

Dominant species, rather than diversity, regulates temporal stability of plant communities

Takehiro Sasaki · William K. Lauenroth

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Abstract A growing body of empirical evidence suggests that the temporal stability of communities typically increases with diversity. The counterview to this is that dominant species, rather than diversity itself, might regulate temporal stability. However, empirical studies that have explicitly examined the relative importance of diversity and dominant species in maintaining community stability have yielded few clear-cut patterns. Here, using a long-term data set, we examined the relative importance of changes in diversity components and dominance hierarchy following the removal of a dominant C4 grass, *Bouteloua gracilis*, in stabilizing plant communities. We also examined the relationships between the variables of diversity and dominance hierarchy and the statistical components of temporal stability. We found a significant negative relationship between temporal stability and species richness, number of rare species, and relative abundance of rare species, whereas a significant positive relationship existed between temporal stability and relative abundance of the dominant species. Variances and covariances summed over all species significantly increased with increasing species richness, whereas they significantly decreased with

increasing relative abundance of dominant species. We showed that temporal stability in a shortgrass steppe plant community was controlled by dominant species rather than by diversity itself. The generality of diversity–stability relationships might be restricted by the dynamics of dominant species, especially when they have characteristics that contribute to stability in highly stochastic systems. A clear implication is that dominance hierarchies and their changes might be among the most important ecological components to consider in managing communities to maintain ecosystem functioning.

Keywords *Buchloe dactyloides* · Grassland · Mass ratio hypothesis · Removal experiment · Shortgrass steppe

Introduction

Temporal stability, which has been defined as a lack of fluctuations over time (Tilman 1999; Lehman and Tilman 2000), is a fundamental property of any ecosystem and has therefore been the subject of many studies during the last few decades. A growing body of empirical evidence suggests that the temporal stability of communities, measured as lack of fluctuations in total biomass or abundance in communities over time, often increases with diversity (Tilman 1999; Cottingham et al. 2001; Valone and Hoffman 2003; Tilman et al. 2006). Theory predicts that greater community stability can result from the manner in which temporal variance in species abundances scales with abundance (portfolio effect); from increasingly negative covariance in the abundances of competing species at higher diversity (covariance effect); and/or from the manner in which species abundances scale with diversity (overyielding effect; greater total biomass in

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T. Sasaki (✉)
Graduate School of Life Sciences, Tohoku University, 6-3 Aoba,
Aramaki, Aoba-ku, Sendai 980-8578, Japan
e-mail: sasa@m.tains.tohoku.ac.jp; sasa67123@gmail.com

W. K. Lauenroth
Department of Botany, University of Wyoming, Laramie,
Wyoming 82071-2000, USA

communities at higher diversity) (Tilman 1999; Lehman and Tilman 2000).

A counterview is that dominant species, rather than diversity itself, might enhance community stability, as predicted by Grime's mass ratio hypothesis (Grime 1998). This hypothesis holds that ecosystem functioning, including stability, is largely controlled in the short term by dominant species, whereas minor vegetation components such as subdominant and rare species may regulate stability in the long term by influencing the recruitment of dominant species (Grime 1998). Whereas the effects of diversity on ecosystem functioning have received much attention, the importance of community dominance hierarchies and their changes in maintaining ecosystem functioning is poorly understood (Smith and Knapp 2003; Hillebrand et al. 2008; Grman et al. 2010).

Loss of dominant species can reduce competition for limiting resources, favor diversity, and modify the dominance hierarchy in communities, with an additional increase in the abundance of subdominant and rarer species (Collins et al. 1998; Bakker and Olff 2003). If the diversity effect on community stability prevails in a given system, the increase in diversity caused by the removal of dominant species should lead to increased community stability. However, a few empirical studies that have explicitly examined the relative importance of diversity and dominant species in the maintenance of community stability have shown that the removal of or a reduction in the abundance of dominant species often increases diversity in communities but does not change temporal stability (Leps 2004; Polley et al. 2007). These empirical investigations suggest that the effect of diversity on temporal stability can be constrained by the dynamics of a dominant species in some ecosystems. Yet, we lack a strong case in which the dominant species enhances the temporal stability of communities. Consequently, few studies have examined the importance of dominant species in stabilizing communities.

