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Variation of grazing-induced vegetation changes across a large-scale productivity gradient

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Keywords
Beta-diversity; Dissimilarity; Life forms; Normalized difference vegetation index; Patagonian steppes; Productivity; Río de la Plata grasslands; Species richness

Abbreviations
NDVI = normalized difference vegetation index; ANPP = above-ground net primary productivity; RUE = radiation use efficiency

Nomenclature
sensu Zuloaga et al. 2008

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Abstract

Questions: Does the magnitude of grazing-induced changes in species composition vary with habitat productivity? How does the sign and magnitude of grazing effects on species richness and beta-diversity change with increasing productivity? Do major life forms exhibit consistent responses to grazing along productivity gradients?

Location: Steppes and grasslands of southern South America in Argentina and Uruguay.

Methods: We evaluated grazing effects on plant composition, species richness, beta-diversity and life-form abundances along a ten-fold, regional productivity gradient and within subregions of contrasting productivity, using a common sampling protocol for 23 paired grazed vs ungrazed plots. The annual integral of the normalized difference vegetation index was used as a surrogate for above-ground net primary productivity.

Results: Compositional dissimilarity between grazed and ungrazed plots, as well as grazing-induced differences in plant richness and beta-diversity all increased with habitat productivity. Grazing decreased species richness in low-productive steppes but enhanced the richness of high-productive grasslands. On average, grazing reduced beta-diversity in high-productive sites but not in low-productive sites. Dominant species were more strongly suppressed by grazing towards productive grasslands. Grazing generally decreased shrub species cover, whereas graminoid and forb cover did not consistently change with grazing through the productivity gradient.

Conclusions: Our results indicate that the overall grazing effects on vegetation structure increased along a regional productivity gradient. Yet the sign of grazing impacts on species richness and beta-diversity shifted with habitat productivity, in agreement with models of herbivore-mediated co-existence and species colonization in productive systems. Further, we found that narrowing the spatial extent of analysis to the subregion generally obscured grazing–productivity relationships. Biodiversity conservation programmes should carefully weigh the varied impacts of livestock grazing across productivity gradients.

Introduction

Large herbivores exert a major influence on grassland ecosystem structure and function (Milchunas & Lauenroth 1993; Oesterheld et al. 1999). Grazing effects on plant community attributes like floristic composition, species diversity and life-form abundances can vary widely among sites, and it remains unclear whether they fit a general pattern. This variation of grazing impacts has been associated with differences in habitat productivity or resource supply (Milchunas et al. 1988; Proulx & Mazumder 1998), herbivore type (Olff & Ritchie 1998; Bakker et al. 2006), management (Bullock et al. 2001), species pool size (Frank 2005), plant dominance (Hillebrand et al. 2007) and spatial scale (Chaneton & Facelli 1991; Olff & Ritchie 1998). However, the paucity of studies testing for herbivore effects across broad habitat gradients through standardized protocols hinders the ability to find generalized responses, such as those suggested by global meta-analyses (e.g. Milchunas & Lauenroth 1993; Chase et al. 2000; Hillebrand et al. 2007).

Several models concur in predicting an increase in the magnitude of grazing impacts on vegetation structure with increasing productivity. Conceptual models focusing on plant traits emphasize trade-offs in species responses to resource supply, competition and herbivory (Milchunas et al. 1988; Proulx & Mazumder 1998; Cingolani et al. 2005). Dominant plants in resource-rich habitats are assumed to be adapted to light competition, which in turn makes them susceptible to large herbivores (Coughenour 1985; Osem et al. 2002). In productive systems such as mesic grasslands, grazers prevent exclusion of less competitive plants by feeding selectively on dominant ones, thus facilitating species co-existence and diversity (Harper 1969; Pacala & Crawley 1992; Hillebrand et al. 2007). Grazing disturbance of dense grassland canopies additionally increases plant richness by promoting colonization of ruderal species (Huston 1979; Bakker et al. 2006). Conversely, in low-productivity systems, like semi-arid steppes and deserts, dominant plants are adapted to soil resource shortages (e.g. drought), and may exhibit high resistance to grazing (Coughenour 1985). Under such conditions, grazing may reduce plant richness by eliminating subordinate or rare palatable species (Milchunas et al. 1988; Pacala & Crawley 1992; Osem et al. 2002). Proulx & Mazumder (1998) suggested that herbivore-mediated competitive release does not occur in unproductive habitats, because nutrient limitations reduce the growth potential of subordinate species (see Huston 1979). Overall, these mechanisms predict a reversal in direction of grazing effects on plant richness along productivity gradients. Moreover, divergent selection for traits conferring light competition ability vs grazing resistance (Coughenour 1985) should lead to higher grazing-induced changes in species composition in high- than in low-productivity systems (Milchunas et al. 1988; Milchunas & Lauenroth 1993; Bakker et al. 2006).

On the other hand, dynamic regulation models emphasize energy transfer across trophic levels and focus on herbivore impacts on producer biomass (Chase et al. 2000; Oksanen & Oksanen 2000). The 'ecosystem exploitation' model (Oksanen et al. 1981) predicts higher control of plant biomass by mammalian herbivores as habitat productivity increases in two trophic level systems. This would reflect increased herbivore biomass and consumer pressure with productivity; a pattern observed across both natural and managed grasslands (Oesterheld et al. 1992). Simple food chain models, however, do not address grazing effects on plant composition and diversity. More realistic, 'heterogeneous' food web models incorporate compositional turnover among producers, reflecting differential responses to grazing of edible and inedible species (Leibold 1996). Trophic models with producer heterogeneity predict increased species dissimilarity between grazed and ungrazed areas with increasing productivity (Chase et al. 2000). They also postulate a unimodal pattern of plant richness along productivity gradients, as herbivores facilitate co-existence at intermediate productivity but extirpate edible species, favouring dominance by resistant plants in high productivity habitats (Leibold 1996).

Grazing-induced changes in species composition and diversity may reflect predictable responses by plant life forms (PLFs) characterized by different functional traits (Sala 1988; Díaz et al. 2007). Such patterns have been documented for particular systems (e.g. Noy-Meir et al. 1989; Rusch & Oesterheld 1997), but may also arise at broader scales. For example, grassland encroachment by shrub species has been attributed to heavy grazing in both dry and mesic environments (Milchunas & Lauenroth 1993; Van Auken 2000; Roques et al. 2001; Briggs et al. 2005). Invasion by low-growing forbs and annual grasses has been noted in temperate sub-humid grasslands of the Americas (Milchunas et al. 1988; Mack 1989). Nevertheless, regional studies often report idiosyncratic PLF responses to grazing across environmental gradients (Stohlgren et al. 1999; Anderson et al. 2007), and hence the matter remains unsolved.

Lastly, grazing may influence the spatial heterogeneity of species composition, or beta-diversity (Adler et al. 2001; Anderson et al. 2011). Grazing has been shown to increase (Bakker et al. 2003) or reduce (Chaneton & Facelli 1991; Adler & Lauenroth 2000; Frank 2005) within-community heterogeneity. Such inconsistent results would reflect the scale dependency of grazing impacts on vegetation (Olff & Ritchie 1998; Adler et al. 2001; Dorrough et al. 2007). Large herbivores are predicted to affect spatial heterogeneity, depending on the interaction between grazing pattern and the scale of habitat patchiness (Adler et al. 2001). Thus, when grazing is homogeneous relative to small-scale plant patchiness, and promotes colonization by resistant species, beta-diversity is expected to decrease under grazing (Olff & Ritchie 1998). Yet, to our knowledge, only one grassland study (Frank 2005) has examined

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whether grazing altered beta-diversity in a consistent way along a primary productivity gradient.

Previous works looking at grazing impacts along habitat or productivity gradients relied on meta-analyses of grazed vs ungrazed treatments from disparate ecosystems (Milchunas & Lauenroth 1993; Proulx & Mazumder 1998; Chase et al. 2000; Bakker et al. 2006; Hillebrand et al. 2007; cf. Frank 2005; Anderson et al. 2007). While this approach can detect broad response trends, differences in measuring protocols and sampling scale might confound among-site comparisons (Brown & Allen 1989; De Bello et al. 2007). Here we use a standardized sampling scheme to examine grazing-related changes in grassland attributes across a productivity gradient in southern South America. The study region comprises the Río de la Plata sub-humid grasslands and the Patagonian semi-arid shrub/grass steppes (Soriano 1992; Paruelo et al. 2007; Fig. 1). Effects of livestock grazing on plant composition and diversity have been reported for both subregions (e.g. Facelli et al. 1989; Perelman et al. 1997; Rusch & Oesterheld 1997; Chaneton et al. 2002; Altesor et al. 2005, 2006; Cesa & Paruelo 2011); however, no attempt has been made so far to synthesize grazing response patterns within or across subregions.

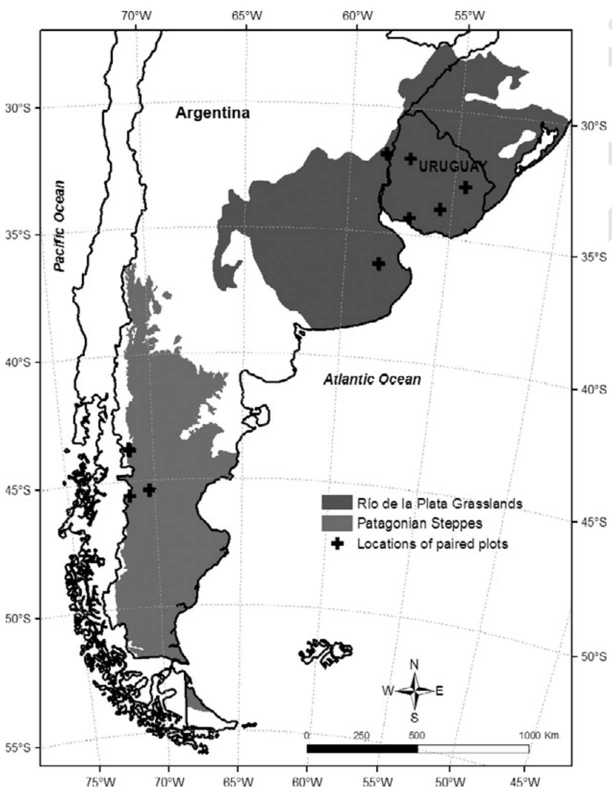

Fig. 1. Location of study sites in grass and shrub-grass steppes of Patagonia (Argentina) and Rio de la Plata grasslands (Argentina and Uruguay).

