CrossMark

COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Functional diversity increases ecological stability in a grazed grassland

Lauren M. Hallett[1,3,4] · Claudia Stein[1,2] · Katharine N. Suding[1,3]

Abstract Understanding the factors governing ecological stability in variable environments is a central focus of ecology. Functional diversity can stabilize ecosystem function over time if one group of species compensates for an environmentally driven decline in another. Although intuitively appealing, evidence for this pattern is mixed. We hypothesized that diverse functional responses to rainfall will increase the stability of vegetation cover and biomass across rainfall conditions, but that this effect depends on land-use legacies that maintain functional diversity. We experimentally manipulated grazing in a California grassland to create land-use legacies of low and moderate grazing, across which we implemented rainout shelters and irrigation to create dry and wet conditions over 3 years. We found that the stability of the vegetation cover was greatly elevated and the stability of the biomass was slightly elevated across rainfall conditions in areas with histories of moderate grazing. Initial functional diversity—both in the seed bank and aboveground—was also greater in areas that had been moderately grazed. Rainfall conditions in conjunction with this grazing legacy led to different functional diversity patterns over time. Wet conditions led to rapid declines in functional diversity and a convergence on resource-acquisitive traits. In contrast, consecutively dry conditions maintained but did not increase functional diversity over time. As a result, grazing practices and environmental conditions that decrease functional diversity may be associated with lasting effects on the response of ecosystem functions to drought. Our results demonstrate that theorized relationships between diversity and stability are applicable and important in the context of working grazed landscapes.

Keywords California rangeland · Compensatory dynamics · Land-use legacy · Rainfall variability · Seed bank

Communicated by Stephan Hattenschwiler.

✉ Lauren M. Hallett
  lauren.m.hallett@gmail.com

1   Department of Environmental Science Policy
    and Management, University of California, Berkeley, 137
    Mulford Hall, Berkeley, CA 94720, USA

2   Department of Biology and Tyson Research Center,
    Washington University in St. Louis, St. Louis, MO 63130,
    USA

3   Institute of Arctic and Alpine Research, University
    of Colorado Boulder, Boulder, CO 80303, USA

4   Environmental Studies Program and Department of Biology,
    University of Oregon, Eugene, OR 97403, USA

Introduction

Understanding the factors governing ecological stability has long been a central focus of ecology (MacArthur 1955; Tilman et al. 1996; Cottingham et al. 2001), and a developing consensus indicates that biodiversity may be key to promoting ecosystem stability (Hooper et al. 2005; Naeem et al. 2009; Cardinale et al. 2012). For instance, species or functional groups may affect ecosystem properties in similar ways, but have different responses to the environment (Yachi and Loreau 1999; Díaz and Cabido 2001; Mori et al. 2013). The various environmental responses represented in a community, called functional response diversity (Díaz and Cabido 1997; Suding et al. 2008), can help to stabilize ecosystem properties. Specifically, a diverse representation of

environmental responses increases the likelihood that some species are present that can compensate for an environmentally driven decline in others (Yachi and Loreau 1999; Gonzalez and Loreau 2009). A key challenge is to apply this relationship in the context of maintaining the stable provisioning of ecosystem services (Thompson and Starzomski 2007; Mori et al. 2013; Balvanera et al. 2014).

There is need to understand and manage for ecological stability in the face of a climate that is predicted to become more extreme and variable (IPCC 2013). The effects of climate change will likely be dependent on the legacies of land use, such as grazing, plowing, or burning, particularly in managed and working landscapes (Foster et al. 2003; Quétier et al. 2007). Specifically, land-use legacies might influence which functional groups are available to respond to climate variability via changes in the seed bank, extant community, or microsite availability (Chillo et al. 2011; Mori et al. 2013). Importantly, management that aims to maximize ecosystem services under optimal climate conditions may potentially alter resilience to non-optimal conditions (Côté and Darling 2010) (Fig. 1). For example, a common goal for rangeland

management is to promote highly productive forage species. However, drought years can negatively affect productive dominant species, whereas less productive subordinate species, particularly forbs, do relatively well in drought years due to decreased competition (Kardol et al. 2010; Mariotte et al. 2013; Dudney et al. 2016). Management that reduces subordinate functional groups may therefore lower the potential stability of ecosystem functions across future climate conditions (Mariotte 2014) (Fig. 1).

In addition to management, environmental change can generate shifts in functional trait representation and diversity over time. For example, reductions in environmental stress (e.g., nutrient enrichment or increased water availability) are often associated with functional diversity loss (Suding et al. 2005) and overall shifts toward more resource-acquisitive traits (Sandel et al. 2010; Eskelinen and Harrison 2015). These changes may alter diversity–stability relationships over space and time. For example, in rangelands high rainfall is optimal for promoting forage production within a given year. Several consecutive years of optimal conditions, however, may lead to community declines in stress-tolerant traits and reduced resilience to future drought conditions. Alternatively, residual diversity of stress-tolerant species in the vegetative community or seed bank may facilitate recovery during periods of sustained drought.

