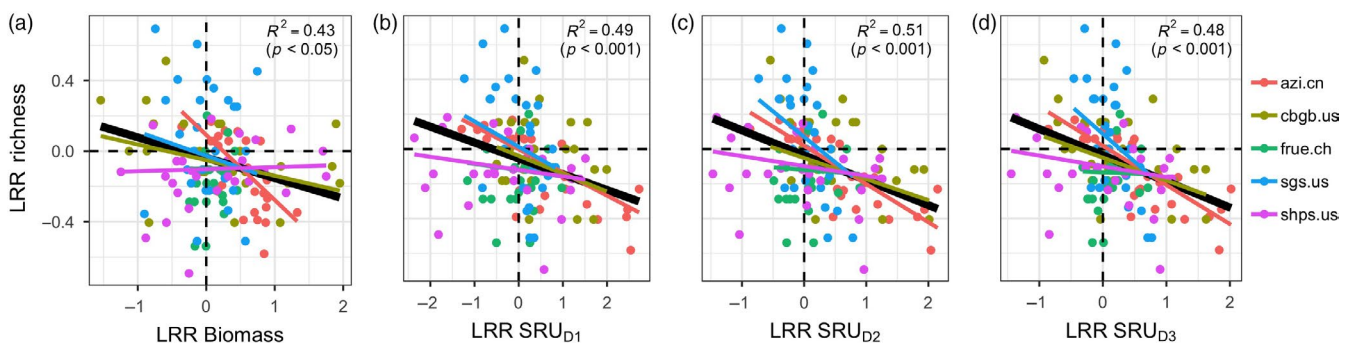
FIGURE 5 Relationships of changes in biomass (a) and changes in SRU for the most (b), the two most (c) and the three most (d) dominant species with changes in plant species richness in response to human disturbance across five sites that are part of the international Nutrient Network. The sites include a tallgrass prairie (cbgb.us), a shortgrass prairie (sgs.us) and a shrub steppe (shps.us) in North America, a pasture (frue.ch) in Europe and an alpine grassland (azi.cn) in Asia (Table S1). Black lines are the fixed-effect linear regression slopes among sites from the mixed effects model with block nested within site as a random effect; coloured lines show patterns within sites. Conditional R^2 represents model variation explained by the combination of fixed and random effects. Log response ratios (LRR) are calculated as in Figure 1c [Colour figure can be viewed at wileyonlinelibrary.com]

increases in community biomass or SRU, the best predictions were obtained when only a few dominant species were included. Thus, predictions based on changes in the dominant species (SRU_D, $Biomass_D$) were much better than those based on the entire community (SRU_C, $Biomass_C$). Our results support the mass ratio effect (Grime, 1998) and earlier studies reporting that only a few dominant species drive community structure, composition and functioning (Hoover, Knapp, & Smith, 2014; Smith & Knapp, 2003; Winfree, Fox, Williams, Reilly, & Cariveau, 2015). Most interestingly, we found that the best predictions were obtained when considering the SRU of only dominant species regardless of the identity of the dominant species. Below, we show that this is due to a dilution effect of the intermediate species and an opposing effect of the rare species.

Although of less practical utility and partly related to the relationships of the community and dominant species, we found that changes in the rare species (SRU_R and $Biomass_R$) can also be used as good predictors of changes in plant species richness, but in the opposite direction indicated by both dominant species (SRU_D and $Biomass_D$) (Figure 4c,d) and the total community (SRU_C and $Biomass_C$) (Figure 4a,b). This result indicates that human disturbances have opposing impacts on dominant versus rare species, leading to opposite predictions of changes in species richness. Decreases in plant species richness are thus due to a simultaneous general increase in the dominant species abundance, as well as a decrease in the rare species abundance, regardless of which plant species are involved (Clark & Tilman, 2008; Smith & Knapp, 2003). The contrasting contributions of dominant and rare species to predicting changes in plant species richness together with a dilution effect of the intermediate species explains why weaker predictions are obtained when utilizing the entire community data, as opposed to only the dominant species (Zhang et al., 2015). In sum, our study shows that the aggregation of measures of species' cover and height of a few dominant species can provide a powerful, non-destructive and robust tool to assess competitive outcomes in response to human disturbance. For example, the total biomass or SRU of two communities may show little response to human disturbance, but the community with the greater changes in biomass or SRU of a few dominant species will experience a greater change in species richness and evenness.