The goal of this study was to evaluate the magnitude and direction of grazing effects on species composition, richness, beta-diversity and PLFs (grasses, shrubs, forbs) along a ten-fold productivity (and precipitation) gradient in southern South America. We expected the magnitude of grazing-induced changes in species composition to increase with site productivity. We predicted that grazing effects on species richness would shift from negative in low-productivity sites to positive in high-productivity sites. We also predicted that beta-diversity and PLFs would not show a directional pattern in grazing effects across a productivity gradient, as these attributes appear to be context-dependent, regardless of productivity (Stohlgren et al. 1999; Adler et al. 2001; cf. Frank 2005). Our approach was to test whether pair-wise differences between grazed and ungrazed plots were correlated with site productivity across the whole study region and within low- and high-productivity subregions.

Methods

Study region

The study area encompassed the grasslands and steppes located between 30° and 46° S in Uruguay and Argentina (Fig. 1). The whole region spans a mean annual precipitation (MAP) gradient ranging from <200 mm in Patagonia to more than 1200 mm in the northeastern section of the Río de la Plata grasslands (RPG; Soriano 1992). Mean annual temperature (MAT) varies from 5 °C in the southernmost location in Patagonia, to 19 °C in the northeasternmost location of RPG. These subregions represent different phytogeographic units, although their extant floras share common Antarctic lineages, while the RPG are enriched by neotropical taxa (Burkart 1975; Cabrera & Willink 1976). The Patagonian steppes are dominated by C_3 tussock-forming grasses and short-stature shrubs (León et al. 1998). The RPG comprise a mix of C_3 and C_4 tussock and prostrate grasses, and a species-rich ensemble of herbaceous forbs (Soriano 1992; Perelman et al. 2001), while shrubs are generally sparse, except for some localities (Altesor et al. 2006). Field estimates of above-ground net primary productivity (ANPP) range from ca. 60 g m^{-2} yr^{-1} in Río Mayo, Patagonia (Fernández et al. 1991) to ca. 750 g m^{-2} yr^{-1} in the Argentine Pampas (Hidalgo & Cauhepé 1991).

There is scarce evidence on the recent (pre-Hispanic) evolutionary history of grazing for the study region (Cingolani et al. 2005; Oesterheld & Semmartin 2011). A diverse and abundant megafauna of vertebrate herbivores occupied southern South America prior to the Late Pleistocene extinctions (McFadden 1997; Barnosky & Lindsey

2010). Since then, the main native grazers have been *Ozotoceros bezoarticus* (pampas deer), nowadays reduced to small protected populations in RPG, and *Lama guanicoe* (guanaco), which is still common in Patagonia (Cabrera & Willink 1976; Paruelo et al. 2007). Most importantly, the whole region has been grazed by domestic herbivores (cattle, sheep, horses) for nearly two centuries. Steppe vegetation in Patagonia has been largely devoted to livestock grazing, with agriculture being restricted to irrigated valleys (Paruelo et al. 2007). In contrast, over one third of the original RPG has been transformed to agriculture, while remnant grasslands are managed for livestock (Baldi & Paruelo 2008).

Study design and vegetation sampling

We selected 23 paired, grazed and ungrazed plots located in nine sites where natural grasslands or steppes were the dominant vegetation type (Table 1, Fig. 1). The sites in Patagonia comprised the grassy steppes of the Sub-Andean district and the shrub–grass steppes of the Occidental district (León et al. 1998). The RPG sites were located on the Flooding Pampa, the Mesopotamic Pampa and the Uruguayan Campos (Soriano 1992). The present study did not consider the Monte and Espinal phytogeographic provinces (Cabrera 1976), which are dominated by xerophytic woodlands and shrublands. Thus we restricted the analysis to prairies, grass steppes and shrub–grass steppes (Paruelo et al. 2007). We only considered sites where one or more grazing exclosures had been established by fencing out all domestic herbivores for at least 5 yr (hereafter, ungrazed plots). There were 1–5 pairs of grazed vs ungrazed plots per site, which were regarded as true replicates for the purpose of analysis, including eight pairs in Patagonia and 15 pairs in RPG (Table 1). For each pair, the exclosure and the adjacent grazed area were located within the same physiographic unit and soil patch. We ensured that the grazed plot was representative of the larger paddock by avoiding any excessively trampled patches or animal trails. Mowed grasslands and fire-managed sites were discarded. While evaluating grazing effects through a paired-plot design has some drawbacks (Stohlgren et al. 1999), this approach minimizes the risk of confounding differences attributed to grazing with other sources of spatial variation in vegetation (soil properties, topography, species pool).

The cover of all vascular plant species was recorded along three 5-m-long linear transects placed parallel to the fence dividing the grazed and ungrazed plots within a pair. Transects were established at least 4 m away from each side of the fence, and were 1 m apart from each other. The horizontal projection of the canopy of each individual plant item intercepted by the linear transect was measured to the nearest 0.1 cm. We also used plant cover data collected beforehand within the same sites. Overall, we compiled data from previous works for ten paired plots (Chaneton et al. 2002; Altesor et al. 2006; Cesa & Paruelo 2011), while 13 additional areas were newly sampled. Plant cover data for the three Patagonian sites were originally taken using 30-m-long transects. To make data comparable between subregions, cover data were extracted for three 5-m-long segments chosen at random from each original transect in Patagonia. Nomenclature followed Zuloaga et al. (2008); a full species list can be found in Appendix S1.

We used the annual integral of the normalized difference vegetation index (NDVI) as a surrogate for above-ground net primary productivity (ANPP) at the site scale. NDVI is a spectral index calculated as,

$$\mathrm{NDVI} = \frac{IR - R}{IR + R}$$

where R represents the reflectance in the red portion and IR the reflectance in the infrared portion of the electromagnetic spectrum. This index shows a positive and linear relationship with the fraction of photosynthetically active radiation absorbed by green vegetation, and hence with primary productivity (Prince 1991; Di Bella et al. 2004;

Table 1. General description of study sites in the Río de la Plata grasslands (RPG) and Patagonian steppes (PAT) of southern South America.

Site name	Lat./Long.	Subregion	No. of paired *G*/*UG* plots	MAP (mm)	MAT (°C)	ANPP (g m^{-2} yr^{-1})
El Palmar (national park)	31.871/58.289	RPG	3	1300	18.9	663.4–785.1
El Relincho (private ranch)	34.341/56.980	RPG	5	1099	17.4	624.8–701.7
Cerro colorado (experimental station, SUL)	33.881/55.559	RPG	1	1161	16.3	707.0
Glencoe (experimental station, INIA)	32.011/57.169	RPG	2	1406	17.3	646.5–652.5
Las chilcas (private ranch)	36.245/58.289	RPG	2	861	14.9	638.8–676.0
Quebrada de los cuervos (protected area)	32.912/54.447	RPG	2	1293	16.8	577.4–598.3
Media luna (private ranch)	45.591/71.427	PAT	2	325	7.3	181.4–232.8
Río mayo (experimental station, INTA)	45.393/70.273	PAT	3	154	8.0	9.9–31.2
Tecka (private ranch)	43.763/71.319	PAT	3	324	7.9	80.1–250.4

G/*UG*, paired grazed and ungrazed plots per site; MAP, mean annual precipitation; MAT, mean annual temperature; ANPP, above-ground net primary productivity (range).

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Piñeiro et al. 2006). We obtained NDVI data from the MODIS (Moderate Resolution Imaging Spectroradiometer) sensor onboard the EOS Terra satellite. The MODIS [4] Land Science Team (http://modis-land.gsfc.nasa.gov/) produces an NDVI composite image every 16 d with a spatial resolution of 250 m × 250 m. We used a NDVI time series corresponding to the period 2000–2006. Each NDVI image was filtered using its associated 'per pixel' quality image (Roy et al. 2002), and only those pixels without clouds or shadows, and with low levels of aerosols in the atmosphere were analysed. NDVI values were obtained only from grazed plots using the complete MODIS pixel nearest to a study site. For each site, we calculated the annual integral of NDVI (NDVI-I) by summing the products of 7-yr average NDVI for each period and the proportion of the year represented by that period (usually 16 d in MODIS time series; Paruelo et al. 1997). We used Monteith's model (Piñeiro et al. 2006) to provide an estimate of ANPP from the NDVI-I data. We used a linear relationship to transform NDVI-I into the fraction of photosynthetically active radiation absorbed by green vegetation (Ruimy et al. 1994). Incoming photosynthetically active radiation data were obtained from weather stations near the study sites (see Table 1). We used radiation use efficiency (RUE) values equal to 0.42 g dry matter MJ^{-1} for the RPG (Piñeiro et al. 2006) and 0.3 g dry [5] matter MJ^{-1} for Patagonia (Paruelo et al. 2004), estimated from NDVI data of Landsat images and field biomass harvests.

Data analyses

We used Sørensen's quantitative distance measure to evaluate pair-wise differences in plant species composition between grazed and ungrazed plots (MjM Software; Gleneden Beach, OR, US). In addition, we examined grazing effects on two components of plant community diversity, namely, species richness (S_{mean}) and beta-diversity (β). Species richness was represented by the mean number of species recorded per sample transect within a plot. Beta-diversity was measured as

$$\beta = \frac{ST}{S_{mean}}$$

where ST is the total number of species found in a plot and S_{mean} is the mean richness as defined previously (Whittaker 1972). In this context, beta-diversity reflects the spatial variation of species composition within a community (Anderson et al. 2011). Further, species were classified into three major plant life forms (PLFs): shrubs, graminoids and forbs. PLF cover and richness, and dominant species cover, were calculated by averaging their respective values among transects within a plot. Species accounting for more than 50% of the total cover in an ungrazed plot were regarded as 'dominant'; thus the number of dominant species for any given pair of plots varied from one to five species.

