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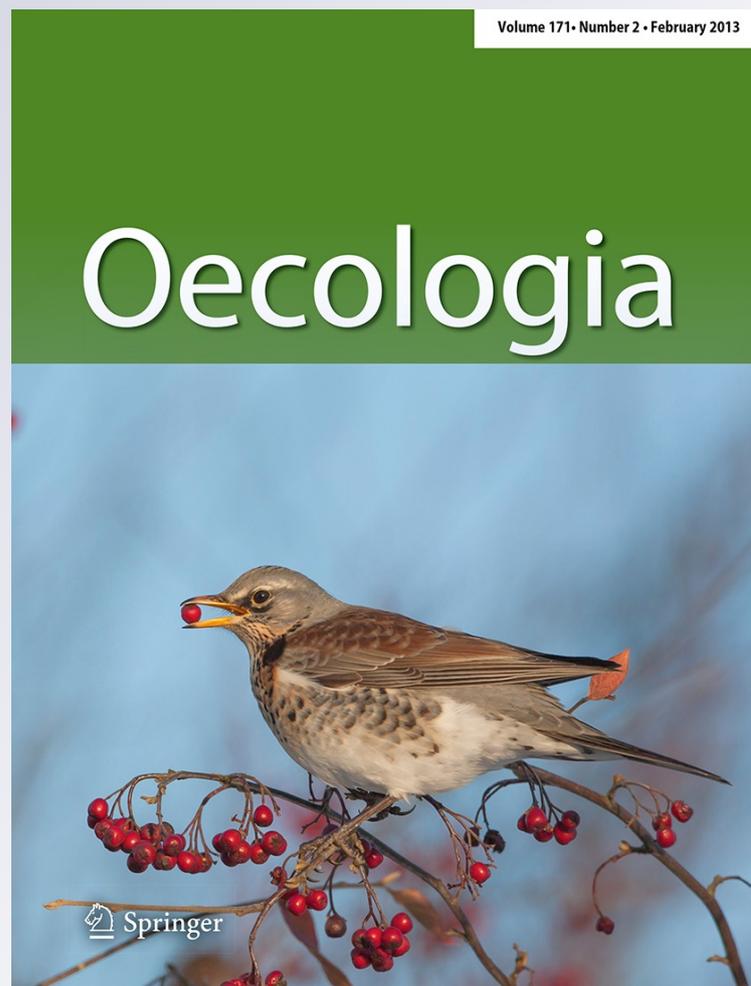
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A long-term experimental test of the dynamic equilibrium model of species diversity

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Abstract The dynamic equilibrium model of species diversity predicts that ecosystem productivity interacts with disturbance to determine how many species coexist. However, a robust test of this model requires manipulations of productivity and disturbance over a sufficient timescale to allow competitive exclusion, and such long-term experimental tests of this hypothesis are rare. Here we use long-term (27 years), large-scale (8 × 50-m plots), factorial manipulations of soil resource availability and sheep grazing intensity (disturbance) in grasslands to test the dynamic equilibrium model. As predicted by the model, increased productivity not only reduced plant species richness, but also moderated the effects of grazing intensity, shifting them from negative to neutral with increasing productivity. Reductions in species richness with productivity were associated with dominance by faster growing (i.e. high

specific leaf area) and taller plants. Conversely, grazing favoured shorter plants and this effect became stronger with greater productivity, consistent with the view that grazing can lead to weaker asymmetric competition for light. Our study shows that the dynamic equilibrium model can help to explain changes in plant species richness following long-term increases in soil resource availability and grazing pressure, two fundamental drivers of change in grasslands worldwide.

Keywords Alpha diversity · Disturbance · Functional trait · Productivity · Species coexistence

Introduction

The mechanisms determining local species richness, or the number of species found in a community, have long challenged ecologists (Hutchinson 1961). This is illustrated by the more than 100 different hypotheses about species richness regulation that have been reported in the literature (Palmer 1994). Among these different hypotheses, the most prominent are underpinned by the availability of resources that limit ecosystem productivity and the disturbances that remove ecosystem biomass (Grime 1973; Connell 1978; Huston 1979; Tilman 1982). However, neither of these factors alone is likely to determine species richness (Adler et al. 2011), particularly given the strong potential for interactions among resources and disturbance.

The dynamic equilibrium model of species diversity (Huston 1979) explicitly addresses the interaction between productivity and disturbance. Under this hypothesis, competitive interactions will lead to the exclusion of all but the most competitive species if allowed to proceed to equilibrium; therefore, productivity should generally decrease

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species richness due to faster rates of competitive displacement. On the other hand, disturbances may slow down this process by removing biomass, thus preventing competitive dominance (Grime 1973; Huston 1979). Importantly, the dynamic equilibrium model predicts that the strength and direction of disturbance effects on species richness depend on productivity (Huston 1979). At low productivity, disturbance should decrease richness, because small population sizes coupled with slow rates of recovery will lead to local extinctions, whereas at high productivity it should increase richness by suppressing competitive dominance (Huston 1979, 1994).