In this work, using a long-term data set, we examine the relative importance of changes in diversity components and dominance hierarchy following the removal of the dominant species in stabilizing plant communities under natural variations in rainfall. We do this using various measures of species diversity, functional diversity, and dominance hierarchy (the relative abundances of dominant, subdominant, and rare species) and by revealing significant relationships between these variables and the temporal stability of communities. Furthermore, we examine the relationships between the variables of diversity and dominance hierarchy and the statistical components of temporal stability (summed variance, which is the sum of the temporal variance of each species; summed covariance, which is the sum of the temporal covariances between all pairs of species in a community; and summed abundance, which is

the sum of the abundance of each species). Finally, we discuss the potential mechanisms that might be responsible for the relationships between the variables of diversity and dominance hierarchy and temporal stability.

Materials and methods

Site description

We examined the temporal stability of plant communities over a 9-year period (1998–2006) following the removal of the dominant species, *Bouteloua gracilis*, from a long-term experimental site (Central Plains Experimental Range, Shortgrass Steppe Long-Term Ecological Research site) located 60 km northeast of Fort Collins, Colorado (40°49'N, 107°47'W). The climate is semi-arid with a long-term (68 years) mean annual precipitation of 341 mm (CV = 29%), and a mean annual temperature of 9.6°C (CV = 11%) (Munson and Lauenroth 2009). Across the experimental period, the site experienced strong fluctuations in annual precipitation (see Munson and Lauenroth 2009). The plant community is dominated by the C4 shortgrasses *B. gracilis* (blue grama) and *Buchloeë dactyloides* (buffalo grass), with C3 grasses, forbs, and shrubs composing the subdominant and relatively rare portion of the plant community (Munson and Lauenroth 2009). The possession of a C4 photosynthetic pathway may thus distinguish these dominant species from other species. Other general descriptions of the study site are available in Munson and Lauenroth (2009).

Data sets

A split-plot factorial design was established in 1997 consisting of six sites, with two grazing treatments (a pair of adjacent grazed and ungrazed locations) within each site and two removal treatments (removal of *B. gracilis* or control) within each grazing treatment. Each site by grazing by removal treatment combination was replicated twice, for a total of 48 3 × 3 treatment plots. The sites were selected randomly and were located approximately 6 km apart. Soils at the sites contained 63% sand, 15% silt, and 22% clay on average, and the slope was <3% at all sites. Cattle were the most important large herbivore grazers in the experiment. The grazing treatment was moderate summer grazing with the objective of removing 40% of aboveground net primary production (Milchunas et al. 2008). All tillers and root crowns of *B. gracilis* were removed by clipping at the soil surface once in 1997 from the subplots, with all other vegetation left undisturbed (note that we removed only *B. gracilis* just once in 1997). Plant density (number of individuals) was measured annually in

late June and early July from 1998 to 2006 by species in a fixed 1×1 m quadrat in the center of the subplots. For clonal species, an individual plant was defined as a group of tillers connected by a crown (Coffin and Lauenroth 1988; Fair et al. 1999). Most studies of temporal stability in plant communities have used biomass rather than density as the community property for calculating temporal stability (e.g., Tilman et al. 2006). Although we would have preferred to use biomass for the analyses, we could not because such data were not available. Nonetheless, previous studies in a physiognomically and climatically similar long-term experimental site at the Sevilleta Wildlife Refuge in New Mexico (Ernest et al. 2000) reported that density was correlated strongly with cover and biomass. We therefore used density data in all of the following analyses.