The magnitude of grazing effects (ΔGE) on each structural attribute of vegetation (Smean, β and PLF cover and richness) was calculated for each pair of plots as

$$\Delta GE = \frac{(G - UG)}{UG}$$

where G and UG denoted attribute values for the grazed and ungrazed plots, respectively. Further, the grazing effect on the cover of each dominant species in ungrazed plots (ΔGE dc) was expressed as [6]

$$\Delta GE\mathrm{dc} = \frac{(G - UG)}{(G + U)}$$

The aggregated response to grazing of those species classified as 'dominant' was obtained by the weighted average of the relative change in cover of all such species. For rigour, our analysis quantified the effect size of excluding domestic herbivores from long-term grazed, natural vegetation areas.

Simple regression analyses were performed between the response attributes measured in grazed and ungrazed plots. To determine the significance of grazing effects, each regression was compared with the 1:1 line (no grazing effect) by testing whether the slope differed from 1 and the y-intercept differed from 0. To evaluate whether grazing effects varied with productivity, regression analyses were performed using NDVI-I values as the independent variable and Sørensen's distance and ΔGE for each vegetation attribute (S_{mean}, β, PLF cover and richness, dominant species cover) as dependent variables. Although we generated estimates of ANPP for each study site, these analyses used NDVI-I as predictor variate to avoid artifacts based on the assumption of different RUE. Regressions were performed on the whole data set (n = 23 paired plots), and separately for the Patagonian and RPG subregions (n = 8 and 15, respectively) to determine if the sign of grazing effects shifts between low- and high-productivity systems. All analyses were performed using GraphPad Prism v. 3.0 (GraphPad Software Co., San Diego, CA, US).

Results

Changes in community composition and diversity

The annual NDVI-I varied from 0.223 to 0.732 across study sites, which corresponded to ANPP values ranging between 9.9 g m^{-2} yr^{-1} (Río Mayo, Patagonia) and 785.1 g m^{-2}

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yr^{-1} (El Palmar, RPG; Table 1). The magnitude of grazing-induced changes in plant species composition showed a significant trend along the productivity gradient (Fig. 2). Compositional differences between paired grazed and ungrazed plots increased with the annual NDVI-I of the site ($F_{1,21}$ = 81.46, P < 0.001). Analyses within subregions indicated that the relationship was positive and highly significant for RPG ($F_{1,13}$ = 24.06, P < 0.001), but was negative and marginally non-significant for Patagonia ($F_{1,6}$ = 5.33, P = 0.07).

Mean species richness ranged between 3.7 and 33.7 species per 5-m transect. Species richness in grazed plots was positively related to that observed in their ungrazed counterparts ($F_{1,21}$ = 43.16, P < 0.0001; Fig. 3a). The slope of the regression line was not different from 1 ($F_{1,25}$ = 0.76, P = 0.39), while the intercept was higher than 0 ($F_{1,26}$ = 4.44, P = 0.045). Thus, on average, grazing exerted a positive effect on species richness across the whole richness gradient, with 17 of the 23 paired plots showing higher richness in the grazed than in the ungrazed condition. Notably, however, most paired plots in Patagonia fell below the richness equality line (Fig. 3a). The magnitude of grazing impact on plant richness was strongly and positively associated with site productivity ($F_{1,21}$ = 39.7, P < 0.0001; Fig. 4a). Grazing caused a 36% decrease in species richness at the least productive end of the gradient, whereas it increased richness up to a 106% at the most productive grassland sites. Interestingly, at the subregion level, the grazing effect on species richness increased significantly with NDVI-I across the Patagonian steppes ($F_{1,6}$ = 13.44, P = 0.01), varying from slightly negative to nearly neutral. In contrast, grazing enhanced species richness in RPG regardless of observed variation in NDVI-I ($F_{1,13}$ = 1.27, P = 0.27; Fig. 4a).

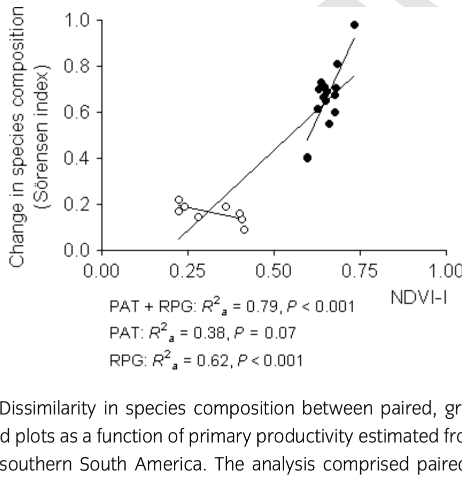

 Fig. 2. Dissimilarity in species composition between paired, grazed and ungrazed plots as a function of primary productivity estimated from NDVI-I data in southern South America. The analysis comprised paired plots in semi-arid Patagonian steppes (PAT, empty circles) and in sub-humid Río de la Plata grasslands (RPG, solid circles). Regression statistics are shown for the whole data set and for each study subregion.

Beta-diversity correlated significantly between grazed and ungrazed plots ($F_{1,21}$ = 17.54, P < 0.001; Fig. 3b). Overall, beta-diversity was lowered by grazing in 18 of the 23 paired plots. The regression slope was below 1 ($F_{1,25}$ = 25.5, P < 0.001), meaning that the grazing effect on beta-diversity became stronger on high beta-diversity sites (Fig. 3b). Grazing-induced changes in beta-diversity

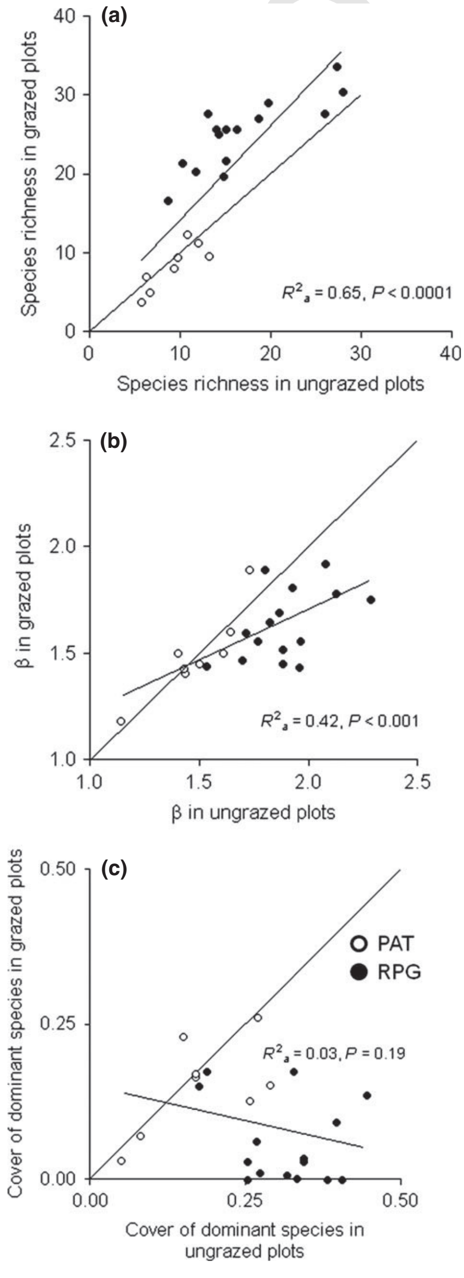

Fig. 3. Relationship between (**a**) species richness, (**b**) beta-diversity and (**c**) dominant species cover recorded in adjacent, grazed and ungrazed plots located in semi-arid Patagonian steppes (PAT, empty circles) and in sub-humid Río de la Plata grasslands (RPG, solid circles). The equality line indicates no change attributed to grazing.

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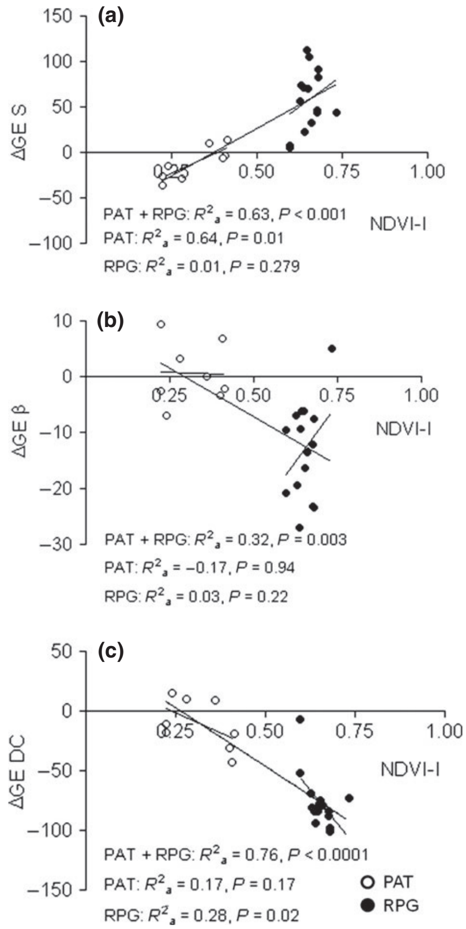

Fig. 4. Percentage change in the magnitude of grazing effects on (**a**) species richness, (**b**) beta-diversity and (**c**) dominant species cover, as a function of primary productivity estimated from NDVI-I data. Paired plots were located in semi-arid Patagonia steppes (PAT, empty circles) and sub-humid Río de la Plata grasslands (RPG, solid circles). Regression statistics are shown for the whole data set and for each study subregion.

were inversely related to NDVI-I across the whole region ($F_{1,21}$ = 11.27, P = 0.003; Fig. 4b), while differences in beta-diversity within subregions did not depend on productivity (RPG: $F_{1,13}$ = 1.63, P = 0.22; Patagonia: $F_{1,6}$ = 0.006, P = 0.94). On average, grazing did not consistently affect beta-diversity in Patagonia, but reduced community heterogeneity in RPG (Fig. 4b).