Here, we test how legacies of grazing and climate variability influence ecological stability in a California grassland. We focus on whether grazing practices can lead to overall stability in biomass production and vegetation cover across rainfall conditions by enhancing functional diversity. Maintaining biomass production despite rainfall variability is essential for foraging, and maintaining vegetation cover is critical to reduce soil erosion (Busby and Cox 1994; Allen-Diaz and Jackson 2000). We first hypothesize that grazing practices that maintain a mix of resource-acquisitive and stress-tolerant species will increase the stability of biomass and cover across drought and non-drought conditions, but at the expense of lower production in non-drought conditions (Chillo et al. 2011; Mori et al. 2013). Second, we hypothesize that consecutive years with high rainfall conditions will result in loss of functional diversity and traits associated with drought tolerance. We focus on functional diversity changes initiated by different experimental grazing intensities, across which we manipulate rainfall via rainout shelters and irrigation over 3 years.
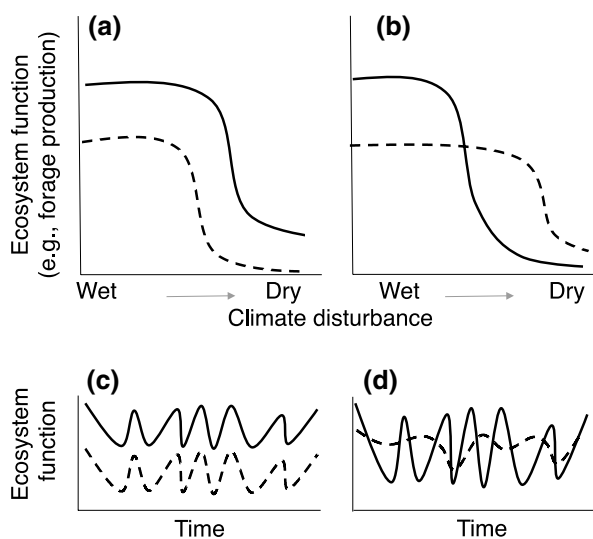
Fig. 1 Potential relationships between functional diversity, ecosystem function and stability under variable climate conditions. *Solid lines* indicate communities with traits that maximize forage production (e.g., resource acquisitive, high growth traits) at the expense of functional diversity; *dashed line* indicates communities with high functional diversity (e.g., a mix of resource-acquisitive and stress-tolerant traits). **a** Relationship between forage production and climate given the assumption that traits that maximize production under optimal (wet) conditions also maximize production in non-optimal (dry) conditions. **b** Hypothesized relationship between forage and climate in which communities with a mix of resource-acquisitive and stress-tolerant species have relatively lower production in optimal conditions but relatively higher production in non-optimal condition. **c** Ecosystem function in a variable environment over time for scenario **a**. **d** Ecosystem function in a variable environment over time for scenario **b**; functionally diverse communities are more stable

Methods

Site description

We conducted the experiment in a valley grassland at the University of California Sierra Foothill Research Extension

Center (SFREC), Browns Valley, California, USA (39º 15′N, 121º 17′W). The site is characterized by a Mediterranean climate with cool, wet winters and hot, dry summers. The average annual rainfall is 730 mm, most of which falls during the growing season from October through April. The annual rainfall is highly variable, however, ranging between 230 and 1310 mm over the past 50 years (sfrec. ucanr.edu/Data/Weather/).

The site is relatively flat with a loamy, xeric alfisol soil type (California Soil Resource Lab, http://casoilresource. lawr.ucdavis.edu/gmap/). Vegetation at the site is characteristic of contemporary California grasslands; it is dominated by annual exotic grasses with six to eight subordinate forb species. Dominant grasses consist primarily of *Avena fatua*, *Bromus hordeaceus*, and *Festuca perennis*, and subordinate forbs consist primarily of *Erodium botrys* and *Trifolium hirtum* (Pitt and Heady 1978) (table S1). The site had been grazed by cattle for 150 years prior to our experiment, but we fenced it to enable controlled grazing manipulations during the study.

Grazing legacies

In May 2008, we established a gradient that simulated the effects of grazing using a combination of trampling by cattle and mechanical mowing and subsequent removal (Fig. S1; described in detail by Stein et al. 2014, 2016). Manipulating grazing levels within the same pasture allowed us to isolate the effects of grazing from potentially confounding site attributes such as soil type or slope. The "low" level was trampled twice per year, once in late March when plants started flowering and a second time in June/July after most plants were senesced. The "moderate" level was both mowed and trampled in March and June/July. The timing of the treatments (i.e., toward the end of the growing season and following senescence) were designed to reflect the impact of California's year-round grazing practices. Both grazing levels were replicated four times and paired in blocks for a total of eight 10 m × 3 m plots. Residual dry matter (RDM), the plant material that remains just before the start of a new growing season and a standard measure of grazing intensity (Bartolome et al. 2007), was significantly reduced by almost one-third in the moderate grazing plots (Stein et al. 2014). We maintained these treatments through September 2012, when we stopped the treatments and characterized effects on aboveground vegetation and on the soil seed bank. All applicable institutional and/ or national guidelines for the care and use of animals were followed.

To characterize the effect of grazing treatments on aboveground vegetation, we measured species composition at peak biomass during the final year of the manipulation (May 2012). We visually estimated cover in one

1 m × 1 m subplot within each grazing plot, characterizing the cover of each species by class from 0.5, 1, 2, 5, and 10 through 100 in 10% increments. Total species cover could be greater than 100 owing to canopy overlap or less than 100 owing to bare ground. To ensure that we fully captured the effect of grazing on compositional changes, we also measured the germinable seed bank. In September 2012, we collected five soil cores (5 cm depth, 5.08 cm diameter) in each grazing plot for a total of 40 cores. Because we collected samples just prior to the first germinating rains, they reflect seeds available for the growing season following 4 years of experimental grazing. We spread each soil core over Sunshine Mix 1 (Sun Gro Horticulture, Agawam, MA) in a half-flat (27 cm × 27 cm), watered it twice weekly, and grew its contents in the greenhouse for 3 months. We took a census of seedlings weekly, counting the number of individuals that emerged by species.

Rainfall treatments

In October 2012, we implemented a 3-year rainfall manipulation using rainout shelters and irrigation to create dry and wet conditions (Fig. S2). In each of the eight 10 m × 3 m grazing legacy plots, we established two paired rainfall treatments and one control for a total of 16 dry and 16 wet 1.3 m × 2.6 m subplots (i.e., eight pairs of dry/wet subplots per grazing level) and 8 1.3 m × 2.6 m controls (i.e., four control subplots per grazing level) that we maintained across three growing seasons. There are many approaches to assess ecological stability in the face of climate variability, ranging from analysis of long-term data in relation to precipitation (e.g., Tilman and Downing 1994; Hallett et al. 2014) to experimentally creating variable environments (e.g., Gherardi and Sala 2015). We chose to compare stability across paired dry and wet treatments within year to assess the consequences of shared starting conditions on different potential rainfall trajectories. We maintained treatments over 3 years to increase replication across annual rainfall conditions and to test if community cover, production and functional trait composition adjusted in response to rainfall treatments (Smith et al. 2015). For example, if trait composition responded rapidly to rainfall we would expect convergence in total cover across treatments over time. Alternatively, if the legacy effect of grazing had strong, lasting effects on composition, we would expect similar treatment responses across all 3 years.