Data analysis

We selected variables associated with either diversity or dominance hierarchy. For the variables of diversity, we calculated 9-year mean values of species richness (the number of species), the number of rare species (species with less than 1% of total cumulative density in all control-subplot quadrats in all years), species diversity (Simpson's diversity index; Magurran 2004), species evenness (Simpson's evenness index; Magurran 2004), and functional diversity (the adaptation of an index of species dissimilarity; Botta-Dukat 2005; De Bello et al. 2006; Lavorel et al. 2008) for each quadrat. We then averaged these values from each of two quadrats within each of two treatment subplots (i.e., $n = 24$). Simpson's diversity index (D), and Simpson's evenness index (E) were calculated as follows for each quadrat:

$$D = 1 - \sum_{i=1}^S P_i^2 \quad (1)$$

$$E = \frac{1}{\sum_{i=1}^S P_i^2 \times S} \quad (2)$$

where S is the number of species found in each quadrat and P_i is the proportional density represented by the i th species. To quantify functional diversity, we selected species functional traits such as life history (annual, biennial, herbaceous perennial, or woody), growth form (grass, forb, subshrub, or shrub), photosynthetic pathway (C3 or C4), N-fixing ability (legume or non-legume), and lateral spread (erect, tussock, branched, or prostrate). Previous studies have indicated that these traits are key to determining the role of species in stabilizing communities, both temporally and spatially, in grassland ecosystems (Crawley et al. 1999; White et al. 2000; Symstad and Tilman et al. 2001; Weigelt

et al. 2008). We collected the information for these traits from an existing local flora guide (McGregor and Barkley 1986). Each option for these nominal traits was recorded as a separate column in the traits' category data. Where multiple membership of categories within a nominal trait was possible (e.g., for life history), the sum of the scores for a species across that trait was set to 1 (Pakeman 2004; De Bello et al. 2005). For example, species that could behave as annuals or biennials would have a score of 0.5 as annuals and 0.5 as biennials, with a total of 1 for the life history trait. In brief, functional diversity (FD) was then calculated as follows for each quadrat:

$$FD = \sum_{i=1}^S \sum_{j=1}^S d_{ij} P_i P_j \quad (3)$$

where d_{ij} is the pairwise dissimilarity between species i and j , numerically given as the species Euclidean distance. Thus, FD is the sum of the dissimilarity in the trait space among all possible pairs of species, weighted by the product of the species' relative abundance.

For the variables of dominance hierarchy, we also calculated the 9-year mean values of the relative abundance of dominant species; of subdominant species (species with more than 1% of total cumulative density in all control-subplot quadrats in all years; *B. gracilis* and *B. dactyloides* were considered dominant species and therefore excluded from the abundance analysis of subdominant and rare species; Munson and Lauenroth 2009); and of rare species (species with less than 1% of total cumulative density in all control-subplot quadrats in all years) for each quadrat. We then averaged these values from each of two quadrats within each of two treatment subplots (i.e., $n = 24$).

We calculated the inverse of CV (ICV), that is, the mean density divided by the standard deviation of density, as a measure of temporal stability of community (Tilman 1999; Tilman et al. 2006). Increased values of ICV indicated greater stability. To explore more closely how diversity and dominance hierarchy could affect temporal stability in communities, we also calculated a temporal stability index (TSI; Lehman and Tilman 2000; Valone and Hoffman 2003), defined as:

$$TSI = \frac{\sum \text{Abundance}}{\sqrt{(\sum \text{Variances} + \sum \text{Covariances})}} \quad (4)$$

where abundance and variances are summed over all species in a community and covariances are summed over all pairs of species. Higher values of TSI also indicate greater stability. For the case of diversity, TSI increases with diversity if, all else being equal, more diverse communities (1) have lower summed variances (portfolio effect), (2) have lower summed covariances (covariance effect), or (3) have greater abundance (here, more individuals; overyielding effect) than

less diverse communities (Tilman 1999; Lehman and Tilman 2000; Cottingham et al. 2001; Valone and Hoffman 2003). To calculate the ICV and TSI, we pooled the data from each of two quadrats within each of two treatment subplots (i.e., $n = 24$).