Grazing clearly reduced the cover of dominant species in 15 out of 23 cases, and this resulted in dominant species cover in grazed plots not being significantly related to that in ungrazed plots ($F_{1,21}$ = 1.82, P = 0.19; Fig. 3c). Grazing-induced changes in dominant species were strongly negatively related to NDVI-I for the whole data set ($F_{1,21}$ = 53.70, P < 0.0001), so that dominant species became more negatively affected by grazing towards the most productive sites (Fig. 4c). While this trend was apparent among the RPG sites ($F_{1,13}$ = 6.73, P = 0.02), grazing impact on dominant species in Patagonia was not significantly related to cross-site differences in NDVI ($F_{1,6}$ = 1.44, P = 0.27).

Changes in life-form abundance

Graminoids were the dominant PLF throughout the study region. Species richness within PLFs showed a wider variation for graminoids (from 2 to 23.3 spp. per transect) than for forbs (0–11.6 spp. per transect) and shrubs (0–5 spp. per transect). Both graminoid and shrub richness in grazed plots were positively related to richness values in ungrazed plots (graminoids: $F_{1,21}$ = 106.7, P < 0.0001; shrubs: $F_{1,21}$ = 58.83, P < 0.0001; Fig. 5a,b). Graminoid richness was higher in grazed than in ungrazed plots in 16 out of 23 paired plots. The slope for the graminoid model was higher than 1 ($F_{1,25}$ = 8.35, P = 0.007), meaning that the positive effect of grazing on graminoid richness increased towards more species-rich areas (Fig. 5a). In contrast, grazing reduced shrub species richness in 19 of the 23 paired plots. The slope for shrubs did not differ from 1 ($F_{1,25}$ = 0.09, P = 0.76), while the intercept was significantly lower than 0 ($F_{1,26}$ = 4.30, P = 0.05), indicating a proportional decrease in shrub richness with grazing across the richness gradient (Fig. 5b). The forb richness regression between grazed and ungrazed plots was marginally non-significant ($F_{1,21}$ = 3.84, P = 0.06). Forb species richness was higher in grazed than in ungrazed plots in 13 out of 23 cases, and these increases mostly occurred in the lower richness sites of the RPG (Fig. 5c).

Graminoid cover was significantly correlated between grazed and ungrazed plots ($F_{1,21}$ = 22.83, P < 0.001), whereas shrub and forb species cover were not (Fig. 5d–f). The regression for graminoid cover did not differ from the 1:1 line, denoting the lack of a definite grazing impact on the main vegetation matrix. Indeed, about the same number of cases fell on each side of the equality line for both subregions (Fig. 5d). Shrub cover decreased in 21 out of 23 cases, showing small or no changes in the low-productivity areas, but a pronounced decrease in the most productive areas (Fig. 5e). Although forb cover tended to be higher with grazing in 14 of the 23 cases, such differences were generally quite small (see Fig. 5f).

Grazing-induced changes in graminoid richness were independent of NDVI-I across the whole data set, and the same was true for the RPG subregion (Table 2). Yet, the effect on graminoid richness was positively related to NDVI-I across Patagonian steppes. In contrast, the magnitudes of grazing effects on shrub and forb richness were negatively and positively related to NDVI-I on a regional scale, respectively (Table 2). These relationships were not significant within subregions. Grazing-induced changes in

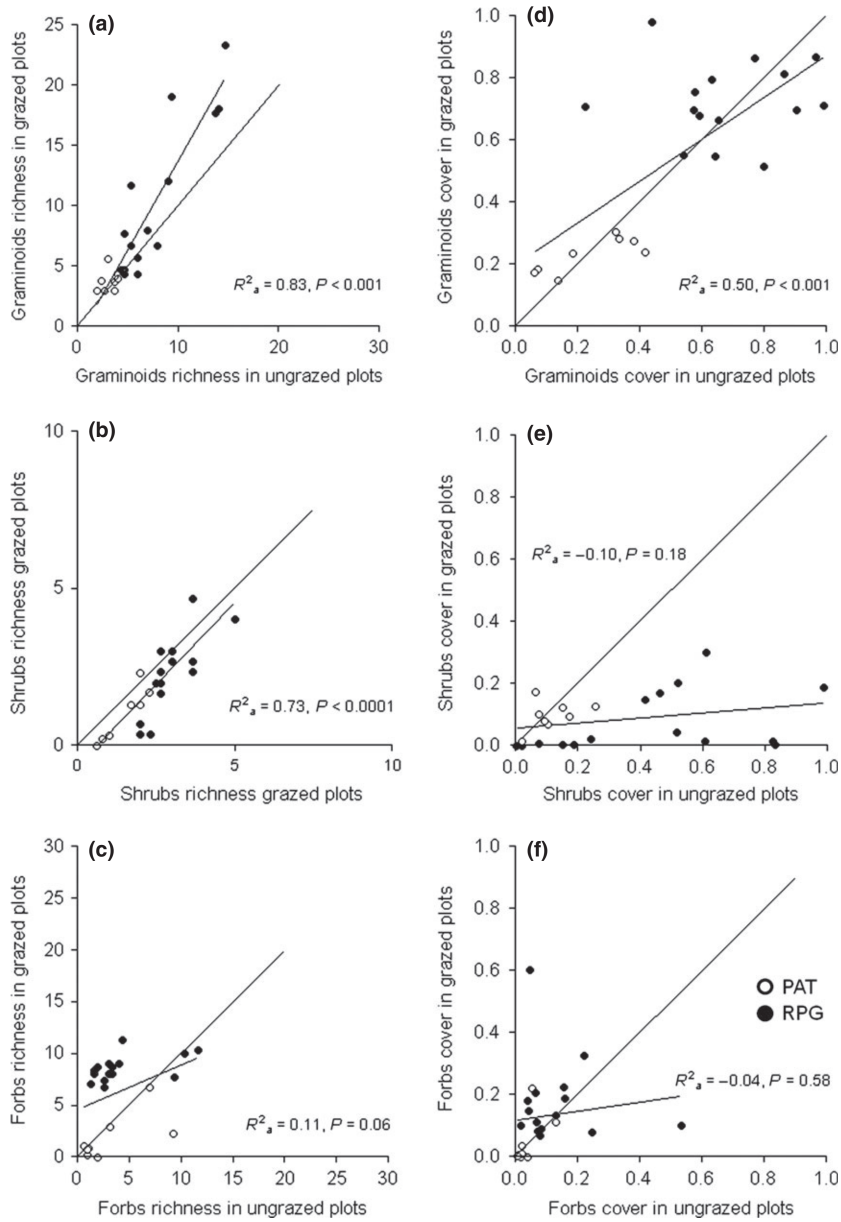

Fig. 5. Relationship between species richness and cover of graminoids (**a**, **d**), shrubs (**b**, **e**) and forbs (**c**, **f**) recorded in adjacent grazed and ungrazed plots. 13 The equality line denotes no change attributed to grazing. Plots were located in semi-arid Patagonia steppes (PAT, empty circles) and in sub-humid Río de la Plata grasslands (RPG, solid circles).

graminoid and forb cover did not vary significantly with NDVI-I, whereas the change in shrub cover was negatively correlated with NDVI for the whole data set but not within subregions (Table 2).

Discussion

Our results generally support the hypothesis that grazing impacts on vegetation structure increase with habitat productivity. We found that the magnitude of grazing-related differences in species composition, mean richness, beta-diversity and dominant species cover, all increased over a ten-fold productivity gradient encompassing sub-humid grasslands and semi-arid steppes in southern South America (Figs 2, 4). In addition, the sign of the grazing effect on species richness shifted from negative to positive with increasing productivity. Overall, these patterns correspond with predictions of conceptual models for large-herbivore effects on grasslands (Milchunas et al. 1988; Osem et al. 2002), as well as those of dynamic regulation models

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Table 2. Statistics for the relationship between grazing-induced changes in plant life form richness (ΔS) and cover (ΔC) and primary productivity estimated from NDVI-I.

Variable	Life form	Whole data set			RPG		PAT	
		$F_{1,21}$	P	R^2_a	$F_{1,13}$	P	$F_{1,6}$	P
ΔS	Graminoids	0.07	0.79	−0.05	0.01	0.90	0.01	0.93
ΔS	Forbs	**13.33**	**0.001**	**0.32**	1.44	0.25	1.62	0.25
ΔS	Shrubs	**8.37**	**0.009**	**0.24**	0.60	0.45	2.36	0.17
ΔC	Graminoids	0.074	0.79	−0.03	2.206	0.16	**15.39**	**0.01**
ΔC	Forbs	0.05	0.82	−0.05	0.24	0.64	0.23	0.65
ΔC	Shrubs	**8.84**	**0.007**	**0.25**	0.11	0.74	0.90	0.38

Numbers in bold denote significant regression models ($P < 0.05$).

for heterogeneous food webs (Leibold 1996; Chase et al. 2000). Our findings for species dissimilarity, plant richness and dominant species also agree with quantitative meta-analyses of grazed vs ungrazed community changes along gradients of resource supply and primary productivity (Milchunas & Lauenroth 1993; Proulx & Mazumder 1998; Chase et al. 2000; Hillebrand et al. 2007). However, unlike these meta-analyses, we applied a common sampling protocol and used the same descriptor for site productivity throughout the study region. Therefore, differences among sites were not confounded by factors such as spatial scale, productivity measure or vegetation response variable (see Olff & Ritchie 1998; Stohlgren et al. 1999; Anderson et al. 2007).

Grazing-induced changes in species composition

At the whole-region scale, a large fraction of the variation in species dissimilarity between paired grazed and ungrazed areas was accounted for by site productivity. We estimated productivity from satellite NDVI-I data for the nominal, grazed condition. Thus, our measures reflected differences in actual primary production, rather than potential productivity for ungrazed areas. A similar pattern had been reported for other regional (Bakker et al. 2006; Anderson et al. 2007) and global analyses (Milchunas & Lauenroth 1993; Chase et al. 2000). These studies found a remarkably lower amount of variation in grazing-induced species turnover being explained by productivity or environmental moisture ($R^2 = 0.21–0.39$), compared to that reported here ($R^2_a = 0.79$). Several factors might contribute to this result, including the use of common indices to estimate ANPP and species dissimilarity across all sites at a fixed spatial scale, that grasslands and steppes considered for study are climatically determined and had similar evolutionary histories of grazing, and the fact that they have been chronically grazed by domestic herbivores for over a century.