The rainout shelters were constructed with solid, clear polyethylene roofs that fit over a 1.3 m × 2.6 m area. Shelters had angled roofs and were approximately 1 m tall (Fig. S2). After the first germinating rains of the season, we erected the roofs shortly before rainfall events and removed them afterward; the roofs were only erect for approximately 10% of the growing season. Shelter runoff

was collected and used to irrigate wet treatment plots of the same size. We maintained rainfall treatments over the course of three growing seasons (October 2012–May 2015). Due to extreme drought in the 2013–2014 growing season, we periodically irrigated the wet plots using non-chlorinated well water. Each year of the rainfall treatment, we hand-mowed all plots to RDM levels comparable with the moderate grazing treatment. We initially monitored the effect on soil moisture using two 15-cm-deep time domain reflectometer (TDR) probes in each plot; starting in March 2013, we monitored soil moisture with 30-cm-deep continuously logged probes in a quarter of the plots (CS650-L Soil Water Content Reflectometer, Campbell Scientific, Logan, UT), and from March 2013 to May 2014 we measured soil moisture with 5-cm-deep continuously logged probes (ec50 probes, Decagon Devices, Pullman, WA). We analyzed the 30-cm-deep soil moisture data with repeated-measures ANOVA with treatment and year as fixed effects, and plot, shelter pair and time point as random effects.

We estimated species cover in a 0.5 m × 0.5 m subplot situated in the center of each dry and wet plot in mid-April each year using our previous cover classes. Peak biomass varies by functional group over the growing season, with forbs reaching peak biomass in March and grasses in May. Due to space limitations in the shelters we opted to measure biomass allometrically instead of sampling biomass multiple times each year. To this end, in 2013 we established two 0. 25 m × 0.25 m subplots within each plot in which we created forb and grass-dominated communities via seed addition and weeding. We harvested each community at its peak, dried and weighed the biomass for 48 h at 60 C, and subsequently estimated community biomass by relating the percent cover of forbs and grasses to the biomass (g/m^2) produced by the functional group in a given rainfall treatment.

Functional traits

To test treatment effects on functional trait composition and diversity, we paired our species composition data with species-level functional trait data. Functional trait data were collected from ten plants per species grown without competition a greenhouse; for a full description of trait collection methods see Butterfield and Suding (2013). We focused on seven functional traits that relate to plant resource responses: height (Ht), specific leaf area (SLA), leaf dry matter content (LDMC), root density (Dens), coarse root diameter (DiamC), specific root length of coarse (>0.2 mm diameter; SRLC) and fine (>0.2 mm diameter; SRLF) roots. Trait data overlapped with 93.6 ± 0.011% of our cover data. Prior to subsequent analyses, we averaged trait values within a species and standardized values around trait means.
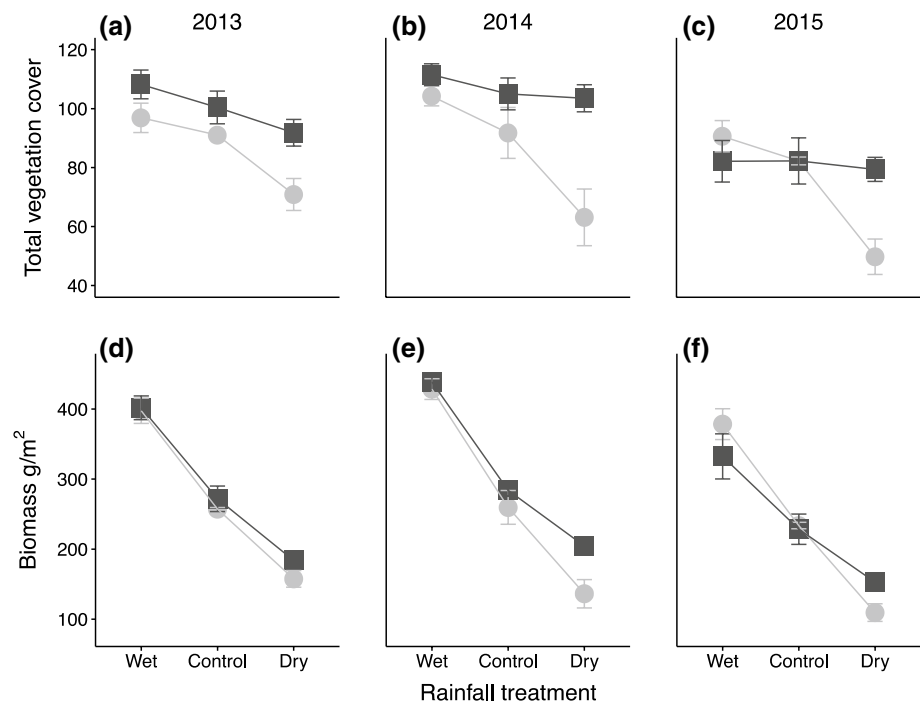
Analysis

To test how grazing legacy and rainfall conditions interact to affect ecosystem function, we aggregated biomass and cover within each plot and conducted two ANOVA with biomass and cover as the response variables, grazing legacy, rainfall treatment, a grazing × rainfall interaction and year as fixed effects and grazing block, grazing plot, shelter pair and plot as nested random effects. Because we had an unbalanced number of control plots relative to wet and dry plots, we omitted them from these and subsequent analyses. To characterize ecological stability, we calculated the coefficient of variation (CV) of biomass and cover for each paired wet and dry plot (a lower CV indicates higher stability). We assessed the legacy effect of grazing on stability using ANOVA with CV as the response variable, grazing (low, moderate) and year as fixed effects and grazing block, grazing plot and shelter pair as nested random effects.

To relate these patterns with functional diversity, we calculated diversity as Rao's quadratic entropy (Rao's Q) among all traits for each community and time point (e.g., pre-rainfall treatment germinable seed bank plots and aboveground vegetation plots, and post-rainfall treatment aboveground vegetation plots each year). We used Rao's Q because it includes species abundances and can reflect multiple traits (Botta-Dukát 2005). To test the initial effect of grazing legacy on the functional diversity of the germinable seed bank and aboveground vegetation, we used ANOVA with diversity as the response variable, grazing (low, moderate) as a fixed effect and grazing block, grazing plot and plot as nested random effects. To test the subsequent effect of rainfall treatments on functional diversity within each grazing treatment, we used ANOVA with diversity as the response variable, rainfall treatment (wet, dry), year and a rainfall × year interaction as fixed effects and grazing plot, shelter pair and plot as nested random effects.