We performed a split-plot ANOVA to compare the effects of grazing (the whole plot treatment) and removal (the subplot treatment) on the variables of temporal stability (ICV and TSI), diversity, and dominance hierarchy. In a split-plot ANOVA, we considered site as a blocking factor. Although the experiment was originally set up to investigate the effects of cattle grazing and removal of dominant species on vegetation dynamics in the shortgrass steppe, initial analyses indicated that grazing was not a significant factor in the responses of community attributes such as density and cover to the removal treatments (Munson and Lauenroth 2009). In general, cattle grazing has been found to have a very small influence on shortgrass steppe plant communities (Milchunas et al. 2008). Our analyses also revealed that grazing was not a significant factor in the responses of diversity, dominance hierarchy, and temporal stability to the removal treatments (see “Results” and Table S1 of the Electronic supplementary material). However, some of the variables of diversity and dominance hierarchy differed significantly among the sites (Table S1). Therefore, to increase the generality of our analyses and facilitate a mechanistic understanding of how particular community attributes affect the temporal stability of communities, we ran single-variable linear mixed-effects models for each variable of diversity and dominance hierarchy by adding site and grazing treatment nested within site as random effects.

To evaluate the confounding effects of directional responses of vegetation to the removal treatment on the results, we also examined the relationships between each variable of diversity and dominance hierarchy and temporal stability, using subset data from 2002 to 2006. Although repeated photography indicated that *B. gracilis* recovered rapidly owing to regrowth from perennial organs rather than vegetative spread from the edges of the plot or seedling establishment in the removal plots, the cover of *B. gracilis* was generally significantly higher in the control than removal plots from 1998 to 2006, indicating that our removal treatment has a long-lasting effect (Munson & Lauenroth 2009). Moreover, our additional analysis indicated that the change in the relative abundance of dominant species by the removal treatment represented the change in the relative abundance of *B. gracilis* rather than *B. dactyloides* (Table S1). Nevertheless, there was no significant difference in basal cover of all vegetation between the control and removal plots from 2002 to 2006 (Munson and Lauenroth 2009). Therefore, we considered that vegetation dynamics would be governed by directional responses to

the removal treatment from 1997 to 2001, whereas the directional changes were small from 2002 to 2006.

Finally, to determine the potential mechanisms that might be responsible for the relationships between the variables of diversity and dominance hierarchy and temporal stability, we assessed the contributions of these variables to the statistical components of TSI, summed variances, summed covariances, and summed abundances. By adding site and grazing treatment nested within site as random effects, we also ran single-variable linear mixed-effects models for each variable of diversity and dominance hierarchy that was revealed to affect significantly the temporal stability. For all linear mixed-effect models, we obtained *P* values by using Markov chain Monte Carlo simulations (Baayen et al. 2008).

All statistical analyses were performed with R software (version 2.9.2; R Development Core Team 2009).

Results

Temporal stability (ICV and TSI) and the relative abundance of dominant species were significantly higher (Fig. 1i, j, f), whereas species richness, number of rare species, and the ratio of subdominant species were significantly lower in the control than in removal plots (Fig. 1a, d, g). We could not generally detect an effect of grazing treatment or an interaction effect between grazing and removal treatment on these variables (see Table S1). Species diversity, species evenness, functional diversity, and the relative abundance of rare species did not vary significantly between the control and removal plots (see Table S1 and Fig. 1b, c, e, h).

We found a significant negative relationship between TSI and species richness, number of rare species, and relative abundance of rare species (Fig. 2a, d, h), whereas a significant positive relationship existed between TSI and the relative abundance of dominant species (Fig. 2f). The relationships between TSI and species diversity, species evenness, functional diversity, and relative abundance of subdominant species were not significant (Fig. 2b, c, e, g). These relationships were consistent when we used ICV as a measure of the temporal stability of communities (results not shown). In addition, these results were robust when we based the analyses on the subset data from 2002 to 2006 (see Fig. S1 of the Electronic supplementary material); species richness, number of rare species, and the relative abundance of rare species were significantly negatively related to TSI (Fig. S1a, d, a, h), whereas the relative abundance of dominant species was significantly positively related to TSI (Fig. S1f).