The analyses per subregion showed that productivity positively influenced the magnitude of grazing impact on species composition across the RPG sites. In contrast, the relationship was not significant for the Patagonian steppes, although both subregions comprised a similar range of NDVI-I values (Fig. 2). It thus appears that the role of site productivity in modulating community responses to grazing would be mostly important in high-productivity habitats. In productive sub-humid grasslands, selective herbivory suppresses tall-growing dominant plants and often favours invasion by low-growing ruderal species (Milchunas et al. 1988; Collins et al. 1998; Bakker et al. 2006). This may drive large changes in dominant species cover and overall community composition, as recorded here for the RPG subregion (Fig. 4c; see Rusch & Oesterheld 1997; Chaneton et al. 2002; Altesor et al. 2005).

Alternatively, low-productivity systems are often dominated by more grazing-resistant plants, such as tough tussock grasses and spiny shrubs (Milchunas et al. 1988; Milchunas & Lauenroth 1993). This idea is consistent with the reduced change in dominant species observed between grazed and ungrazed plots in Patagonia (Figs 3c, 4c). In unproductive systems, low resource supply and a small species pool may further limit colonization rates, and thus compositional turnover in response to grazing (Leibold 1996; Proulx & Mazumder 1998; Oesterheld & Semmartin 2011). Lastly, different magnitudes of grazing impacts on plant species composition may be expected if habitat productivity controls herbivore biomass and consumption rates (see Oesterheld et al. 1992, 1999), as predicted for grazers in two-trophic level ecosystems (Oksanen et al. 1981; Chase et al. 2000; Oksanen & Oksanen 2000).

Reversal of grazing impact on species richness with habitat productivity

Our second prediction stated that the direction of species richness differences between grazed and ungrazed plots would shift across the productivity gradient. Present results clearly supported this pattern. Mean richness increased with grazing in productive RPG but was decreased or not affected by grazing in Patagonian steppes (Fig. 4a). Other studies investigating grazing effects on species diversity along landscape or regional gradients found a qualitatively similar response to productivity (Osem et al. 2002; Frank 2005; Bakker et al. 2006). The increased richness of grazed productive grasslands was associated with a drastic reduction in dominant species cover and the number of colonizing forbs and prostrate grasses (Fig. 5c; see Facelli et al. 1989; Chaneton et al. 2002; Rodríguez et al. 2003; Altesor et al. 2005). The results for RPG agree with models of herbivore-mediated co-existence in competitive systems (Huston 1979; Leibold 1996; Collins et al. 1998; Bakker et al. 2006). As productivity increases, light competition becomes more prevalent as a determinant of vegetation structure, and this would render high-productive plant communities more susceptible to grazing (Milchunas et al. 1988; Osem et al. 2002; Frank 2005).

Conversely, the slightly negative impact of grazing on plant richness in Patagonia involved the loss of a few subordinate palatable grasses and ephemeral forbs (Perelman et al. 1997; Cesa & Paruelo 2011). Low primary production in Patagonian steppes (Table 1) determines that above-ground biomass remains below ca. 300 g m^{-2}, a threshold proposed by Huisman & Olff (1998), above which light limitation would reduce the establishment of many plant species. Osem et al. (2002) postulated that dominant species in unproductive systems are well adapted to competition for soil resources, and so allocate more carbon to below-ground organs, which makes them less vulnerable to grazing (see also Coughenour 1985; Leibold 1996). In such systems, grazing would decrease diversity by removing subordinate and rare species (Milchunas et al. 1988). Alternatively, severe resource limitations may prevent plant regrowth after herbivory, thus increasing the risk of species loss under sustained grazing (Proulx & Mazumder 1998; Frank 2005).

Intriguingly, for the Patagonia data set, grazing reduced species richness at the lowest productivity sites but had little richness effect at the highest productivity sites (see Figs 3a, 4a). This pattern may explain the marginally negative slope of the relationship between species dissimilarity and productivity found in Patagonia (Fig. 2). In this subregion, shifts in species composition would be primarily driven by grazing-induced changes in species richness, whereas compositional shifts in the RPG typically involve substantial changes in the abundances of both dominant and subordinate species (e.g. Chaneton et al. 2002). The reduced effect of grazing on compositional similarity at intermediate productivity sites (most productive sites of Patagonia) corresponded with a zone of the gradient where both species richness and composition changed slightly.

Neither a difference in graminoid species richness nor in shrub richness helped to explain patterns of total species richness in response to grazing. Shrub richness declined with grazing throughout the productivity gradient, whereas graminoid richness showed no pattern with productivity, although their numbers did increase in the most productive RPG sites (Table 2, Fig. 5). It seems likely that compensatory dynamics among species with contrasting growth traits or palatability precluded any differences in graminoid richness between grazed and ungrazed areas (Chaneton et al. 2002; Díaz et al. 2007).

Grazing reduced beta-diversity across the productivity gradient

We found that grazing predictably reduced the spatial heterogeneity (beta-diversity) of plant communities as habitat productivity increased from semi-arid steppes in Patagonia to sub-humid grasslands in the Río de la Plata Basin. This component of community diversity (Whittaker 1972; Anderson et al. 2011) was largely neglected by existing models and meta-analyses focusing on grazing–productivity relationships. Hence, we had no early expectations on how ANPP might influence the effect of grazing on beta-diversity. Results showed no significant (average) effect of livestock grazing on beta-diversity towards less productive sites, but a decrease in spatial heterogeneity of grazed areas in higher productivity grasslands (Figs 3b, 4b). Nevertheless, our analyses indicated that this pattern was primarily determined by coarse-scale differences between the study subregions.

One possibility may be that grazing effects on beta-diversity reflect some fundamental differences between RPG and Patagonia in the relative scales of grazing pattern and grain of underlying habitat heterogeneity (Sala 1988; Adler et al. 2001). If the spatial pattern of grazing is coarser than existing small-scale environmental variation, then grazing may act to homogenize species composition (e.g. Adler & Lauenroth 2000; Dorrough et al. 2007). Previous work in the flooding Pampa (RPG) suggested that grazing reduces the spatial variation of floristic composition by suppressing patchy dominance by tall tussock grasses, and by increasing the frequency of invasive forbs and grazing-resistant grasses (Chaneton & Facelli 1991; Chaneton et al. 2002; see also Olff & Ritchie 1998). These effects appear to override within-site differences in microtopography and soil properties (Chaneton et al. 2005). In managed systems, the scale of grazing pattern is influenced by stocking rate, paddock size and herbivore body size, which may all depend on the ecosystem carrying capacity (Oesterheld et al. 1999). RPG paddocks overlap with coarse landscape patterns of topographic and edaphic variation (Perelman et al. 2001), and are much smaller than those typical of Patagonian steppes. Also, RPG paddocks are grazed by cattle, with a relatively uniform grazing pressure year-round.

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By contrast, large paddocks in Patagonia contain a remarkable heterogeneity associated with topographic relief and location of water sources. This creates a spatially variable grazing pressure reinforced by animal movement (mostly sheep) between winter and summer ranges (Paruelo et al. 2007).

Only one study had previously reported how grazing affects beta-diversity along a productivity gradient. Frank (2005) examined the effect of native herbivores on grassland beta-diversity over a 500 g m^{-2} ANPP gradient in Yellowstone National Park (USA). In his study, grazing exerted a non-linear effect on beta-diversity (Whittaker's index), as spatial heterogeneity decreased with grazing at both low- and high-productivity sites, but was increased by grazing at intermediate sites (Frank 2005). Interestingly, this pattern correlated with the observed impact of grazing on local species richness. Thus, taken together, our data for South American rangelands and those of Frank (2005) for Yellowstone grasslands indicate that a full understanding of the influence of habitat productivity on vegetation responses to grazing should focus on spatial species turnover both among and within communities. Nevertheless, we stress the need for further work to determine how herbivores affect community beta-diversity along productivity gradients.

Idiosyncratic plant life-form responses to grazing

We set out to examine whether different life forms exhibit consistent responses to grazing across regional and subregional productivity gradients. Patterns in life-form abundance may help to understand grazing-induced changes in vegetation structure beyond individualistic species responses (Noy-Meir et al. 1989; Milchunas & Lauenroth 1993; Díaz et al. 2007). However, we found little evidence for predictable, grazing-related differences in the cover of major plant life forms across sites of varying productivity (Table 2, Fig. 5).

The only clear trend was the increasingly positive effect of removing livestock on shrub species cover that took place across the whole productivity gradient. Unexpectedly, grazing reduced shrub cover in most rangeland sites, and this effect was stronger in sub-humid grasslands than in semi-arid steppes (see Fig. 5d). Shrubs accounted for over 20% of the ground cover in half of the grazing exclosures included in our study (Altesor et al. 2006; Cesa & Paruelo 2011). This finding contradicts the widely held view that grazing promotes woody species encroachment in both arid and mesic grasslands worldwide (McPherson et al. 1988; Milchunas & Lauenroth 1993; Van Auken 2000; Roques et al. 2001; Briggs et al. 2005). Mechanisms behind the increased cover of shrubs in ungrazed areas remain largely unexplored. Yet, at least for the RPG subregion, these might involve reduced water infiltration associated with soil compaction and direct physical damage on woody seedlings from cattle trampling.