To investigate how treatments affected functional composition, we used principal component analysis (PCA) to characterize the functional trait relationships among species along two axes. We treated the first two PCA axes as "traits" and used species' PCA scores as "trait values" to calculate two single-trait indices: community weighted mean (CWM) and single-trait functional dispersion for each plot and time point. We used ANOVA to test the effect of grazing on trait CWMs of the germinable seed bank and aboveground vegetation using grazing (low, moderate), with grazing block, grazing plot and plot as random effects. We tested for rainfall effects on CWMs within grazing treatments using ANOVA with CWM as the response variable, rainfall treatment (wet, dry), year and rainfall × year as fixed effects and grazing plot, and shelter pair and plot as nested random effects. We used density maps to visualize the relationship between CWM and diversity in response

Fig. 2 Total cover (**a–c**) and biomass (**d–f**) responses to rainfall and grazing legacy over 3 years (±SE). *Dark squares* indicate a legacy of moderate grazing and *light circles* indicate a legacy of low grazing

to rainfall and across grazing histories and years. We conducted all analyses in R v 3.2.2 using library ("FD") to calculated functional diversity metrics (Laliberte and Legendre 2010) and library ("nlme") to conduct mixed-effect models (Pinheiro et al. 2015). We explored interaction effects using a Tukey test in library ("multcomp") (Hothorn et al. 2008).

Results

Rainfall treatments

The 3 years of our rainfall manipulation all experienced below-average rainfall, with 510 mm falling in the 2013 growing season, 398 mm in the 2014 growing season and 403 mm in the 2015 growing season (California Irrigation Management Information Services, http://www.cimis.water.ca.gov/cimis/welcome.jsp). Because we applied rainfall from the dry plots to the wet plots, we estimate that the wet treatments received between 800 and 1000 mm of rain each year of the experiment, reflective of the upper range of rainfall observed at the site, whereas we estimate that the shelters in conjunction with the natural drought created conditions reflective of the lower range of rainfall at the site. The rainfall treatments resulted in significant differences in soil moisture throughout the growing season ($F_{1,1879} = 847$, $P < 0.0001$), with on average 41.7% soil moisture in the wet plots over the growing season compared to 31.8 in the dry at a depth of 30 cm (Fig. S3).

Similar patterns, but with a lower mean, were observed at 5-cm depth (Fig. S4). Average soil moisture was slightly higher in 2015 than in previous years ($F_{1,1879} = 51.3$, $P < 0.0001$; Fig. S3).

Ecosystem function and stability

Total vegetation cover differed by rainfall treatment and grazing legacy (rain × grazing legacy, $F_{1,14} = 16.94$, $P = 0.001$; Fig. 2). In areas with a legacy of low grazing, total cover was high under wet conditions but substantially reduced under dry conditions (Fig. 2; z-value = 7.78, $P < 0.0001$). In contrast, in areas with moderate grazing legacies, total cover was high and did not significantly differ across rainfall conditions (Fig. 2). Total cover was lower in 2015 relative to previous years ($F_{2,62} = = 18.2$, $P < 0.0001$).

Total biomass similarly differed by rainfall treatment and grazing legacy (rain × grazing legacy, $F_{1,14} = 8.84$, $P = 0.01$; Fig. 2). There was a consistent, direct effect in which biomass production was lower under dry compared to wet conditions (Fig. 2; $F_{1,14} = 629.9$, $P < 0.0001$). The degree of biomass decline under drought differed by grazing treatment; specifically, under dry conditions biomass was elevated in areas with moderate as opposed to low grazing histories (Fig. 2; z-value = 2.7, $P = 0.039$), whereas biomass did not differ between grazing legacies under wet conditions (Fig. 2). Biomass production was lowest in 2015 ($F_{2,62} = 13.5$, $P < 0.0001$).
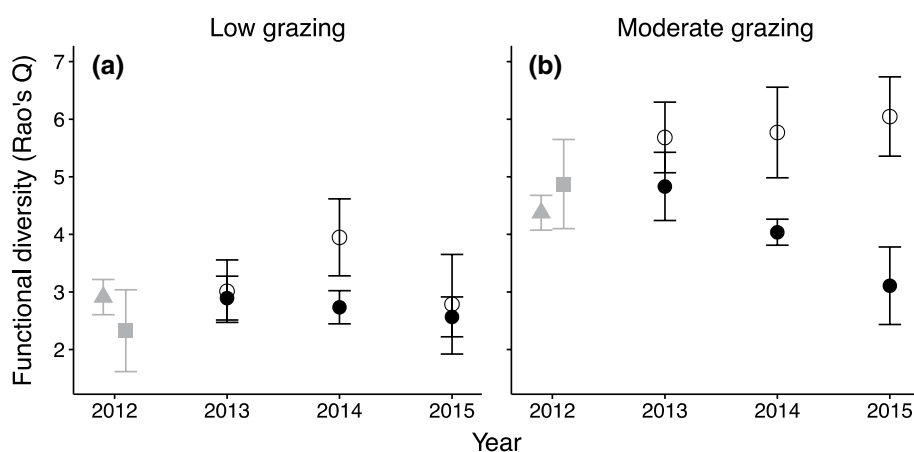
Fig. 3 Legacy effects of 4 years of (**a**) low levels and (**b**) moderate levels of experimental grazing on functional diversity, and subsequent responses of functional diversity to rainfall treatments over time. Measurements in 2012 reflect the functional diversity of the germinable seed bank (*gray triangles*) and aboveground vegetation (*gray squares*) before rainfall manipulations. Measurements from 2013 through 2015 represent changes in the functional diversity of aboveground vegetation in response to rainfall treatments (*open circles* indicate dry treatment, *filled circles* indicate wet treatment)

Stability of cover was marginally and stability of biomass was significantly higher across rainfall treatments in areas with moderate compared to low grazing histories (cover: $F_{1,3} = 7.39$, $P = 0.073$; biomass: $F_{1,3} = 12.9$, $P = 0.037$). This result was associated with dampened declines in both cover and biomass under drought in areas with histories of moderate compared to low grazing (Fig. 2).

Functional diversity

Functional diversity of the germinable seed bank was significantly greater in areas that had been moderately as opposed to lightly grazed (triangles in Fig. 3; $F_{1,3} = 11.5$, $P < 0.043$). The functional diversity of aboveground vegetation was also greater in areas with a legacy of moderate grazing, although this trend was marginally significant (squares in Fig. 3; $F_{1,3} = 7.8$, $P = 0.069$). The functional diversity of the vegetation remained low and did not significantly respond to rainfall treatments in areas with a legacy of low grazing (left panel in Fig. 3). In contrast, in areas with a legacy of moderate grazing, there was a rainfall effect ($F_{1,7} = 5.6$, $P = 0.050$) driven by a rainfall × year interaction ($F_{2,28} = 4.4$, $P = 0.021$) in which functional diversity remained consistently high in the dry treatments, but significantly declined over time in the wet treatments (right panel in Fig. 3).