The dynamic equilibrium model of species diversity has been highly influential, having been cited >1,500 times (ISI Web of Knowledge June 2012). Yet despite its influence, there are still few strong experimental tests of this model. Testing the key prediction of the model, i.e. the interactive effect of productivity and disturbance, requires an experimental design where multiple levels of productivity are crossed with multiple levels of biomass removal (Huston 1994; Proulx and Mazumder 1998). Examples of previous rigorous tests include a short-term experiment in old-field communities (Huston 1980) that provided early support for the model. In contrast, a similar but longer (6 years) experiment showed that plant species richness varied quadratically with disturbance in unfertilized controls (peaking at intermediate levels), but was unaffected by disturbance at higher fertility (Wilson and Tilman 2002). Other studies have used a variety of experimental systems, including microbial (Rashit and Bazin 1987; Kneitel and Chase 2004; Scholes et al. 2005; Haddad et al. 2008) and marine (Widdicombe and Austen 2001; Worm et al. 2002; Svensson et al. 2007) assemblages. Several of these studies have provided support for the dynamic equilibrium model (Rashit and Bazin 1987; Widdicombe and Austen 2001; Worm et al. 2002; Kneitel and Chase 2004; Haddad et al. 2008), while others have not (Scholes et al. 2005; Svensson et al. 2007).

Although previous experimental tests of the dynamic equilibrium model have contributed to our understanding of how productivity and disturbance together influence species richness, they suffer from some limitations, at least when applied to grassland ecosystems. First, the use of highly simplified synthetic communities (e.g. Rashit and Bazin 1987; Scholes et al. 2005; Haddad et al. 2008) makes it difficult to extrapolate results to more complex ecosystems. For results to be more directly relevant to biodiversity management, more realistic experiments are needed, such as imposing changes in productivity and disturbance that mimic the real-world changes faced by ecosystems (e.g. as a result of agricultural intensification). Second, some previous experimental tests in grasslands (e.g. Huston 1980; Wilson and Tilman 2002) did not use grazing as a

disturbance (but see Proulx and Mazumder 1998; Worm et al. 2002; Frank 2005; Bakker et al. 2006), even though grazing is the most extensive land use on Earth (Asner et al. 2004; Foley et al. 2005) and a major disturbance factor in grasslands (Bouwman et al. 2005). While the dynamic equilibrium model makes no distinction between the different types of processes that remove ecosystem biomass (e.g. fire, flooding or grazing), grazing and other biotic disturbances may influence plant species richness in more complex ways than other intense, non-selective disturbances such as fire (Huston 1994; Olf and Ritchie 1998; Svensson et al. 2010). Third, because competitive exclusion and disturbance- or stress-caused extinctions can be slow processes, longer term experiments are required. Finally, few studies have considered how species' functional traits can explain the effects of productivity and disturbance on species richness (Haddad et al. 2008). In particular, plant traits that relate to relative growth rate (RGR) and competitive ability, such as specific leaf area (SLA) and plant height, vary predictably along productivity and disturbance gradients and influence plant interactions (Grime 1979; Gaudet and Keddy 1988; Lambers and Poorter 1992; Westoby 1999; Aerts 1999).

In this study, we use long-term (27 years), realistic manipulations of soil resource availability and grazing intensity in grasslands (Scott 1999) to provide a strong test of the dynamic equilibrium model of species diversity. The experiment consisted of the initial sowing of a common plant species pool (25 species) into resident natural grassland vegetation in 1982, with annual manipulations of soil resource availability (five fertilizer levels, with the lowest level receiving no fertilizer, and the highest also being irrigated to represent high-intensity agriculture) leading to contrasting productivities that were crossed with three sheep-grazing intensity (disturbance) levels leading to different proportions of aboveground productivity grazed. These experimental manipulations are particularly relevant, since increases in agricultural inputs and grazing pressure by livestock are the two most fundamental drivers of change in grasslands worldwide (Bouwman et al. 2005).

We measured: (1) total plant species richness and relative abundances, (2) total net primary productivity (NPP; both above- and belowground), and (3) grazing intensity (proportion of aboveground productivity grazed by sheep) in years 26–27 of the experiment. In addition, we explored changes in SLA and plant height. We hypothesised that:

1. At average grazing intensity, plant species richness would decline at high productivity, reflecting faster rates of competitive displacement (Huston 1979).
2. Grazing intensity would decrease plant species richness at low productivity, but increase it at high productivity by suppressing competitive dominance

(Huston 1979; Olf and Ritchie 1998; Proulx and Mazumder 1998; Worm et al. 2002), i.e. there would be a significant positive productivity \times grazing intensity interaction.