Finally, we assessed the contributions of species richness, number of rare species, and relative abundances of

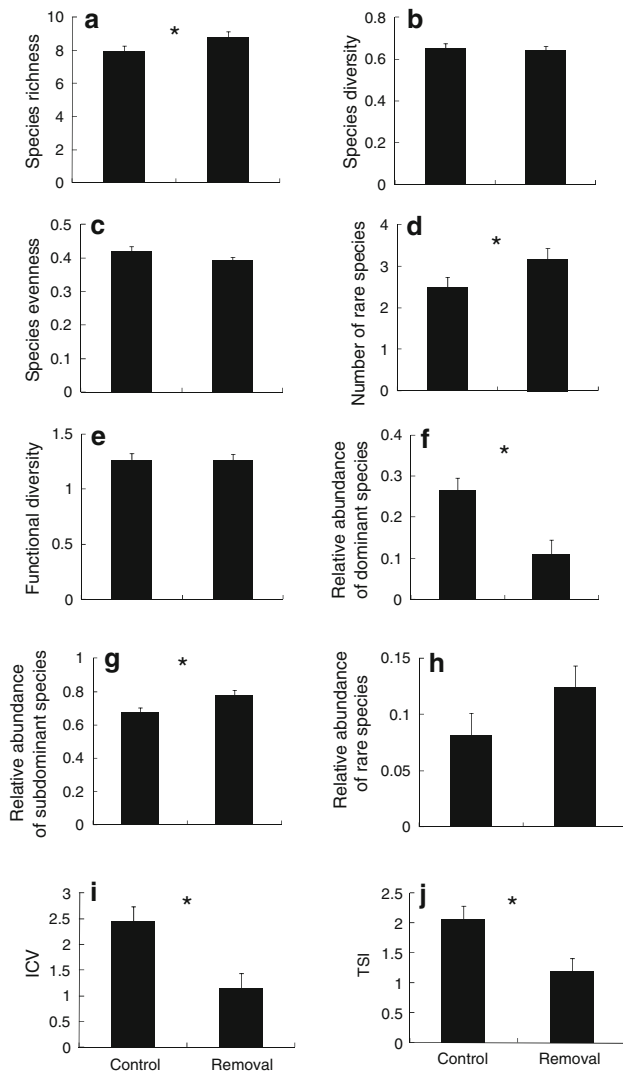


Fig. 1a–j Differences in the variables of diversity (species richness, species diversity, species evenness, number of rare species, and functional diversity (a–e), respectively), dominance hierarchy (relative abundances of dominant, subdominant and rare species (f–h), respectively), and temporal stability of communities (ICV, inverse of CV and TSI, temporal stability index (i and j) between control and removal plots. Bars show means + standard errors. Significant differences are indicated by an asterisk ($P < 0.05$). Higher ICV and TSI indicate greater stability. Results of a split-plot ANOVA to compare the effects of grazing (the whole plot treatment), and removal (the subplot treatment) on these variables are given in the Electronic supplementary material (Table S1)

dominant and rare species to the statistical components of TSI. Summed variances significantly decreased with increasing relative abundance of dominant species (Fig. 3c). Summed covariances significantly increased with increasing species richness and number of rare species (Fig. 3e, f), but significantly decreased with increasing relative abundance of dominant species (Fig. 3g). Summed abundance significantly decreased with increasing relative abundance of dominant species (Fig. 3k).

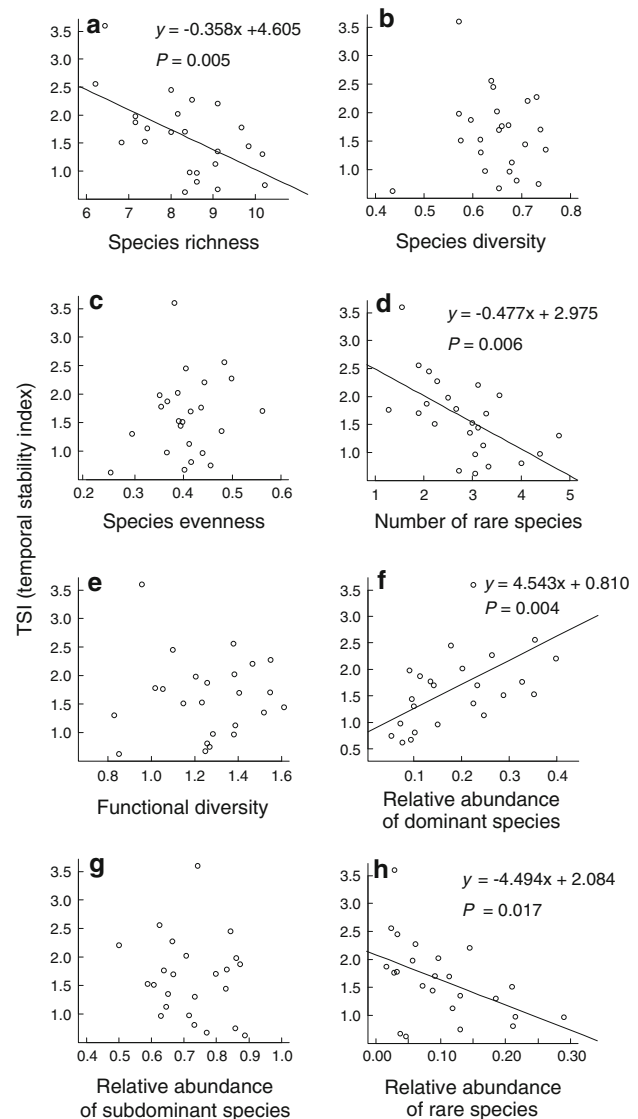


Fig. 2a–h Relationships between the TSI (temporal stability index) and each variable of diversity (species richness, species diversity, species evenness, number of rare species, and functional diversity (a–e), respectively) and dominance hierarchy (relative abundances of dominant, subdominant and rare species (f–h), respectively). Solid lines indicate significant linear fits from single-variable mixed-effects models ($P < 0.05$). P values were obtained by using Markov chain Monte Carlo simulations. Higher TSI indicates greater stability. These results were robust when we based these analyses on the subset data from 2002 to 2006 (see Fig. S1 of the Electronic supplementary material)

Discussion

Removal of the dominant species increased species richness, number of rare species, and relative abundance of subdominant species (Fig. 1a, d, g), but it did not affect species diversity, species evenness, functional diversity, and relative abundance of rare species in communities (Fig. 1b, c, e, h). The reduction in dominant species abundance was compensated for by an increase in subdominant