Functional composition

The cumulative variance explained by the first two axes of the PCA of functional traits was 65.4% (Fig. 4). The first axis, which explained 38.8% of the variance, was
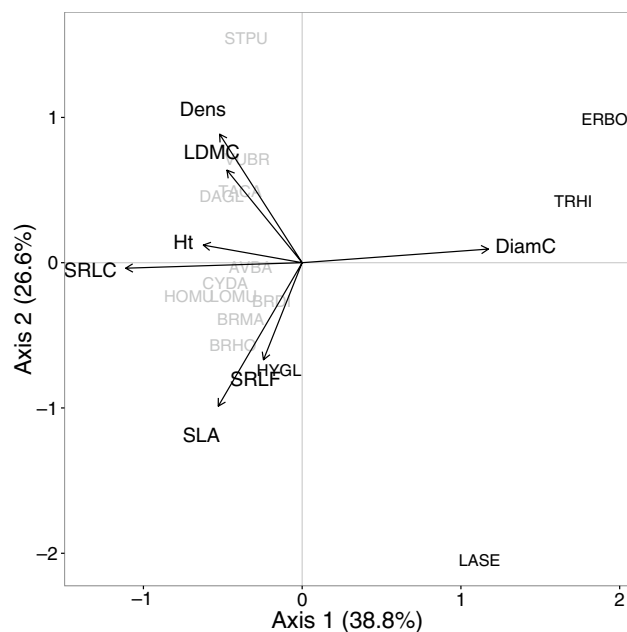
Fig. 4 Principal coordinate analysis of seven functional traits for plant species present in our California grassland experiment. Trait abbreviations are: *Ht* height, *SLA* specific leaf area, *LDMC* leaf dry matter content, *Dens* root density, coarse root diameter (DiamC), specific root length of coarse (>0.2 mm diameter; SRLC) and fine (>0.2 mm diameter; SRLF) roots. Forb species are *dark gray* and grass species are *light gray*; see Table S1 for species names

associated with a shift from resource-acquisitive to stress-tolerant traits. Two resource-acquisitive traits—SRLC and height—loaded low on axis 1, and a stress-tolerant trait—root diameter—loaded high on axis 1 (Fig. 4). The second axis, which explained 26.6% of the variance, was also associated with a resource-acquisitive to stress-tolerant
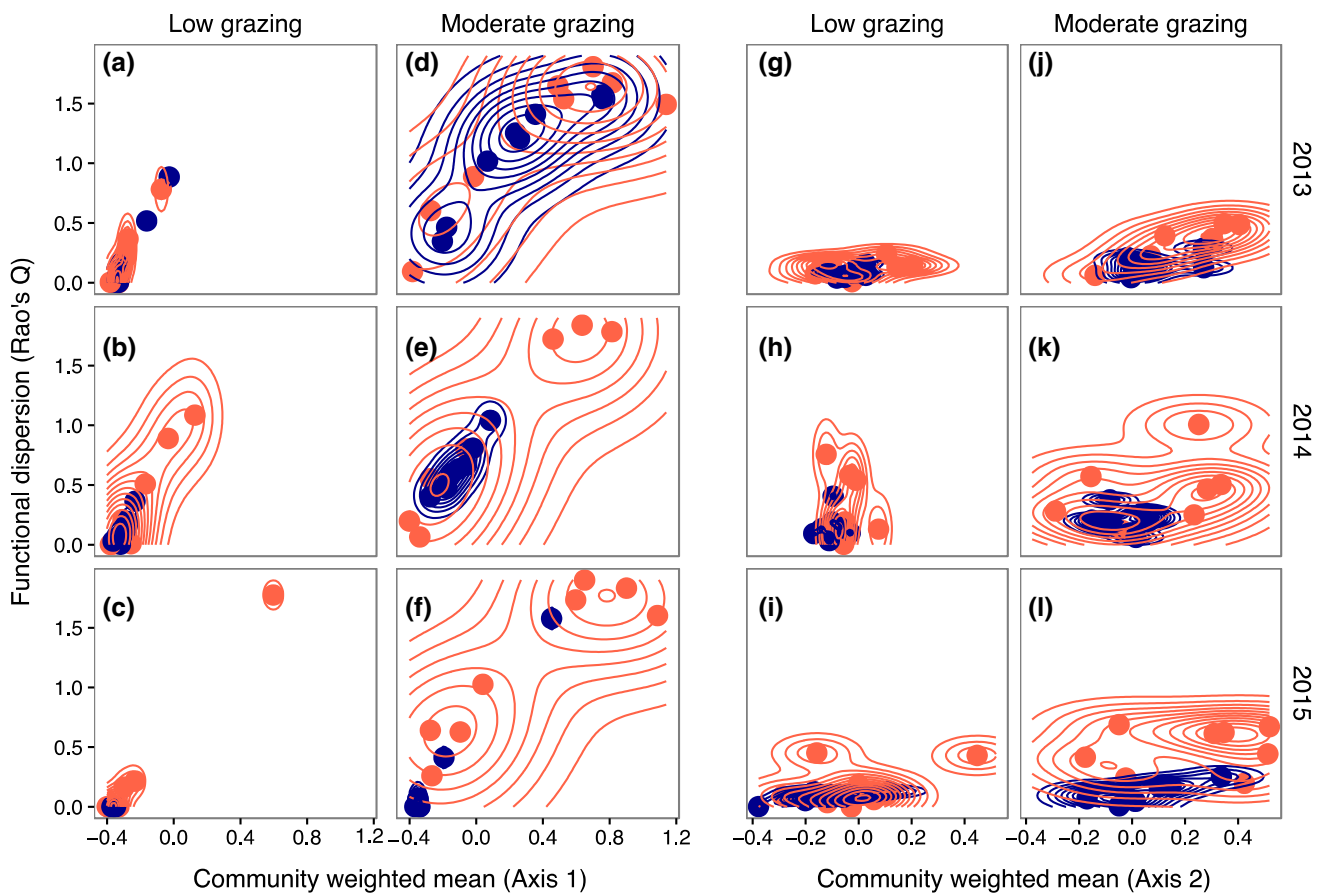
Fig. 5 The community-weighted mean of trait PCA axes in relation to trait dispersion over time and in relation to grazing legacy and rainfall conditions (*light red* indicates dry treatments, *dark blue* indicates wet): (**a–c**) axis 1 with a legacy of low grazing; (**d–f**) axis 1 with a legacy of moderate grazing; (**g–i**) axis 2 with a legacy of low grazing; (**j–l**) axis 2 with a legacy of moderate grazing. *Filled circles* indicate plot values; density contours indicate the range of variation among plots. Both PCA axis 1 and axis 2 are associated with shifts from resource acquisitive to stress-tolerant traits (PCA presented in