Our in depth single-site analysis suggests that the best predictions are obtained when including the first three dominant species for biomass and the first five dominant species for SRU. However, it is interesting to note that the predictive power is already higher than the community-based approach when including only the most dominant species for biomass or the two most dominant species for SRU. Our analysis of multiple sites further demonstrates that the good predictions of diversity based on only the single most dominant species in a plot hold up across a wide range of different plant communities. Similarly, for all sites, including the two most dominant species in the analysis, yielded higher predictive ability as compared to each of community biomass and SRU_D based on only the single most dominant species. While we cannot exclude that higher predictive power could be obtained based on the four or the five most dominant species in some cases, our multi-site analysis shows that including the three most dominant species led to slightly less precise diversity predictions as compared to using only the two most dominant species. This is in line with our single-site study, which shows that including more species will eventually lead to poorer predictions, due to the diluting effects of intermediate species and the opposing effects of rare species.

The observation that communities are composed of a few locally dominant species and many locally rare species is one of the most universal ecological principles (McGill et al., 2007). Moreover, our method is generic in that it does not focus on the responses of any particular species or group of species in a community. Rather, it considers that changes in competitive abilities of a few species dominating in a particular community (SRU_D), regardless of species identity, are driving changes in community composition. We, therefore, expect our results to apply across a wide range of habitats and ecosystems. Indeed, our results clearly show, across multiple study sites differing in their habitats and locations, that SRU_D gives better predictions of changes in species richness than community biomass. Future studies could determine how such an approach performs under a wider variety of anthropogenic drivers, and the number of dominant species required to reach the strongest predictions.

Our results suggest that the higher predictive power of SRU comes from the aggregation of two key factors with their independent contributions, together acting as a collective wrapper for plant competitive responses in multiple dimensions. Particularly, cover and height represent the competitive ability for space and light in the horizontal dimension and for light in the vertical dimension (Damgaard, 2011). The finding that cover and height are only weakly correlated (Figure S1) suggests that SRU is a better predictor than biomass because it combines two factors that, to a large extent, represent different species' resource accumulation strategies and independently contribute to asymmetric competition for light and community-level thinning (Hautier et al., 2009; Kaarlejarvi, Eskelinen, & Olofsson, 2017; Suding et al., 2005; Yang et al., 2015). As such, SRU represents a very useful and reliable wrapper of multiple factors related to plant competitive abilities, but future studies will be required to assess the exact suite of factors and underlying mechanisms that make SRU such a good predictor of plant species dynamics.

The SRU_D approach is highly simplified; for example, while it precisely measures changes in trait plasticity (height) in response to human disturbance, it ignores the contribution to plant diversity dynamics of intraspecific trait plasticity within a community. Moreover, while plants exhibit an enormous range of shape and volume (Ingram & Hudson, 1994), our approach simplifies plants' form into a volume representing a cylinder. Despite its simplicity, our model captures the variation in cover and the highly plastic response of height, a plasticity that is not available from trait databases and that needs to be measured in the field (Kattge et al., 2011), into a robust and generalizable predictor of competitive outcomes in response to multiple human disturbances across a wide range of habitats.

Not only does our approach allow for the accurate tracking of management success with respect to promoting species richness, it

also stresses how management measures tailored to reducing the SRU of dominant species could represent successful interventions for enhancing biodiversity. Thus, our study suggests that selective harvesting of the dominant species, or introduction of natural enemies (e.g. herbivores, plant or soil pathogens and (hemi)parasites) acting in a density-dependent manner or having a greater effect on the dominant species in a community could promote coexistence and diversity. For example, specialist pathogens or negative biotic soil-effects can promote coexistence by limiting the abundance of the dominant plant species (Allan, van Ruijven, & Crawley, 2010; Creissen, Jorgensen, & Brown, 2016; Heinze, Bergmann, Rillig, & Joshi, 2015). If fast-growing species dominate the community, the introduction of (hemi)parasitic species likely to infect dominant species via abundance-based mechanisms (e.g., due to increased encounter rates) could help grassland restoration (Bardgett et al., 2006; Bullock & Pywell, 2005; DiGiovanni, Wysocki, Burke, Duvall, & Barber, 2017; Pywell et al., 2004). This is because the reduction in competitive dominance of the dominant species by selective harvesting or natural enemies impairs future resource uptake, competitive ability and future abundance of the target dominant species and helps other species, especially rare species, to establish and persist (Allan et al., 2010; Bullock & Pywell, 2005; Hautier, Hector, Vojtech, Purves, & Turnbull, 2010; Heinze et al., 2015). Thus, our results have implications for the development of restoration and management strategies as well as providing an accurate and tractable tool for monitoring subsequent changes in species richness.

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AUTHORS' CONTRIBUTIONS

P.Z. and Y.H. conceived the study and analysed the data, with input from all authors; P.Z., Y.H., X.Z., X.Z., C.C., G.D., Z.G. and J.F. collected the data used in this study; P.Z. and Y.H. wrote the paper with input from all authors.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.1bm144m (Zhang et al., 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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