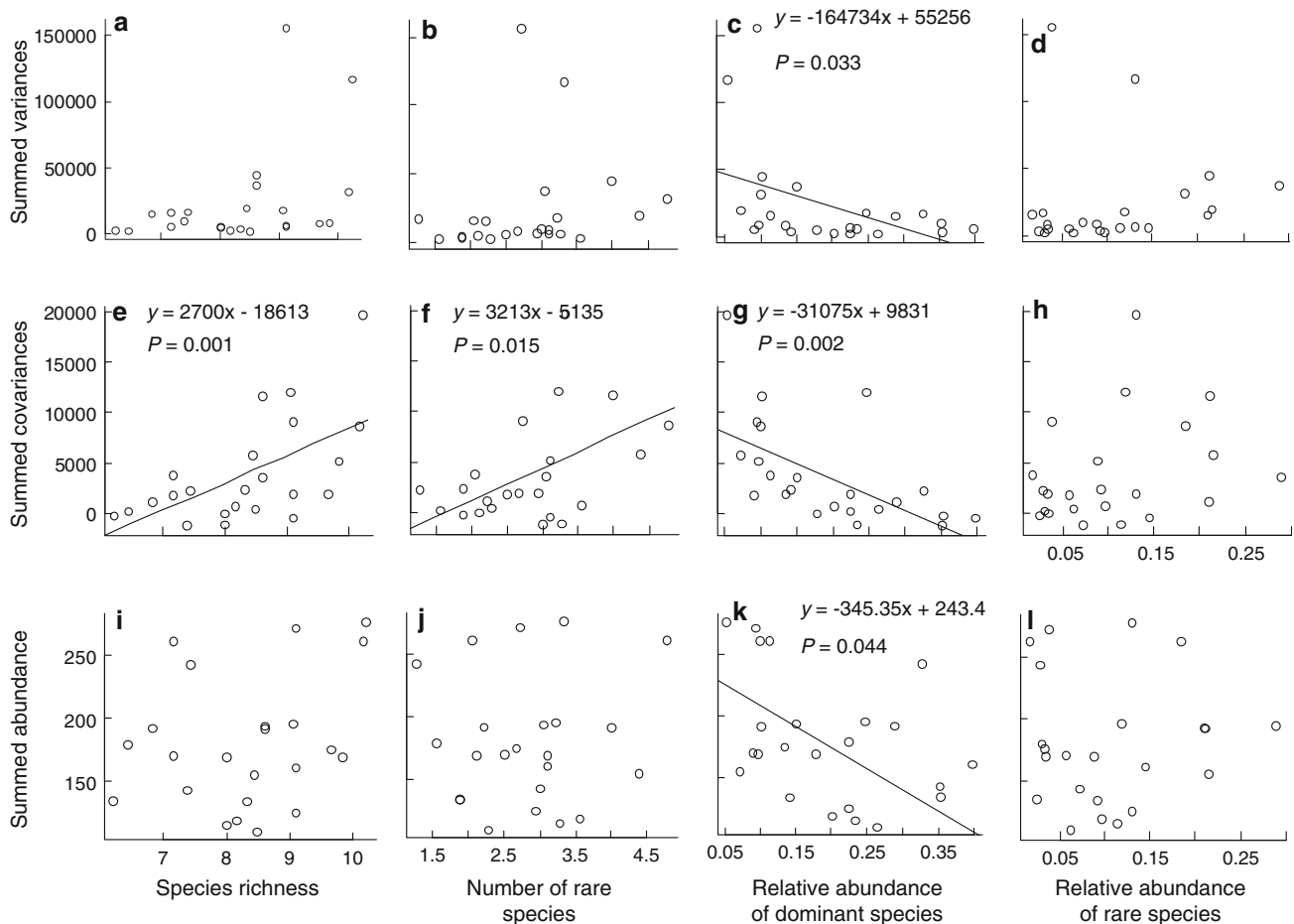


Fig. 3a–l Relationships between TSI (temporal stability index) components (summed variances, covariances, and abundance) and species richness (**a**, **e**, **i**), number of rare species (**b**, **f**, **j**), and relative abundances of dominant (**c**, **g**, **k**) and rare species (**d**, **h**, **l**), which were

significantly related to TSI (see Fig. 2). Solid lines indicate significant linear fits when applying single-variable mixed-effects models ($P < 0.05$). P values were obtained using Markov chain Monte Carlo simulations

species abundance without a significant change in species evenness and diversity. Increases in the abundance of subdominant species in plots were largely due to the increases in abundance of particular grass species (almost all of them were subdominant) that were already present before *B. gracilis* removal (Munson and Lauenroth 2009). For example, *Carex eleocharis*, *Sporobolus cryptandrus*, and *Agropyron smithii* increased rapidly in abundance in the removal plots, but almost exclusively in plots in which they had occurred before dominant species removal (Munson and Lauenroth 2009). As a consequence, subdominant species that can increase greatly in abundance when dominant species are removed might be limited in number in each plot; this would explain the lack of significant changes in species evenness and species diversity. The change in species richness following dominant species removal was probably largely driven by the recruitment of rare species that had relatively low abundance. Moreover, new rare species might not have had unique traits; this

would have explained the lack of changes in functional diversity. Overall, loss of dominant species may reduce competition for limiting resources, favoring species richness and modifying the dominant hierarchy in communities, with an additional increase in the abundance of subordinate and rarer species (Collins et al. 1998; Bakker and Olff 2003). Nonetheless, the increase in species richness triggered by the removal of dominant species led to a decrease in temporal stability in communities.