- Effects on plant species richness of productivity and grazing intensity would be associated with specific shifts in plant traits, namely: (1) increased dominance by fast-growing, competitive species (reflected by increases in community-weighted SLA and plant height with higher productivity), and (2) a greater decrease in plant height with grazing intensity with higher productivity, reflecting stronger suppression of competitive dominance (especially with regard to asymmetric competition for light) by grazing at high productivity.

Materials and methods

Study area and site

The study was conducted at Mount John, west of Lake Tekapo in the Mackenzie Basin of New Zealand's South Island (43°59'S, 170°27'E, 820 m above sea level). The climate is semi-continental with an average of 1,772 degree-days above 5 °C and a mean annual temperature of 8.7 °C, with 14.9 °C in January (warmest) and 1.7 °C in July (coldest). Mean annual rainfall is 601 mm, uniformly distributed throughout the year. The average annual moisture deficit is 445 mm (Coulter 1975). Soils are humose, orthic brown (Hewitt 1998), between 45 and 90 cm deep, and were developed from greywacke and argillite rock till material. The dominant vegetation type prior to human settlement is likely to have been short-tussock grassland with a variable woody component, probably near the tall-tussock (*Chionochloa* spp.)/short-tussock (*Festuca novae-zelandiae* Hack. Cockayne) grassland transition (McGlone 2001). Early human occupation began around 700–800 years ago, and has been linked with increased fire frequency (McGlone 2001). Extensive grazing by sheep was introduced to the area in the 1850–1860s and remains the most prevalent land use today.

Experimental design

The experiment is described in detail elsewhere (Scott 1999) and is only briefly summarised here. In 1982, a homogeneous mixture of 25 grass and legume pasture species was over-sown, using a rotary hoe drill, within a ~3-ha area of depleted fescue tussock (*F. novae-zelandiae*) grassland dominated by the exotic mouse-ear hawkweed (*Hieracium pilosella* L.). The trial followed a split-plot

design consisting of two spatial replications (blocks; each 50 \times 250 m), each split into five whole plots (50 \times 50 m) receiving one of the following five nominal fertilizer treatments: 0, 50, 100, 250 and 500 kg ha⁻¹ year⁻¹ of sulfur-fortified superphosphate. The use of this fertilizer is typical of Australasian legume-based pasture systems, which rely on N fixation by legumes to build soil N levels. The actual mean P and S rates applied over the first 10 years of the experiment, in terms of applied P + S, were: 0 + 0, 4.1 + 17.6, 8.9 + 26.0, 22.7 + 54.5 and 46.8 + 114.8 kg ha⁻¹ year⁻¹ for the 0, 50, 100, 250 and 500 kg ha⁻¹ year⁻¹ treatments, respectively (Scott 1999). The whole plots receiving 500 kg ha⁻¹ year⁻¹ were also irrigated fortnightly from November to May of each year to simulate the highest intensity agriculture in the region. Fertilizer was applied annually for the first 20 years of the experiment.

Each whole plot was further split into six 8 \times 50-m subplots (hereafter referred to as "plots") corresponding to a two-way factorial design involving sheep grazing intensity (lax, moderate and hard) and stocking type (mob vs. sustained). In mob-grazing plots, a larger number of sheep (with actual numbers depending on available feed-on-offer of the moderate plot) were introduced to plots for 3–4 days, while sustained-grazing plots received fewer sheep for a longer period (e.g. several weeks). However, only mob-stocking plots were considered in the present study.

Grazing intensity levels corresponded to a 1:2:4 sheep-grazing days ratio in years 2–4 of the experiment and 2:3:4 in subsequent years. Plots were always grazed in groups of three, corresponding to the three mob-stocked grazing intensity levels per whole plot. For each grazing event (i.e. when vegetation had reached approximately 30 cm in height), sheep numbers were adjusted based on available feed-on-offer of the moderate grazing treatment, using expert knowledge (D. Scott). The duration of grazing was the same for all three plots, but was adjusted based on residual bulk of the moderate grazing treatment (i.e. height of 1–2 cm). Grazing treatments occur in November–May each year. Depending on the fertilizer level, there were between four and nine grazing cycles during our sampling period (October 2007–April 2009).

Soil characteristics

Four soil samples (0–20 cm depth) were collected in each plot at random locations along a central longitudinal transect in September 2008. A composite soil sample per plot was bulked and sent to a commercial laboratory (Hill Laboratories, Hamilton, New Zealand) for nutrient analyses: pH, anaerobically mineralisable N, Olsen P, SO₄-S, total N and total C.

Vegetation sampling and plant species richness

Sampling of all vascular plant species present within each plot was undertaken in November 2007 and 2008 (Laliberté et al. 2010). Twenty 1 × 1-m quadrats were positioned randomly along two longitudinal transects in each plot. Transects were 3 m apart from each other and 2 m from the closest fence. Cover of all vascular plant species present in each 1 × 1-m quadrat was recorded using a seven-point semi-quantitative scale (1, ≤0.1 %; 2, 0.1–0.9 %; 3, 1–5 %; 4, 6–25 %; 5, 26–50 %; 6, 51–75 %; 7, 76–100 %). The median of a class was used as a cover estimate and data were transformed to relative abundances. Relative abundance data from 2007 to 2008 were averaged to give a single value for analysis. Plant species richness was estimated as the number of species in each 1 × 1-m quadrat.

Plant functional traits

From a broader set of measured plant functional traits (Laliberté et al. 2012), we selected SLA (the ratio of leaf area per unit leaf dry mass, i.e. $\text{m}^2 \text{kg}^{-1}$) as a primary marker of plant functional composition because of its strong correlation with plant RGR (Lambers and Poorter 1992). In addition, we selected plant height as a secondary marker of plant functional composition (Laliberté et al. 2012) because of its relationship with competitive ability for light (Gaudet and Keddy 1988). SLA, leaf area and leaf dry matter content were measured on at least ten individuals per plant species (spread among the five fertilizer treatments), following a standardised protocol (Garnier et al. 2001). Height of mature plants was measured from ground level to the tip of the highest photosynthetic organ on at least ten individuals from each species spread among the five different fertilizer treatments (Garnier et al. 2007). These traits were measured on all vascular plant species found in all experimental plots in November 2007, at the end of the autumn to the spring regrowth period, and just prior to the start of the annual grazing treatments. This corresponds roughly to the period of peak standing biomass in this experiment. We used community-weighted mean trait values of SLA and plant height in the analyses (Garnier et al. 2004). Community-weighted traits represent the expected trait value for an individual (in our case, a unit of cover) chosen at random in a community (Garnier et al. 2004). These data were estimated at the 8 × 50-m plot scale.

Aboveground NPP and grazing intensity

Aboveground NPP (ANPP) was estimated during an 18-month period (October 2007–April 2009), using periodic

measurements with a capacitance probe (GrassMaster II; Novel Ways, Hamilton, New Zealand) that were calibrated against oven-dried live biomass harvests (Murphy et al. 1995) from 100 circular quadrats taken across all plots in October 2007 ($R^2 = 0.737$, $P < 0.0001$). Values of ANPP are also reported on an annual scale, from October 2007 to 2008 (Online Resource 1). Each sampling event consisted of 100 capacitance probe measurements per plot (evenly spread across four longitudinal transects) that were then used to estimate the mean live standing biomass. Capacitance probe measurements were always made directly prior to and after each grazing event in each plot, thus allowing us to quantify the amount of primary productivity consumed or trampled by sheep over that period. Periodic routine measurements (about once a month) were also made between grazing events. Measurements were made when vegetation was dry to prevent overestimation of plant live biomass. All increases in live biomass between two consecutive measurements were summed over the entire sampling period to calculate ANPP (Lauenroth 2000).

Grazing intensity was measured as the proportion of ANPP that was consumed or trampled by sheep over the 18-month sampling period during which ANPP was estimated. This provides a meaningful continuous estimate of grazing intensity that is comparable among sites (Bagchi and Ritchie 2010).

Belowground NPP

Belowground NPP (BNPP) was measured using root ingrowth cores. Four 8-cm diameter × 30-cm deep soil cores per plot (randomly positioned along a central longitudinal transect) were removed in October 2007. The resulting holes were immediately filled with root-free soil enclosed in 1-mm-mesh nylon bags. Root cores were retrieved in May 2008, cut into three sections corresponding to three depths (0–10, 10–20, and 20–30 cm) and each section was washed through a 1-mm sieve to separate soil from roots, which were then oven-dried and weighed. The same procedure, again with four root-ingrowth cores per plot, was repeated for the July 2008–April 2009 period. For each harvested root-ingrowth core, we summed all three depth sections, and then averaged values from all four cores per plot for each sampling period. Finally, values from the two sampling periods were summed. ANPP and BNPP were expressed as $\text{Mg dry matter ha}^{-1}$ (over the 18-month sampling period) and summed to estimate total NPP.

Statistical analyses

We used Poisson generalised linear mixed models (GLMMs) with a logarithmic link (Zuur et al. 2009) to model the effects of productivity and grazing intensity on

species richness. Poisson models were used because: (1) species richness data are counts, (2) the Poisson distribution represents the expected number of counts in a sampling unit, (3) the Poisson distribution is bounded by 0 and thus cannot give negative fitted values (Guisan et al. 2002). Poisson models with logarithmic links have also been used in several studies of species richness (e.g. Mittelbach et al. 2001; Orme et al. 2005). We judged that a logarithmic link (and thus the assumption of exponential effects of productivity or grazing intensity on species richness) was reasonable because high productivity or low grazing intensity can lead to strong light competition in grasslands, which can have disproportionately large negative effects on species richness (since competition for light is strongly asymmetric). However, it could be argued that the implicit assumption of multiplicative effects in our Poisson models is unwarranted, so we re-tested our data using Gaussian GLMMs with an identity link on square-root transformed species richness data (because the variance increased with the mean); we present these results (which do not qualitatively change our conclusions) in the supplementary material. To check assumptions of the Poisson model, we looked for patterns in the Pearson residuals by plotting them against fitted values and all predictors included in the model, and also tested for overdispersion (Zuur et al. 2009). We also conducted additional analyses in which we considered irrigation (binary variable) as an additional predictor because only plots receiving the highest fertilizer level were irrigated. In addition, we also tested the interactive effects of productivity and grazing intensity on plant species richness, but excluded the irrigated plots. The rationale for conducting these additional analyses was to explore the possibility that irrigation had an additional effect on species richness beyond what could be explained by productivity, or to determine whether results were strongly influenced by the presence of irrigated plots. We also conducted analyses that used aboveground productivity instead of total productivity as a predictor of plant species richness, because most previous analyses have only considered aboveground productivity (e.g. Adler et al. 2011).

Gaussian GLMMs with an identity link (Pinheiro and Bates 2000) were used to test for effects on community-weighted SLA and plant height of productivity, grazing intensity, and their interaction. Residuals were inspected visually to assess the presence of trends and heteroscedasticity and appropriate variance structures were specified if needed (Zuur et al. 2009). Second-order polynomial terms of productivity and grazing intensity were included but these were never significant and so are not further considered.

All predictors were centred on their means (i.e. subtracting the mean) to facilitate interpretation and to avoid

multicollinearity problems due to the inclusion of interactions and polynomials. In the presence of an interaction (e.g. productivity \times grazing intensity interaction), the unstandardised regression coefficient for a predictor involved in the interaction represents its average effect on the response variable when the conditioning variable (i.e. the other predictor involved in the interaction) is held at its mean value (Aiken and West 1991). The unstandardised regression coefficient for the interaction, on the other hand, represents the amount of change in the slope of the regression of the response variable on one of the predictors involved in the interaction, following a one-unit change in the other predictor (Aiken and West 1991). We assess significance of fixed effects using Wald Z-tests or *t*-tests, as recommended for fixed effects in GLMMs (Bolker et al. 2009).

Because of the split-plot experimental design, random intercepts per block, fertilizer level within block (i.e. whole plot), and quadrat within whole plot (i.e. sub-plot) were specified. Models were fitted using restricted maximum likelihood. Analyses were conducted using packages nlme (Pinheiro et al. 2010) and lme4 (Bates and Maechler 2010) in the R environment (R Development Core Team 2011).

Results

Aboveground and total productivity, but not belowground productivity, strongly increased from unfertilized to fertilized plots, particularly those that were also irrigated (Fig. 1); hereafter, analyses involve total productivity.

There was a highly significant productivity \times grazing intensity interactive effect on plant species richness ($P \leq 0.001$; Table 1). Indeed, as predicted by the dynamic equilibrium model, grazing intensity strongly reduced plant species richness at low productivity, but this relationship became increasingly positive with greater productivity (Fig. 2). At average grazing intensity, increased productivity significantly reduced species richness (Productivity main term: $P = 0.004$; Table 1). Conversely, grazing intensity had no significant effect on plant species richness at average productivity (Grazing intensity main term: $P = 0.427$; Table 1). A Gaussian linear mixed-effect model with an identity link on square-root transformed species richness data yielded qualitatively similar results (Online Resource 1). We did not find the relationship between grazing intensity and species richness at average productivity to be unimodal, since a second-order polynomial of grazing intensity was not significant ($P = 0.421$; Online Resource 3).

A model that included irrigation (binary variable) as an additional predictor showed that it had a marginally non-significant effect on plant species richness ($P = 0.056$),

Fig. 1 Effects of fertilizer level on **a** aboveground net primary productivity (ANPP), **b** belowground NPP (BNPP), **c** total NPP and **d** plot-scale plant species richness (i.e. over the entire 8 × 50-m plot). Mean ± SE of grazing treatments at all fertilizer levels are shown. Note that the y-axes in **a** and **c** are on logarithmic scales. Different letters among fertilizer levels indicate significant differences ($P < 0.05$) following post hoc Tukey tests

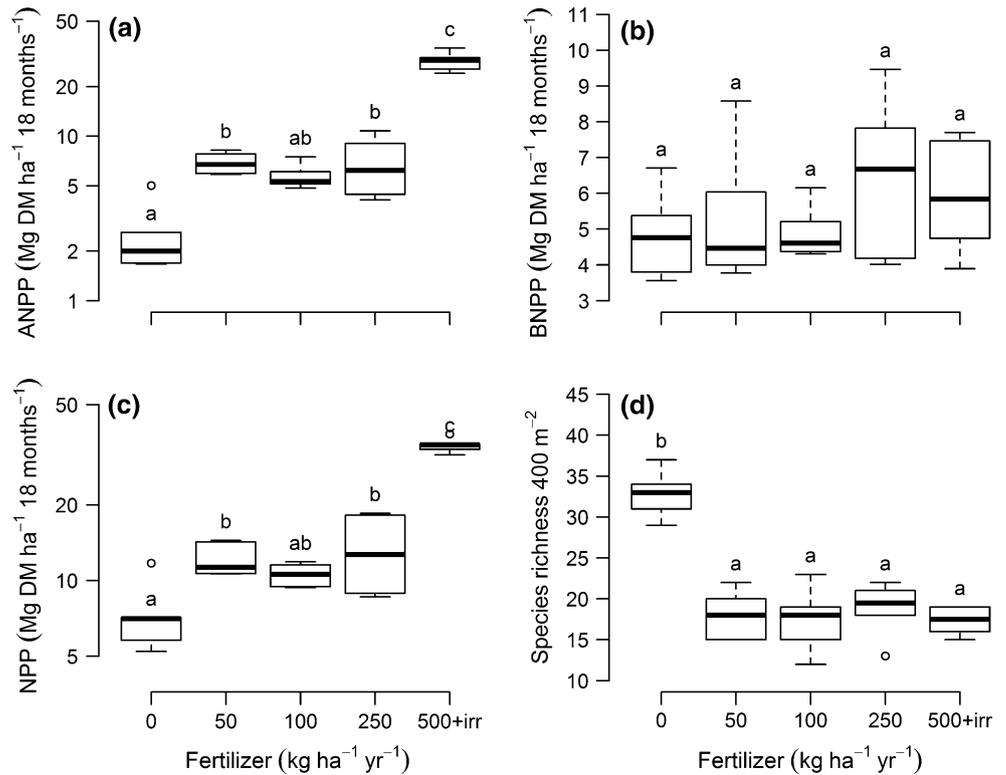


Table 1 Results of Poisson or Gaussian generalised linear mixed models for plant species richness (Poisson model), community-weighted specific leaf area (SLA) (Gaussian model), and community-weighted plant height (Gaussian model)

Fixed effects	β	SE	Z	P	Random effects	σ
Species richness^a						
Intercept	1.649	0.080	20.713	≤ 0.001	Block	0.000
Productivity	-0.031	0.011	-2.847	0.004	Whole plot	0.102
Grazing intensity	0.252	0.317	0.793	0.428	Plot	0.184
Prod. × grazing	0.121	0.038	3.198	0.001		
Fixed effects	β	SE	t	P	Random effects	σ
Community-weighted SLA						
Intercept	18.150	0.821	22.101	≤ 0.001	Block	0.0001
Productivity	0.211	0.061	3.462	0.003	Whole plot	2.326
Grazing intensity	-1.007	1.224	-0.823	0.422	Residual	0.671
Prod. × grazing	-0.101	0.212	-0.476	0.640		
Community-weighted plant height						
Intercept	0.276	0.038	7.167	≤ 0.001	Block	0.000
Productivity	0.015	0.004	4.013	0.001	Whole plot	0.096
Grazing intensity	-0.485	0.082	-5.912	≤ 0.001	Residual	0.048
Prod. × grazing	-0.038	0.013	-2.857	0.011		

In all cases, residuals were inspected visually to check model assumptions

β Unstandardised regression coefficient, *Prod.* productivity

^a No evidence for overdispersion ($\phi = 0.602$, $\chi^2 = 357.5$, $df = 593$, $P = 1$)

while the productivity × grazing intensity interaction remained highly significant ($P \leq 0.001$; Online Resource 4). The productivity × grazing intensity interaction also

remained highly significant ($P \leq 0.001$) when irrigated plots were excluded from the analysis, showing that this result was not solely driven by these plots (Online

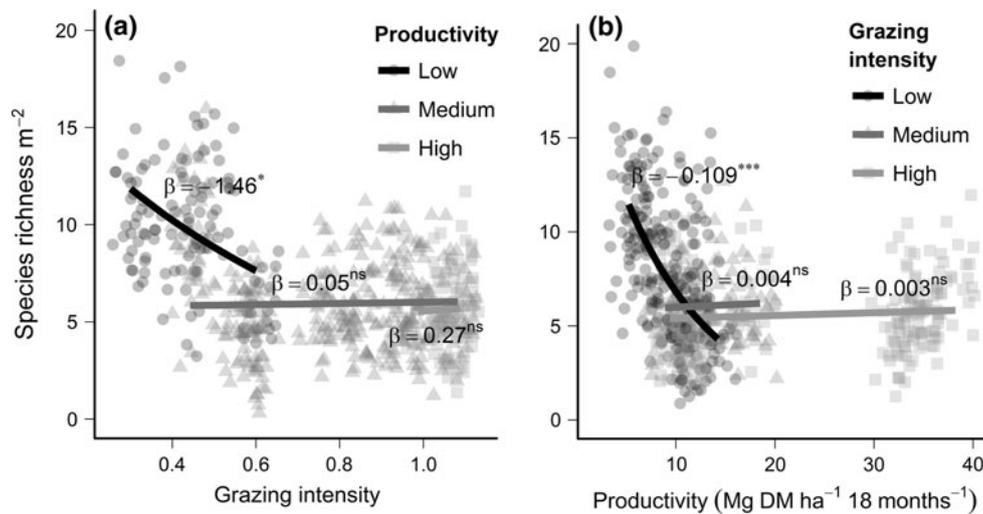


Fig. 2 Effects on plant species richness of **a** grazing intensity at different levels of productivity and **b** productivity at different levels of grazing intensity. In **a** samples were classified into three productivity classes based on Fig. 1 (low productivity—lowest fertilizer level; medium productivity—50, 100, and 250 kg ha⁻¹ year⁻¹ fertilizer levels; high productivity—500 kg ha⁻¹ year⁻¹). In **b** samples were clustered into three grazing intensity levels, using

Ward's method. Grazing intensity represents the proportion of total plant biomass produced that was grazed by sheep over the 18-month sampling period. For each productivity class, lines are predicted values from a Poisson generalised linear mixed model. Points are jittered for visual clarity. Regression coefficients (β) and P -values are shown. * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$, *ns* not significant ($P > 0.05$)

Resource 5). Finally, a model that included ANPP instead of total NPP gave very similar results, in that both the productivity \times grazing intensity interaction and the productivity main term remained highly significant ($P \leq 0.001$), except that in the ANPP model, grazing intensity led to significant increases in species richness at average ANPP ($P = 0.0263$; Online Resource 6).

The effects of productivity and grazing intensity on plant species richness were strongly associated with shifts in plant functional composition (Table 1). First, community-weighted SLA increased with productivity ($P \leq 0.001$), but not grazing intensity ($P = 0.422$), and the productivity \times grazing interaction was not significant ($P = 0.640$). Second, productivity increased community-weighted plant height at average grazing intensity ($P = 0.0014$), while grazing intensity reduced plant height at average productivity ($P \leq 0.0001$). However, grazing intensity reduced plant height more strongly at higher productivity (productivity \times grazing interaction, $P = 0.012$).

Discussion

Our results from this long-term grassland experiment support the predictions from the dynamic equilibrium model of species diversity (Huston 1979, 1994). As predicted by the model, higher productivity not only reduced species richness, but also moderated the effects of disturbance intensity on richness, shifting these effects from negative to neutral with increasing productivity. This

finding supports theoretical models (Huston 1979, 1994) and meta-analyses (Olf and Ritchie 1998; Proulx and Mazumder 1998; Worm et al. 2002) of the effects of grazing on plant species richness. However, in two of these papers (Olf and Ritchie 1998; Proulx and Mazumder 1998), the key prediction that grazing effects on plant species diversity depend on resource availability or productivity was obtained by evaluating or combining results from disparate grazing-impact studies, which were broadly categorised a posteriori on the basis of fertility or productivity (e.g. 'nutrient-poor' vs. 'nutrient-rich' systems; Proulx and Mazumder 1998). In another paper, Bakker et al. (2006) explored the interactive effects of herbivory and primary productivity on plant species richness, but only used two levels of herbivory (grazed vs. ungrazed). In contrast, by using long-term, large-scale, crossed manipulations of multiple levels of resource availability and grazing intensity by large herbivores within a single experiment, our study provides stronger evidence that the effects of grazing intensity on plant species richness depend directly on plant productivity (Huston 1979, 1994; Olf and Ritchie 1998; Proulx and Mazumder 1998; Osem et al. 2002; Frank 2005). Moreover, by using long-term (27-year) manipulations of soil resource availability and grazing intensity that mimic agricultural intensification scenarios in grazing systems, we believe that our results can be extrapolated to real-world grazing systems with greater confidence.