On the other hand, forb and graminoid species exhibited mostly idiosyncratic responses to grazing across our grassland and steppe sites (Fig. 5b,f). We observed similarly large increases and declines of graminoid cover in sites of differing productivity within each study subregion. Most likely, this reflected the functionally heterogeneous composition of the graminoid life form as a whole, which may include both grazing-intolerant and -resistant growth forms, even within the same plant community (Sala 1988; Chaneton et al. 2002; Anderson et al. 2007; Díaz et al. 2007). The lack of a consistent grazing response in forb cover was somewhat unexpected, at least for the RPG sites (see Perelman et al. 2001; Chaneton et al. 2002). Although forb cover tended to increase in grazed areas, this was far from a statistically significant pattern at either the regional or subregional scale (see Fig. 5f, Table 2). Many of the forb species in these rangelands behave as short-lived opportunistic colonizers, and therefore their response to grazing may be highly dependent on local factors (e.g. management) and environmental stochasticity.

Conclusions

We have documented, for an extensive area of South American grasslands and steppes, an overall increase in the magnitude of grazing effects across a regional productivity gradient. We found, however, that narrowing the spatial extent of the analysis to the subregion scale generally obscured the grazing–productivity relationship. The increased uncertainty about grazing responses within subregions may reflect the influence of local factors not controlled for in our study, such as grazing intensity or herbivore type.

It remains unclear as to what are the mechanisms driving the changes in grazing effects with habitat productivity. For instance, by simultaneously looking at different vegetation attributes, we have shown that multiple underlying mechanisms are likely to operate in concert, affecting grazing impacts on different components of community diversity in high- vs low-productive ecosystems. A future challenge would be trying to integrate the relative influences of mechanisms acting on disparate levels, from plant adaptive traits, through herbivore spatial behaviour to energy-constrained (food chain) interactions.

Our results also provide valuable information for biodiversity conservation in managed grazing systems. Livestock grazing can be used as a practical tool for maintaining or even enhancing plant diversity at local scales in the RPG as well as in other mesic grasslands (Collins et al. 1988; Bakker et al. 2006; Schultz et al. 2011). However, changes

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in species richness at small scales may not be reflected at larger scales in these systems. Moreover, grazing may potentially reduce biodiversity at regional scale in mesic grasslands, representing an important issue to consider in the context of conservation management decisions (Landsberg et al. 2002; Dorrough et al. 2007; Lunt et al. 2007).

In contrast to RPG, in low-productive systems such as Patagonian steppes, large grazers may have negative effects on diversity at local scales (also Bakker et al. 2006). Further, our study confirms that grazing effects evaluated in terms of PLF responses cannot be readily extrapolated across climatically different regions (Díaz et al. 2007). Thus, the usefulness of PLFs as a rangeland monitoring tool may be restricted to certain systems. Biodiversity conservation programmes should carefully consider the differential impacts that grazing produces on various vegetation attributes across productivity gradients.

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References

Adler, P.B. & Lauenroth, W.K. 2000. Livestock exclusion increases the spatial heterogeneity of vegetation in Colorado shortgrass steppe. *Applied Vegetation Science* 3: 213–222.

Adler, P.B., Raff, D.A. & Lauenroth, W.K. 2001. The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* 128: 465–479.

Altesor, A., Oesterheld, M., Leoni, E., Lezama, F. & Rodríguez, C. 2005. Effect of grazing on community structure and productivity of a Uruguayan grassland. *Plant Ecology* 179: 83–91.

Altesor, A., Piñeiro, G., Lezama, F., Jackson, R.B., Sarasola, M. & Paruelo, J.M. 2006. Ecosystem changes associated with grazing in sub-humid South American grasslands. *Journal of Vegetation Science* 17: 323–332.

Anderson, T.M., Ritchie, M.E. & McNaughton, S.J. 2007. Rainfall and soils modify plant community response to grazing in Serengeti National Park. *Ecology* 88: 1191–1201.

Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B. D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L. S., Davies, K.F., Harrison, S.P., Fraft, N.J.B., Stegen, J.C. & Swenson, N.G. 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology Letters* 14: 19–28.

Bakker, C., Blair, J.M. & Knapp, A.K. 2003. Does resource availability, resource heterogeneity or species turnover mediate changes in plant species richness in grazed grasslands? *Oecologia* 137: 385–391.

Bakker, E.S., Ritchie, M.E., Olff, H., Milchunas, D.G. & Knops, J. M.H. 2006. Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. *Ecology Letters* 9: 780–788.

Baldi, G. & Paruelo, J.M. 2008. Land-use and land cover dynamics in South American temperate grasslands. *Ecology and Society* 13: 6 [online].

Barnosky, A.D. & Lindsey, E.L. 2010. Timing of Quaternary megafaunal extinction in South America in relation to human arrival and climate change. *Quaternary International* 217: 10–29.

Briggs, J.M., Knapp, A.K., Blair, J.M., Heisler, J.L., Hoch, G.A., Lett, M.S. & McCarron, J.K. 2005. An ecosystem in transition: causes and consequences of the conversion of mesic grassland to shrubland. *BioScience* 55: 243–254.

Brown, B.J. & Allen, T.F.H. 1989. The importance of scale in evaluating herbivory impacts. *Oikos* 54: 189–194.

Bullock, J.M., Franklin, J., Stevenson, M.J., Silvertown, J., Coulson, S.J., Gregory, S.J. & Tofts, R. 2001. A plant trait analysis of responses to grazing in a long-term experiment. *Journal of Applied Ecology* 38: 253–267.

Burkart, A. 1975. Evolution of grasses and grasslands in South America. *Taxon* 24: 53–66.

Cabrera, A.L. & Willink, A. 1976. *Biogeografia de America Latina*. Organización de los Estados Americanos, Washington, DC, US.

Cesa, A. & Paruelo, J.M. 2011. Changes in vegetation structure induced by domestic grazing in Patagonia (southern Argentina). *Journal of Arid Environments* 75: 1129–1135.

Chaneton, E.J. & Facelli, J.M. 1991. Disturbance effects on plant community diversity: spatial scales and dominance hierarchies. *Vegetatio* 93: 143–155.

Chaneton, E.J., Perelman, S.B., Omacini, M. & León, R.J.C. 2002. Grazing, environmental heterogeneity, and alien plant invasions in temperate Pampa grasslands. *Biological Invasions* 4: 7–24.

Chaneton, E.J., Perelman, S.B. & León, R.J.C. 2005. Floristic heterogeneity of Flooding Pampa grasslands: a multi-scale analysis. *Plant Biosystems* 139: 245–254.

Chase, J.M., Leibold, M.A., Downing, A.L. & Shurin, J.B. 2000. The effects of productivity, herbivory, and plant species turnover in grassland food webs. *Ecology* 81: 2485–2497.

Cingolani, A.M., Noy-Meir, I. & Díaz, S. 2005. Grazing effects on rangeland diversity: a synthesis of contemporary models. *Ecological Applications* 15: 757–775.

Collins, S.L., Knapp, A.K., Briggs, J.M., Blair, J.M. & Steinauer, E.M. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science* 280: 745–747.

Doi: 10.1111/jvs.12053

Coughenour, M.B. 1985. Graminoid responses to grazing by large herbivores: adaptations, exaptations and interacting processes. *Annals of the Missouri Botanical Garden* 72: 852–863.

De Bello, F., Leps, J. & Sebastia, M.T. 2007. Grazing effects on the species–area relationship: variation along a climatic gradient in NE Spain. *Journal of Vegetation Science* 18: 25–34.

Di Bella, C.M., Paruelo, J.M., Becerra, J.E., Bacour, C. & Baret, F. 2004. Effect of senescent leaves on NDVI based estimates of fAPAR: experimental and modeling evidence. *International Journal of Remote Sensing* 25: 5415–5427.

Díaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanoves, F., Milchunas, D.G., Skarpe, C., Rusch, G., Sternberg, M., Noy-Meir, I., Landsberg, J., Zhang, W., Clark, H. & Campbell, B. D. 2007. Plant trait responses to grazing – a global synthesis. *Global Change Biology* 13: 313–341.

Dorrough, J.W., Ash, J.E., Bruce, S. & McIntyre, S. 2007. From plant neighbourhood to landscape scales: how grazing modifies native and exotic plant species richness in grassland. *Plant Ecology* 191: 185–198.

Facelli, J.M., Leon, R.J.C. & Deregibus, V.A. 1989. Community structure in grazed and ungrazed grassland sites in the flooding Pampa, Argentina. *American Midland Naturalist* 121: 125–133.

Fernández, R.J., Sala, O.E. & Golluscio, R.A. 1991. Woody and herbaceous aboveground production of a Patagonian steppe. *Journal of Range Management* 44: 434–437.

Frank, D.A. 2005. The interactive effects of grazing ungulates and aboveground production on grassland diversity. *Oecologia* 143: 629–634.

Harper, J.L. 1969. The role of predation in vegetational diversity. *Brookhaven Symposia in Biology* 22: 48–62.

Hidalgo, L.G. & Cauhepé, M.A. 1991. Effect of seasonal rest on the aboveground biomass for a native grassland of the Flooding Pampa, Argentina. *Journal of Range Management* 44: 471–475.

Hillebrand, H., Gruner, D.S., Borer, E.T., Bracken, M.T.S., Cleland, E.E., Elser, J.J., Harpole, W.S., Ngai, J.T., Seabloom, E.W., Shurin, J.B. & Smith, J.E. 2007. Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. *Proceedings of the National Academy of Sciences of the United States of America* 104: 10904–10909.

Huisman, J. & Olff, H. 1998. Competition and facilitation in multispecies plant–herbivore systems of productive environments. *Ecology Letters* 1: 25–29.

Huston, M.A. 1979. A general hypothesis of species diversity. *The American Naturalist* 113: 81–101.

Landsberg, J., James, C.D., Maconochie, J., Nicholls, A.O., Stol, J. & Tynan, R. 2002. Scale-related effects of grazing on native plant communities in an arid rangeland region of South Australia. *Journal of Applied Ecology* 39: 427–444.

Leibold, M.A. 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence and diversity patterns in communities. *The American Naturalist* 147: 784–812.

León, R.J.C., Bran, D., Collantes, M., Paruelo, J.M. & Soriano, A. 1998. Grandes unidades de vegetación de la Patagonia. *Ecología Austral* 8: 125–143.