We found a significant negative relationship between temporal stability and species richness, number of rare species, and relative abundance of rare species (Fig. 2a, d, h). This is counter to the growing body of empirical evidence that suggests that the temporal stability of communities increases with diversity (Tilman 1999; Cottingham et al. 2001; Valone and Hoffman 2003; Tilman et al. 2006). Many theoretical studies have focused on the portfolio and covariance effects (see “Materials and methods”) in demonstrating how increased diversity can confer increased temporal stability

(Tilman 1999; Yachi and Loreau 1999; Hughes and Roughgarden 2000). However, we found no significant relationships between summed variances and species richness and number of rare species (Fig. 3a, b), and we found significant positive relationships between summed covariances and species richness and number of rare species (Fig. 3e, f). Neither the portfolio nor the covariance effect contributed significantly to temporal stability in our communities. Rare species that generally exhibit greater temporal fluctuations than common species should more often exhibit years of zero abundance than common species because of their small population sizes (Lande 1993; Valone and Schutzenhofer 2007), resulting in synchrony in response to high interannual variability in rainfall. This probably dampened the expected stabilizing effect of species richness on temporal stability (Yachi and Loreau 1999). Valone and Barber (2008) also showed that covariances between most pairs of species in natural communities were more often positive than negative, potentially because of shared responses of coexisting species to fluctuations in a common resource base, possibly driven by climatic fluctuations. Moreover, the relationship between summed abundance and species richness was not significant (Fig. 3i), suggesting that overyielding was not important in our communities. A previous study has indicated that functional diversity is a good predictor of the overyielding effect of species richness (Griffin et al. 2009). Our findings suggest that, although we do not know the explicit mechanism, the lack of change in functional diversity, despite the increase in species richness resulting from the removal of dominant species, might explain the absence of an overyielding effect. Thus, there were no operational stabilizing effects of greater diversity; rather, greater species richness supported by an increase in the number of rare species destabilized the communities.

In contrast, we found a significant positive relationship between temporal stability and the relative abundance of dominant species (Fig. 2f). This suggests that the dominant C4 grasses, *B. gracilis* and *B. dactyloides*, rather than diversity itself, regulate community stability. Indeed, the value for the relative abundance of dominant species in our case corresponded exactly to the mean trait value (Garnier et al. 2004) for photosynthetic pathway (C3 or C4). The fact that temporal stability increased significantly with the relative abundance of dominant species—not functional diversity, which incorporates species' dissimilarities as defined by various traits—also supported the importance of dominant species in stabilizing communities, as suggested by Mokany et al. (2008). The relationships between summed variances, covariances, and abundance and the relative abundance of dominant species were all negative (Fig. 3c, g, k). Because C4 plant species generally are tolerant to

drought stresses (Sage 2001), the fluctuations in their population abundance under high interannual variability in rainfall are small. In addition, Fair et al. (1999) reported that *B. gracilis* produces long-lived genets and can therefore maintain its population in the community because its occupation of resource space for long periods prevents the recruitment of other species. Thus, the population stability of *B. gracilis* was probably reflected in the negative relationships between summed variances and covariances and the relative abundance of dominant species. However, increased abundance of dominant species did not contribute to increased community abundance (Fig. 3k). Although an increase in summed abundances also makes it less likely that environmental stochasticity will result in low temporal stability (Tilman 1999; Hughes and Roughgarden 2000), the stabilizing effect underpinned by the negative relationships between summed variances and covariances and the abundance of dominant species was sufficiently strong to stabilize communities.

Thus, our findings showed that temporal stability in communities was largely controlled for nearly a decade by dominant species rather than by diversity itself, supporting Grime's (1998) mass ratio hypothesis. The generality of diversity–stability relationships might be restricted by the dynamics of a dominant species (Leps 2004; Polley et al. 2007), especially when the species has features that distinguish it from others that would contribute to stability in highly stochastic systems. The results were robust when we based the analyses on the subset data from 2002 to 2006 (Fig. S1 of the Electronic supplementary material), suggesting that the confounding effects of directional responses of vegetation to the removal treatment on the results were small. However, our results do not necessarily suggest that diversity is unimportant to community stability. In particular, minor vegetation components such as subdominant and rare species might regulate stability in the longer term by influencing the recruitment of dominant species (Grime 1998). A clear implication from this study is that community dominance hierarchies and their changes might be among the important ecological components that need to be considered when managing communities to maintain ecosystem functioning (Smith and Knapp 2003; Hillebrand et al. 2008; Grman et al. 2010).

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