Even though our experimental plots encompassed a very broad range of productivities, grazing intensity was not

independent of productivity. This was not an artefact but a design feature, given that grazing intensity depends on productivity in natural and agricultural grazing systems (McNaughton et al. 1989). The main consequence of this is that mean grazing intensity was higher at high productivity than at lower productivity (Fig. 2). As a result, the non-significant (but weakly positive) effect of grazing intensity on plant species richness at high productivity may have been due to the restricted range in the predictor variable. Interestingly, the very high mean grazing intensity at high productivity could not offset the negative effect of productivity on species richness. The thick stubble and litter layer, followed by vigorous regrowth following grazing, presumably explains why weaker competitors could not easily re-invade high-productivity plots, despite high intensities of biomass removal due to grazing. The obvious management implication of this result is that potential negative impacts of fertilization and irrigation on plant biodiversity in grazing systems should not be expected to be offset by higher rates of biomass removal via grazing.

Interactive effects of productivity and grazing intensity on plant species richness were related to changes in plant functional traits, as predicted (Haddad et al. 2008). Increases in productivity were associated with dominance by taller plants with higher SLA. Plant height is associated with competitive ability (Grime 1979; Gaudet and Keddy 1988; Westoby 1998), whereas SLA is an important determinant of plant RGR (Lambers and Poorter 1992). Together, these results suggest that compositional shifts toward faster growing, taller plants contributed to more rapid rates of competitive displacement of slower growing species (Huston 1979; Aerts 1999). This would explain the negative effects of productivity on plant species richness observed in our study, and reinforces the idea that effects of productivity on species richness are mediated by changes in species functional traits (Aerts 1999; Haddad et al. 2008).

We also found that grazing intensity decreased plant height, but that this effect became more pronounced at higher productivity. This suggests that grazing can lead to weaker asymmetric competition for light (Aerts 1999). This interpretation is consistent with the view that grazing intensity may increase plant species richness at high productivity by suppressing competitive dominance, as predicted by some models (Grime 1973; Huston 1979; Olff and Ritchie 1998), but not observed in our study. This interpretation is also consistent with the fact that the regression coefficients for the productivity, grazing intensity and the productivity \times grazing interaction terms had larger absolute values (and smaller *P*-values) in the model that included ANPP instead of total NPP as a measure of productivity. However, grazing may also have a positive effect on plant species richness by promoting small-scale

heterogeneity and thus increase colonisation (Olff and Ritchie 1998).

Our finding that higher productivity reduced plant species richness contrasts with results obtained from grassland biodiversity-ecosystem function experiments, where positive effects of biodiversity on productivity have often been observed (Balvanera et al. 2006). However, in our study, soil nutrient availability was experimentally altered and long-term (i.e. 27 years) changes in species richness (from a common potential species pool) were recorded, whereas biodiversity-ecosystem function experiments aim to maintain initial soil conditions constant while experimentally manipulating plant species richness. Empirical studies along productivity gradients in grasslands suggest that productivity is a cause, rather than a consequence, of changes in plant diversity (Grace et al. 2007). Since abiotic controls (e.g. soil resource availability) over productivity are generally more important than biotic controls, any diversity effects on productivity may only be detectable once environmental conditions are held constant (Huston and McBride 2002). For example, a previous analysis involving the same experiment used here showed that changes in soil nutrient availability had much larger direct effects on productivity compared to the relatively minor indirect effects mediated via changes in plant functional diversity, and that functional diversity effects were only positive at high fertility (Laliberté and Tylianakis 2012).

Many potential mechanisms can influence the number of plant species that might coexist (Palmer 1994; Silvertown 2004) including spatial (Whittaker et al. 1973; Ricklefs 1977) and temporal (Warner and Chesson 1985) heterogeneity, frequency-dependent predation or parasitism (Janzen 1970; Connell 1971), partitioning of different forms of soil nutrients such as N (McKane et al. 2002) or P (Turner 2008), and species pool effects (Grime 1979; Zobel 1997; Huston 1999; Grace 2001). In addition, the decline in species richness with productivity could have been partly due to changes in plant density (Stevens and Carson 1999), but in the absence of density data we cannot address this hypothesis. Clearly, some of these factors may also play a role in our grassland system. Nevertheless, our study shows that the interactive effects of productivity and disturbance are consistent with those predicted from the dynamic equilibrium model and explained a significant amount of change in plant species richness following long-term increases in soil resource availability and grazing pressure. This is particularly relevant since these two components of agricultural intensification are the two most important drivers of change in grasslands worldwide (Bouwman et al. 2005). The dynamic equilibrium model thus has implications for biodiversity management in grazing systems—the most extensive land use on Earth (Asner et al. 2004).

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