Fig. 4). Comparing (**a**) and (**d**) highlights that legacies of low grazing were associated with net lower functional diversity and a convergence on resource-acquisitive traits. Comparing rainfall effects from (**d–f**) highlights that wet conditions lead to declines in functional diversity and a convergence on resource-acquisitive traits over time. Finally, the spread of plots in (**d–f**) and (**j–l**) compared to (**a–c**) and (**g–i**), respectively, indicates that moderate grazing legacies lead to higher spatial heterogeneity in addition to higher mean functional diversity. Available in color in the online version of this journal

gradient. Specific leaf area and SRLF, both resource-acquisitive traits, loaded low on axis 2, whereas root density and LDMC loaded high on axis 2 (Fig. 4). Much of the variation was driven by functional group differences, with grass species clustering low and forb species high on axis 1 (Fig. 4; see Fig. S5 for compositional as opposed to functional shifts with grazing legacy and rainfall).

Areas with a history of low grazing had a higher representation of resource acquisitive traits than areas with a history of moderate grazing. Specifically, the CWM of axis 1 of both the initial germinable seed bank ($F_{1,3} = 7.71$, $P = 0.069$) and initial vegetation cover ($F_{1,3} = 8.5$, $P = 0.062$) were higher in areas with a legacy of moderate grazing. The functional composition of the vegetation in areas with a legacy of low grazing remained dominated by resource-acquisitive traits across rainfall conditions. Specifically, areas with a legacy

of low grazing had low axis 1 and axis 2 scores, and there was no significant effect of rainfall treatment on the CWM of either PCA axis (Fig. 5). In contrast, in areas with a legacy of moderate grazing there was a treatment × year interaction in which communities under wet conditions converged on resource-acquisitive traits and those in drought did not. Specifically, there was an interaction in which the CWM of axis 1 remained high in the dry plots, but significantly declined in wet plots over time ($F_{2,28} = 3.4$, $P = 0.048$; Fig. 5). For axis 2, there was a marginally significant direct effect in which the CWM was lower in wet than dry plots ($F_{1,7} = 4.52$, $P = 0.071$). Trait density maps highlighted that convergence on resource-acquisitive traits was associated with lower functional dispersion, and also that there was greater spatial heterogeneity in trait indices in areas with histories of moderate grazing (Fig. 5).

Discussion

We hypothesized that land-use practices that maintain functional diversity will lead to greater stability across optimal and non-optimal climate conditions. Consistent with our hypothesis, areas that experienced grazing practices that maintained greater functional diversity (in particular, that maintained a mix of resource-acquisitive and stress-tolerant traits) showed greater stability in total biomass and vegetation cover across experimental non-drought and drought conditions over the course of 3 years. This effect was stronger for cover than biomass, partly because the stress-tolerant traits favored by drought limit production capacity. We found that several consecutive years with optimal (wet) conditions could lead to a rapid decline in functional diversity and a convergence on resource-acquisitive strategies, whereas functional diversity could be maintained but not recovered by several consecutive years of drought. Consequently, our results indicate that ongoing management may be necessary to maintain functional diversity in wet years to stabilize function over dry years.

Grazing land-use legacies caused a shift in seed bank and aboveground composition, with more intense grazing legacies increasing functional diversity via greater representation of stress-tolerant traits. In particular, grazing legacies increased the relative representation of stress-tolerant forbs relative to resource-acquisitive grasses. Increased residual litter following low grazing can directly suppress germination rates of stress-tolerant forbs such as *Erodium* (Rice 1985; Stamp 1989) while promoting grass seed production (Bartolome 1979; Bartolome et al. 2007). Interestingly, functional diversity remained low in areas with histories of low grazing across all 3 years, even under drought conditions that we expected would favor the stress-tolerant traits that were associated with higher functional diversity. This suggests that loss in functional diversity arising from land management may be long-lasting. Our "moderate" grazing simulation approximated standard sustainable grazing practices (Bartolome et al. 2007; Stein et al. 2014) and was not intense enough to substantially reduce grass seed bank and cover or be considered overgrazing. We expect that land-use practices with even more intense grazing legacies may also reduce functional diversity via the loss of grass representation and result in lower vegetation cover stability, similar to the low intensity legacy here (Sasaki et al. 2009; Carmona et al. 2012).

Management practices that maintain moderate to high functional diversity should be a priority given predictions of increased climate variability with climate change. The rainfall-driven shift between stress-tolerant and resource-acquisitive traits we observed reflect rangeland dogma arising from long-term observations and range manager experience (Talbot et al. 1939; Pitt and Heady 1978). However, there is a long-standing debate about the relative role of grazing and climate in generating shifts between resource-acquisitive and stress-tolerant communities (commonly referred to as "grass" versus "forb" years) (Talbot et al. 1939; Heady 1956; Pitt and Heady 1978; Spiegal et al. 2014). By following an experimental approach, our study demonstrates that rainfall is a fundamental driver of these transitions, but that the potential for aboveground cover responses is predicated on grazing practices that maintain a functionally diverse seed bank. This provides context for the relative roles of management and external drivers in determining species composition in variable systems such as California grasslands. In so doing, it highlights that management practices aimed at maximizing services during periods of high rainfall (e.g., practices that promote highly productive grasses) may exacerbate the degree to which services are reduced during dry periods (via a reduction in subordinate, drought-tolerant species). Moreover, although we expected that the presence of stress-tolerant species would suppress function under optimal conditions, we instead observed comparable function across communities under optimal conditions. This may be attributable to the rapid convergence toward resource-acquisitive traits we observed under wet conditions (Elmendorf and Harrison 2009) and suggests that management may be more critical for maintaining function during periods of drought than for maximizing function under optimal rainfall conditions.