Lunt, I.D., Eldridge, D.J., Morgan, J.W. & Bradd Witt, G. 2007. A framework to predict the effects of livestock grazing and grazing exclusion on conservation values in natural ecosystems in Australia. *Australian Journal of Botany* 55: 401–415.

Mack, R.N. 1989. Temperate grasslands vulnerable to plant invasions: characteristics and consequences. In: Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H., Kruger, F.J., Rejmánek, M. & Williamson, M. (eds.) *Biological invasions: a global perspective*, pp. 155–179. John Wiley & Sons, Chichester, UK.

McFadden, B.J. 1997. Origin and evolution of the grazing guild in New World terrestrial mammals. *Trends in Ecology & Evolution* 12: 182–187.

McPherson, G.R., Wright, H.A. & Wester, D.B. 1988. Patterns of shrub invasion in semiarid Texas grasslands. *American Midland Naturalist* 120: 391–397.

Milchunas, D.G. & Lauenroth, W.K. 1993. A quantitative assessment of the effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* 63: 327–366.

Milchunas, D.G., Sala, O.E. & Lauenroth, W.K. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *The American Naturalist* 132: 87–105.

Noy-Meir, I., Gutman, M. & Kaplan, Y. 1989. Responses of Mediterranean grassland plants to grazing and protection. *Journal of Ecology* 77: 290–310.

Oesterheld, M. & Semmartin, M. 2011. Impact of grazing on species composition: adding complexity to a generalized model. *Austral Ecology* 36: 881–890.

Oesterheld, M., Sala, O.E. & McNaughton, S.J. 1992. Effect of animal husbandry on herbivore-carrying capacity at a regional scale. *Nature* 356: 234–236.

Oesterheld, M., Loreti, J., Semmartin, M. & Paruelo, J.M. 1999. Grazing, fire and climate effects on primary productivity of grasslands and savannas. In: Walker, L. (ed.) *Ecosystems of disturbed ground*, pp. 303–322. Elsevier, Amsterdam, NL.

Oksanen, L. & Oksanen, T. 2000. The logic and realism of the hypothesis of exploitation ecosystems. *The American Naturalist* 155: 703–723.

Oksanen, L., Fretwell, S.D., Arruda, J. & Niemela, P. 1981. Exploitation ecosystems in gradients of primary productivity. *The American Naturalist* 118: 240–261.

Olff, H. & Ritchie, M.E. 1998. Effects of herbivores on grassland plant diversity. *Trends in Ecology & Evolution* 13: 261–265.

Osem, Y., Perevolotsky, A. & Kigel, J. 2002. Grazing effects on diversity of annual plant communities in a semi-arid rangeland: interactions with small-scale spatial and temporal variation in primary productivity. *Journal of Ecology* 90: 936–946.

Pacala, S.W. & Crawley, M.J. 1992. Herbivores and plant diversity. *The American Naturalist* 140: 243–260.

Paruelo, J.M., Epstein, H.E., Lauenroth, W.K. & Burke, I.C. 1997. ANPP estimates from NDVI for the central grasslands region of the U.S. *Ecology* 78: 953–958.

Paruelo, J.M., Jobbágy, E.G., Oesterheld, M., Golluscio, R.A. & Aguiar, M.R. 2007. The grasslands and steppes of Patagonia and the Rio de la Plata plains. In: Veblen, T., Young, K. & Orme, A. (eds.) *The physical geography of South America*, pp. 232–248. Oxford University Press, Oxford, UK.

Perelman, S.B., León, R.J.C. & Bussacca, J.P. 1997. Floristic changes related to grazing intensity in a Patagonian shrub steppe. *Ecography* 20: 400–406.

Perelman, S.B., León, R.J.C. & Oesterheld, M. 2001. Cross-scale vegetation patterns of Flooding Pampa grasslands. *Journal of Ecology* 89: 562–577.

Piñeiro, G., Oesterheld, M. & Paruelo, J.M. 2006. Seasonal variation in aboveground production and radiation use efficiency of temperate rangelands estimated through remote sensing. *Ecosystems* 9: 357–373.

Prince, S.D. 1991. Satellite remote sensing of primary production: comparison of results for Sahelian grasslands 1981–1988. *International Journal of Remote Sensing* 12: 1301–1311.

Proulx, M. & Mazumder, A. 1998. Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology* 79: 2581–2592.

Rodríguez, C., Leoni, E., Lezama, F. & Altesor, A. 2003. Temporal trends in species composition and plant traits in natural grasslands of Uruguay. *Journal of Vegetation Science* 14: 433–440.

Roques, K.G., Connor, T.G. & Watkinson, A.R. 2001. Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology* 38: 268–280.

Roy, D.P., Borak, J.S., Devadiga, S., Wolfe, R.E., Zheng, M. & Descloitres, J. 2002. The MODIS Land product quality assessment approach. *Remote Sensing of Environment* 83: 62–76.

Ruimy, A., Saugier, B. & Dedieu, G. 1994. Methodology for the estimation of terrestrial net primary production from remotely sensed data. *Journal of Geophysical Research* 99: 5263–5283.

Rusch, G.M. & Oesterheld, M. 1997. Relationship between productivity, and species and functional group diversity in grazed and non-grazed Pampas grassland. *Oikos* 78: 519–526.

Sala, O.E. 1988. The effect of herbivory on vegetation structure. In: Werger, M.J.A., van der Aart, P.J.M., During, H.J. & Verboeven, J.T.A. (eds.) *Plant form and vegetation structure*, pp. 317–330. SPB, The Hague, NL.

Schultz, N.L., Morgan, J.W. & Lunt, I.D. 2011. Effects of grazing exclusion on plant species richness and phytomass accumulation vary across a regional productivity gradient. *Journal of Vegetation Science* 22: 130–142.

Soriano, A. 1992. Río de la Plata grasslands. In: Coupland, R.T. (ed.) *Natural grasslands. Introduction and Western Hemisphere*, pp. 367–407. Elsevier, Amsterdam, NL.

Stohlgren, T.J., Schell, L.D. & Vanden Heuvel, B. 1999. Effects of grazing and soil quality on native and exotic plant species in Rocky Mountain grasslands. *Ecological Applications* 9: 45–64.

Van Auken, O.W. 2000. Shrub invasions of North American semiarid grasslands. *Annual Review of Ecology and Systematics* 31: 197–215.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. *Taxon* 21: 213–251.

Zuloaga, F., Morrone, O. & Belgrano, M.J. (eds.) 2008. *Catálogo de las plantas vasculares del cono sur (Argentina, sur de Brasil, Chile, Paraguay y Uruguay). Monographs in Systematic Botany from the Missouri Botanical Garden 107*, 3 Vol., pp. 3486. ????, ????. 8

Supporting Information

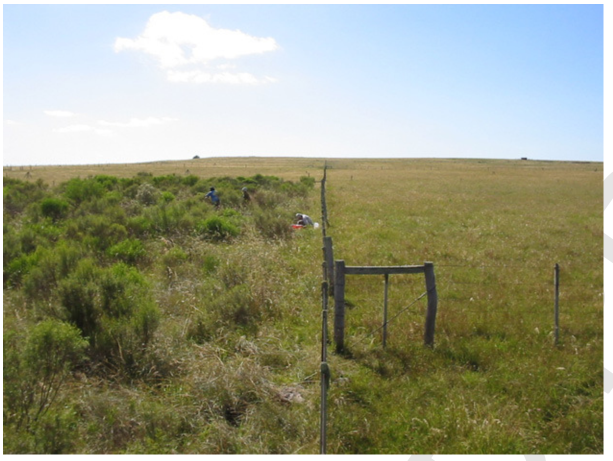
Additional supporting information may be found in the online version of this article:

Appendix S1. List of species recorded in Patagonia and Rio de la Plata grasslands.

Doi: 10.1111/jvs.12053

Graphical Abstract

The contents of this page will be used as part of the graphical abstract of html only. It will not be published as part of main.



In this study we analyzed grazing-induced vegetation changes by comparing 21 grazed- ungrazed pairs across steppes and grasslands of South America. Our results support the hypothesis that grazing impacts on vegetation structure increase with habitat productivity. We found that the magnitude of grazing-related differences in species composition, mean richness 2 and β diversity, all increased over a ten-fold productivity gradient.

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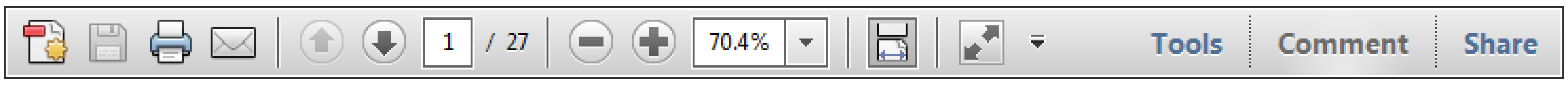
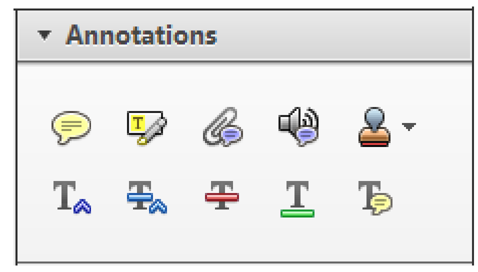
Required software to e-Annotate PDFs: Adobe Acrobat Professional or Adobe Reader (version 7.0 or above). (Note that this document uses screenshots from Adobe Reader X)
The latest version of Acrobat Reader can be downloaded for free at: http://get.adobe.com/uk/reader/

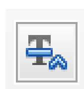
Once you have Acrobat Reader open on your computer, click on the Comment tab at the right of the toolbar:



This will open up a panel down the right side of the document. The majority of tools you will use for annotating your proof will be in the Annotations section, pictured opposite. We've picked out some of these tools below:



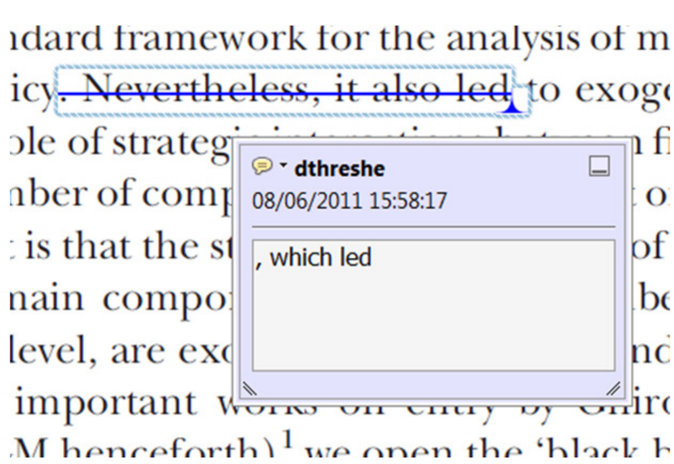
1. Replace (Ins) Tool – for replacing text.