Grazing legacies associated with high functional diversity were also associated with much greater stability in total vegetation cover and slightly more stability in total biomass. Differences in stability patterns for these two functions are likely due to two reasons. First, biomass is more constrained by absolute resource limitation than cover, and so it is unrealistic to expect that biomass would be completely stable across drought and non-drought conditions. Second, the functional traits favored in response to drought are associated with more conservative growth strategies, which should curb their production ability but promote cover. The strong association between diversity and stability of total cover may have longer-term benefits for biomass production. Loss of vegetation cover alters hydrology and increases erosion rates, which can lead to declines in biomass production, especially in drought-prone systems such as California grasslands (Busby and Cox 1994). In addition, although subordinate, stress-tolerant species are limited in their aboveground biomass production and have a disproportionate effect on belowground biomass production and nutrient retention (Mariotte 2014), which are linked with long-term forage production (Briske et al. 2008) as well as carbon sequestration (Silver et al. 2010; Butterfield and Suding 2013).

The relationship between biodiversity and stability has long been a focus of ecology (see review by McCann 2000). Most experimental tests of this relationship in grasslands have involved direct species manipulations in ungrazed systems (e.g., Tilman and Downing 1994; Tilman et al. 2006; Isbell et al. 2009; Polley et al. 2013; Gross et al. 2014). Increasingly, there is need to apply the biodiversity–stability relationship to maintain ecosystem services, but uncertainty about how to translate previous findings for the management of working landscapes (Thompson and Starzomski 2007; Balvanera et al. 2014). Our experiment reduces this uncertainty by testing both the link between management and stability (grazing legacy and total cover and biomass across rainfall conditions) and between management and diversity (grazing legacy and functional diversity). Taken together, our findings suggest that the biodiversity–stability relationship is likely highly applicable for working grazed grasslands. That said, management actions such as grazing may affect multiple other ecosystem attributes concurrently (e.g., soil compaction and microsite heterogeneity that may influence water availability), and we cannot fully isolate the mechanisms leading to higher stability in moderately grazed areas.

Conclusion

Functional response diversity has been suggested as a way to link biodiversity and ecosystem stability (Folke et al. 2004; Mori et al. 2013). Our study highlights that grazing legacy can affect the functional diversity and ecosystem function in response to rainfall. Areas with grazing histories associated with high functional diversity exhibited more stable biomass and cover across rainfall conditions, whereas areas with grazing legacies associated with low functional diversity were less stable and did not recover diversity over time. These results allow us to link theoretical expectation of ecological stability (Yachi and Loreau 1999; Gonzalez and Loreau 2009) to management practices (Bartolome et al. 2007) and are relevant for developing grazing targets that maintain grassland ecosystem stability despite future climate variability.

References

Allen-Diaz B, Jackson RD (2000) Grazing effects on spring ecosystem vegetation of California's hardwood rangelands. J Range Manag 53:215–220. doi:10.2307/4003286

Balvanera P, Siddique I, Dee L et al (2014) Linking biodiversity and ecosystem services: current uncertainties and the necessary next steps. Bioscience 64:49–57

Bartolome JW (1979) Germination and seedling establishment in California annual grassland. J Ecol 67:273. doi:10.2307/2259350

Bartolome JW, Jackson RD, Betts ADK et al (2007) Effects of residual dry matter on net primary production and plant functional groups in Californian annual grasslands. Grass Forage Sci 62:445–452

Botta-Dukát Z (2005) Rao's quadratic entropy as a measure of functional diversity based on multiple traits. J Veg Sci 16:533–540. doi:10.1111/j.1654-1103.2005.tb02393.x

Briske DD, Bestelmeyer BT, Stringham TK, Shaver PL (2008) Recommendations for development of resilience-based state-and-transition models. Rangel Ecol Manag 61:359–367. doi:10.2111/07-051.1

Busby FE, Cox CA (1994) Rangeland health: new methods to classify, inventory, and monitor rangelands. Renew Resour J 12:13–19

Butterfield BJ, Suding KN (2013) Single-trait functional indices outperform multi-trait indices in linking environmental gradients and ecosystem services in a complex landscape. J Ecol 101:9–17. doi:10.1111/1365-2745.12013

Cardinale BJ, Duffy JE, Gonzalez A et al (2012) Biodiversity loss and its impact on humanity. Nature 486:59–67. doi:10.1038/nature11148

Carmona CP, Azcárate FM, de Bello F et al (2012) Taxonomical and functional diversity turnover in Mediterranean grasslands: interactions between grazing, habitat type and rainfall. J Appl Ecol 49:1084–1093. doi:10.1111/j.1365-2664.2012.02193.x

Chillo V, Anand M, Ojeda RA (2011) Assessing the use of functional diversity as a measure of ecological resilience in arid rangelands. Ecosystems 14:1168–1177

Côté IM, Darling ES (2010) Rethinking ecosystem resilience in the face of climate change. PLoS Biol 8:e1000438. doi:10.1371/journal.pbio.1000438

Cottingham KL, Brown BL, Lennon JT (2001) Biodiversity may regulate the temporal variability of ecological systems. Ecol Lett 4:72–85. doi:10.1046/j.1461-0248.2001.00189.x

Díaz S, Cabido M (1997) Plant functional types and ecosystem function in relation to global change. J Veg Sci 8:463–474. doi:10.2307/3237198

Díaz S, Cabido M (2001) Vive la différence: plant functional diversity matters to ecosystem processes. Trends Ecol Evol 16:646–655. doi:10.1016/S0169-5347(01)02283-2

Dudney J, Hallett LM, Larios L et al (2016) Lagging behind: have we overlooked previous-year rainfall effects in annual grasslands? J Ecol. doi:10.1111/1365-2745.12671

Elmendorf SC, Harrison SP (2009) Temporal variability and nestedness in California grassland species composition. Ecology 90:1492–1497

Eskelinen A, Harrison SP (2015) Resource colimitation governs plant community responses to altered precipitation. Proc Natl Acad Sci 112:13009–13014. doi:10.1073/pnas.1508170112

Folke C, Carpenter S, Walker B et al (2004) Regime shifts, resilience, and biodiversity in ecosystem management. Annu Rev Ecol Evol Syst 35:557–581. doi:10.1146/annurev.ecolsys.35.021103.105711

Foster D, Swanson F, Aber J et al (2003) The importance of land-use legacies to ecology and conservation. Bioscience 53:77. doi:10.1641/0006-3568(2003)053[0077:TIOLUL]2.0.CO;2

Gherardi LA, Sala OE (2015) Enhanced precipitation variability decreases grass- and increases shrub-productivity. Proc Natl Acad Sci 112:12735–12740. doi:10.1073/pnas.1506433112

Gonzalez A, Loreau M (2009) The causes and consequences of compensatory dynamics in ecological communities. Annu Rev Ecol Evol Syst 40:393–414. doi:10.1146/annurev.ecolsys.39.110707.173349

Gross K, Cardinale BJ, Fox JW et al (2014) Species richness and the temporal stability of biomass production: a new analysis of recent biodiversity experiments. Am Nat 183:1–12. doi:10.1086/673915

Hallett LM, Hsu JS, Cleland EE et al (2014) Biotic mechanisms of community stability shift along a precipitation gradient. Ecology 95:1693–1700

Heady HF (1956) Changes in a California annual plant community induced by manipulation of natural mulch. Ecology 37:798. doi:10.2307/1933071

Hooper DU, Chapin Iii FS, Ewel JJ et al (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr 75:3–35

Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. Biom J 50:346–363. doi:10.1002/bimj.200810425

IPCC (2013) Climate Change 2013-The Physical Science Basis: Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge

Isbell FI, Polley HW, Wilsey BJ (2009) Biodiversity, productivity and the temporal stability of productivity: patterns and processes. Ecol Lett 12:443–451. doi:10.1111/j.1461-0248.2009.01299.x

Kardol P, Campany CE, Souza L et al (2010) Climate change effects on plant biomass alter dominance patterns and community evenness in an experimental old-field ecosystem. Glob Chang Biol 16:2676–2687. doi:10.1111/j.1365-2486.2010.02162.x

Laliberte E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305. doi:10.1890/08-2244.1

MacArthur R (1955) Fluctuations of animal populations and a measure of community stability. Ecology 36:533. doi:10.2307/1929601

Mariotte P (2014) Do subordinate species punch above their weight? Evidence from above-and below-ground. New Phytol 203:16–21

Mariotte P, Vandenberghe C, Kardol P et al (2013) Subordinate plant species enhance community resistance against drought in semi-natural grasslands. J Ecol 101:763–773. doi:10.1111/1365-2745.12064

McCann KS (2000) The diversity–stability debate. Nature 405:228–233

Mori AS, Furukawa T, Sasaki T (2013) Response diversity determines the resilience of ecosystems to environmental change. Biol Rev 88:349–364. doi:10.1111/brv.12004

Naeem S, Bunker DE, Hector A et al (eds) (2009) Biodiversity, ecosystem functioning, and human wellbeing: an ecological and economic perspective, 1st edn. Oxford University Press, Oxford

Pinheiro J, Bates D, DebRoy S, et al (2015) nlme: Linear and nonlinear mixed effects models

Pitt M, Heady H (1978) Responses of annual vegetation to temperature and rainfall patterns in northern California. Ecology 59:336–350. doi:10.2307/1936378

Polley HW, Isbell FI, Wilsey BJ (2013) Plant functional traits improve diversity-based predictions of temporal stability of grassland productivity. Oikos 122:1275–1282. doi:10.1111/j.1600-0706.2013.00338.x

Quétier F, Thébault A, Lavorel S (2007) Plant traits in a state and transition framework as markers of ecosystem response to land-use change. Ecol Monogr 77:33–52

Rice KJ (1985) Responses of *Erodium* to varying microsites: the role of germination cueing. Ecology 66:1651. doi:10.2307/1938027

Sandel B, Goldstein LJ, Kraft NJB et al (2010) Contrasting trait responses in plant communities to experimental and geographic variation in precipitation. New Phytol 188:565–575. doi:10.1111/j.1469-8137.2010.03382.x

Sasaki T, Okubo S, Okayasu T et al (2009) Management applicability of the intermediate disturbance hypothesis across Mongolian rangeland ecosystems. Ecol Appl 19:423–432

Silver WL, Ryals R, Eviner V (2010) Soil carbon pools in California's annual grassland ecosystems. Rangel Ecol Manag 63:128–136. doi:10.2111/REM-D-09-00106.1

Smith MD, La Pierre KJ, Collins SL et al (2015) Global environmental change and the nature of aboveground net primary productivity responses: insights from long-term experiments. Oecologia 177:935–947. doi:10.1007/s00442-015-3230-9

Spiegal S, Larios L, Bartolome JW, Suding KN (2014) Restoration management for spatially and temporally complex Californian grassland

Stamp NE (1989) Seed dispersal of four sympatric grassland annual species of *Erodium*. J Ecol 77:1005. doi:10.2307/2260819

Stein C, Hallett LM, Harpole WS, Suding KN (2014) Evaluating ecosystem services provided by non-native species: an experimental test in California grasslands. PLoS One 9:e75396. doi:10.1371/journal.pone.0075396

Stein C, Harpole WS, Suding KN (2016) Transitions and invasion along a grazing gradient in experimental California grasslands. Ecology 97:2319–2330. doi:10.1002/ecy.1478

Suding KN, Collins SL, Gough L et al (2005) Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. Proc Natl Acad Sci U S A 102:4387–4392. doi:10.1073/pnas.0408648102

Suding KN, Lavorel S, Chapin FS et al (2008) Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. Glob Chang Biol 14:1125–1140. doi:10.1111/j.1365-2486.2008.01557.x

Talbot MW, Biswell HH, Hormay AL (1939) Fluctuations in the annual vegetation of California. Ecology 20:394. doi:10.2307/1930392

Thompson R, Starzomski BM (2007) What does biodiversity actually do? A review for managers and policy makers. Biodivers Conserv 16:1359–1378. doi:10.1007/s10531-005-6232-9

Tilman D, Downing JA (1994) Biodiversity and stability in grasslands. Nature 367:363–365. doi:10.1038/367363a0

Tilman D, Wedin D, Knops J (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature 379:718–720. doi:10.1038/379718a0

Tilman D, Reich PB, Knops JMH (2006) Biodiversity and ecosystem stability in a decade-long grassland experiment. Nature 441:629–632. doi:10.1038/nature04742

Yachi S, Loreau M (1999) Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. Proc Natl Acad Sci 96:1463–1468