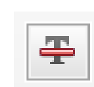
Strikes a line through text and opens up a text box where replacement text can be entered.

How to use it

- Highlight a word or sentence.
- Click on the Replace (Ins) icon in the Annotations section.
- Type the replacement text into the blue box that appears.



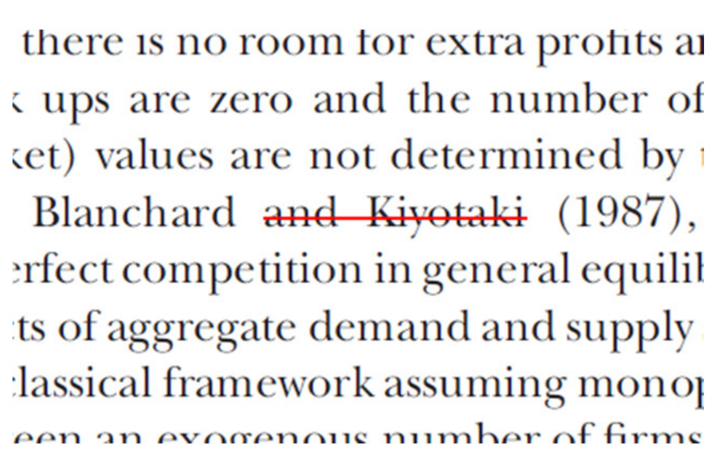
2. Strikethrough (Del) Tool – for deleting text.



Strikes a red line through text that is to be deleted.

How to use it

- Highlight a word or sentence.
- Click on the Strikethrough (Del) icon in the Annotations section.

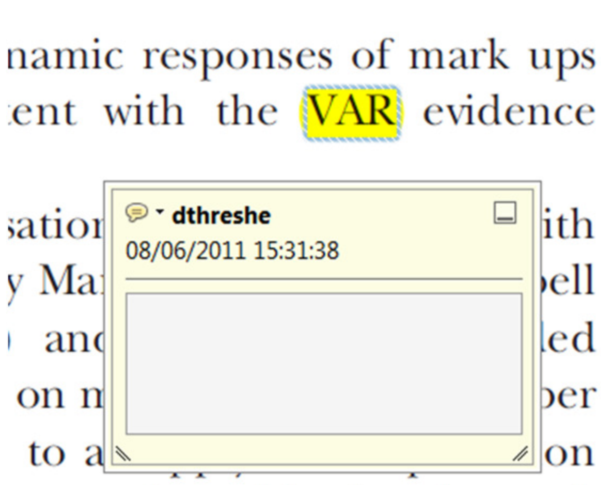


3. Add note to text Tool – for highlighting a section to be changed to bold or italic.

Highlights text in yellow and opens up a text box where comments can be entered.

How to use it

- Highlight the relevant section of text.
- Click on the Add note to text icon in the Annotations section.
- Type instruction on what should be changed regarding the text into the yellow box that appears.

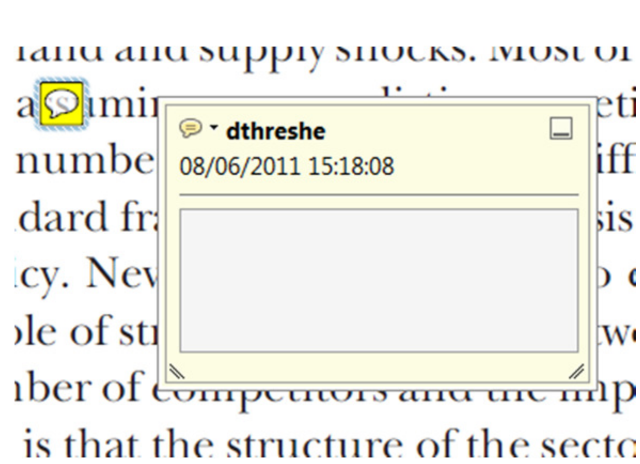


4. Add sticky note Tool – for making notes at specific points in the text.

Marks a point in the proof where a comment needs to be highlighted.

How to use it

- Click on the Add sticky note icon in the Annotations section.
- Click at the point in the proof where the comment should be inserted.
- Type the comment into the yellow box that appears.



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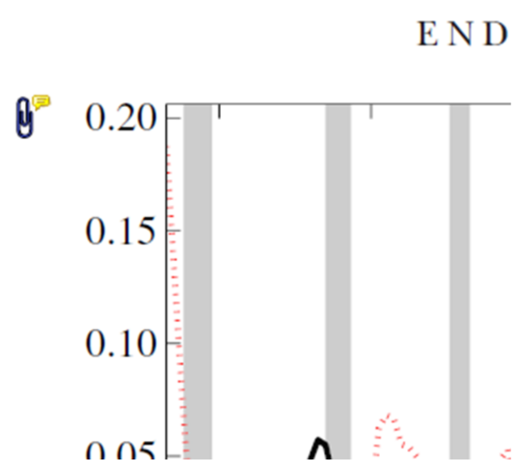
5. Attach File Tool – for inserting large amounts of text or replacement figures.

Inserts an icon linking to the attached file in the appropriate pace in the text.

How to use it

- Click on the Attach File icon in the Annotations section.
- Click on the proof to where you'd like the attached file to be linked.
- Select the file to be attached from your computer or network.
- Select the colour and type of icon that will appear in the proof. Click OK.

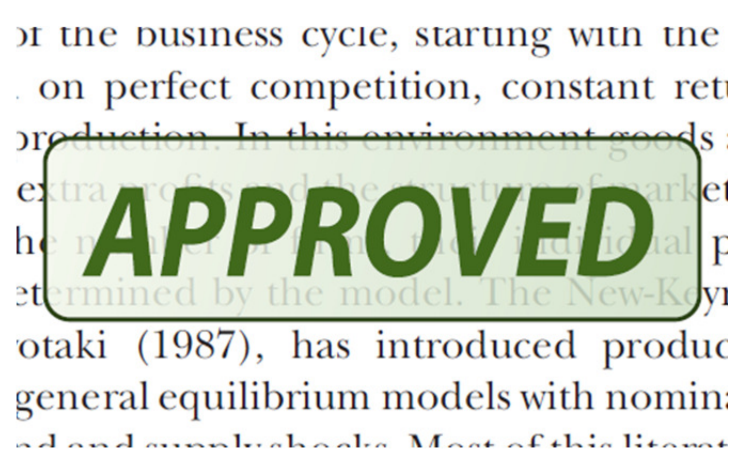


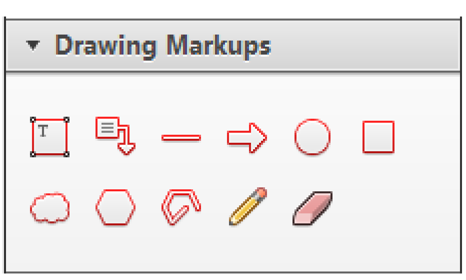
6. Add stamp Tool – for approving a proof if no corrections are required.

Inserts a selected stamp onto an appropriate place in the proof.

How to use it

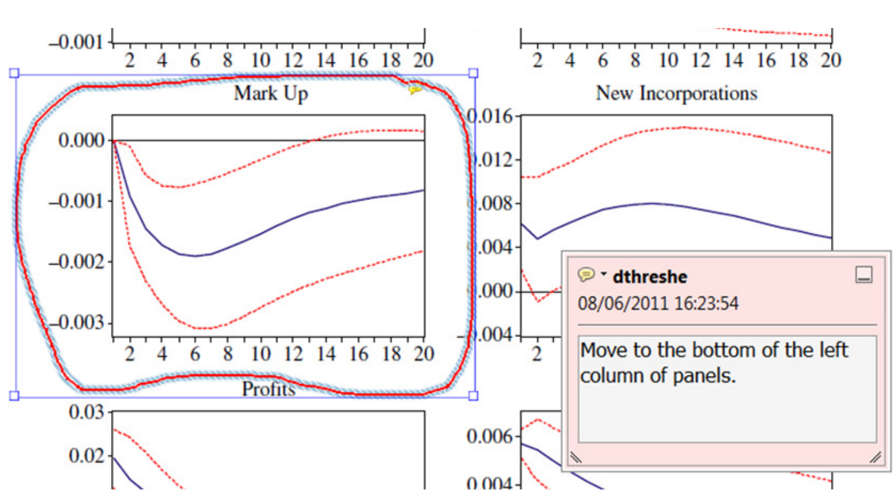
- Click on the Add stamp icon in the Annotations section.
- Select the stamp you want to use. (The Approved stamp is usually available directly in the menu that appears).
- Click on the proof where you'd like the stamp to appear. (Where a proof is to be approved as it is, this would normally be on the first page).





7. Drawing Markups Tools – for drawing shapes, lines and freeform annotations on proofs and commenting on these marks.

Allows shapes, lines and freeform annotations to be drawn on proofs and for comment to be made on these marks..



How to use it

- Click on one of the shapes in the Drawing Markups section.
- Click on the proof at the relevant point and draw the selected shape with the cursor.
- To add a comment to the drawn shape, move the cursor over the shape until an arrowhead appears.
- Double click on the shape and type any text in the red box that appears.

For further information on how to annotate proofs, click on the Help menu to reveal a list of further options: