

# Plant trait responses to grazing – a global synthesis

SANDRA DÍAZ\*, SANDRA LAVOREL<sup>†1</sup>, SUE McINTYRE<sup>‡</sup>, VALERIA FALCZUK\*,  
FERNANDO CASANOVES§, DANIEL G. MILCHUNAS¶, CHRISTINA SKARPE||,  
GRACIELA RUSCH||, MARCELO STERNBERG\*\*, IMANUEL NOY-MEIR<sup>††</sup>,  
JILL LANDSBERG<sup>‡‡2</sup>, WEI ZHANG<sup>‡‡</sup>, HARRY CLARK§§ and BRUCE D. CAMPBELL¶¶

\**Instituto Multidisciplinario de Biología Vegetal (CONICET–UNC) and FCEfyN, Universidad Nacional de Córdoba, C. Correo 495, 5000 Córdoba, Argentina*, <sup>†</sup>*Centre d'Ecologie Fonctionnelle et Evolutive, CNRS, 1919 route de Mende, 34293 Montpellier, Cedex 5, France*, <sup>‡</sup>*CSIRO Sustainable Ecosystems, PO Box 284, Canberra AC 2604, Australia*, <sup>§</sup>*Grupo de Estadística y Biometría, Dpto. de Desarrollo Rural, Facultad de C. Agropecuarias, Universidad Nacional de Córdoba, CC 509, 5000 Córdoba, Argentina*, <sup>¶</sup>*Forest, Range, and Watershed Stewardship Department and Natural Resource Ecology Laboratory, Colorado State University, Ft Collins, CO 80523, USA*, <sup>||</sup>*Norwegian Institute for Nature Research, Tungasletta 2, NO – 7485 Trondheim, Norway*, <sup>\*\*</sup>*Department of Plant Sciences, Faculty of Life Sciences, Tel Aviv University, 69978 Tel Aviv, Israel*, <sup>††</sup>*Institute of Plant Sciences, Faculty of Agricultural, Food and Environmental Quality Sciences, Hebrew University of Jerusalem, PO Box 12, Rehovot 76100, Israel*, <sup>‡‡</sup>*Botany Department, University of British Columbia, Vancouver, BC V6T 1Z4, Canada*, <sup>§§</sup>*AgResearch, Grasslands Research Centre, Private Bag 11008, Palmerston North, New Zealand*, <sup>¶¶</sup>*Hort Research Mt Albert, 120 Mt Albert Road, Private Bag 92 169, Mt Albert, Auckland, New Zealand*

## Abstract

**Herbivory by domestic and wild ungulates is a major driver of global vegetation dynamics. However, grazing is not considered in dynamic global vegetation models, or more generally in studies of the effects of environmental change on ecosystems at regional to global scale. An obstacle to this is a lack of empirical tests of several hypotheses linking plant traits with grazing. We, therefore, set out to test whether some widely recognized trait responses to grazing are consistent at the global level. We conducted a meta-analysis of plant trait responses to grazing, based on 197 studies from all major regions of the world, and using six major conceptual models of trait response to grazing as a framework. Data were available for seven plant traits: life history, canopy height, habit, architecture, growth form (forb, graminoid, herbaceous legume, woody), palatability, and geographic origin. Covariates were precipitation and evolutionary history of herbivory. Overall, grazing favoured annual over perennial plants, short plants over tall plants, prostrate over erect plants, and stoloniferous and rosette architecture over tussock architecture. There was no consistent effect of grazing on growth form. Some response patterns were modified by particular combinations of precipitation and history of herbivory. Climatic and historical contexts are therefore essential for understanding plant trait responses to grazing. Our study identifies some key traits to be incorporated into plant functional classifications for the explicit consideration of grazing into global vegetation models used in global change research. Importantly, our results suggest that plant functional type classifications and response rules need to be specific to regions with different climate and herbivory history.**

*Keywords:* dynamic global vegetation models, functional traits, global plant functional types, grazing history, grazing models, ungulate herbivores

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Correspondence: Sandra Díaz, fax: + 54 351 4332104,  
e-mail: sdiaz@com.uncor.edu

<sup>1</sup>Present address: Laboratoire d'Ecologie Alpine, CNRS, Université Joseph Fourier, BP 53 X, 38041 Grenoble Cedex 9, France.

<sup>2</sup>Jill Landsberg died on 23 May 2005.

## Introduction

Grazing by domestic and wild ungulates is the most globally widespread land use (FAOSTAT data 2004, <http://faostat.fao.org/>). After fire, grazing is the most

important disturbance of vegetation in terms of both area and biomass loss (Huntly, 1991). Grazing is both dependent on (e.g. Day & Detling, 1990; Huntly, 1991) and affects (e.g. Briske, 1996) plant morphological and functional traits. This codependency can generate powerful feedback cycles between the structure and biochemistry of vegetation and the cycling and storage of nutrients (Huntly, 1991; Wardle & Bardgett, 2004). Effects include altered disturbance regimes, especially fire (e.g. Scholes & Archer, 1997; Bachelet *et al.*, 2000; Bond *et al.*, 2003; Bond, 2005), and regional climate (Eastman *et al.*, 2001), and changes to above- and below-ground diversity (Landsberg *et al.*, 1999; Wardle & Bardgett, 2004). For these reasons, changes in grazer densities in response to climate and/or land use change are increasingly considered an important element of global change (Wardle & Bardgett, 2004).

Dynamic global vegetation models (DGVMs) seek to represent vegetation dynamics generically in order to project the effects of global environmental change on the distribution of vegetation types and on key biogeochemical cycles at continental scales (Cramer *et al.*, 2001). An important advance in achieving this has been the simplification of vegetation composition using plant functional groups (Lavorel *et al.*, 2007). However, successful selection of relevant plant functional groups, and representation of vegetation dynamics require identification of the key processes that drive species distribution. Initial developments of DGVMs focussed mainly on plant responses to climate and atmospheric CO<sub>2</sub> concentration, and have successfully captured the distribution of biomes and their contribution to the carbon cycle (Cramer *et al.*, 2001; Sitch *et al.*, 2003). Although recent models successfully include effects of land use change and agricultural land cover modification (McGuire *et al.*, 2001), the approach has been a 'static' one, which incorporates land cover effects, rather than the processes causing the change. The next generation of DGVMs needs to include dynamic simulations of fire and other disturbances (Bond *et al.*, 2003). There have been attempts to incorporate grazing in regional models of vegetation dynamics (Bachelet *et al.*, 2000; Daly *et al.*, 2000; Bond *et al.*, 2003), but grazing is not yet incorporated in DGVMs. A major obstacle to this is the lack of information about which plant traits are positively or negatively associated with grazing at the global scale (Díaz *et al.*, 2002; Skarpe, 2000).

There are thousands of published studies of plant responses to grazing. Those which use plant traits provide a more general and mechanistic basis for understanding plant behaviour (Díaz *et al.*, 2001; Lavorel & Garnier, 2002; see also Vesk & Westoby, 2001), but have generally focused on local conditions. As a result,

most current models of plant trait responses (see Briske, 1996 for review) are extrapolated from these local studies, and there are very few examples of comparisons of grazing effects between regions with contrasting climates and/or evolutionary histories of herbivory (Bock *et al.*, 1995; Adler *et al.*, 2004). Because of this, the validity of many hypothesized trait responses to grazing remains untested at the global level. None of the studies that focus on grazing from a global perspective (Milchunas *et al.*, 1988; Milchunas & Lauenroth, 1993; Briske, 1996; Landsberg *et al.*, 1999) have explicitly tested the generality of plant trait responses to grazing over a range of environments.

Current conceptual models of trait response to grazing provide a framework of our analysis of the global-level consistency of associations between plant attributes and responses to grazing. Of the models available, we restrict our framework to (1) those models that offer explicit predictions of plant trait responses to grazing; and (2) only those predictions that could be tested, at least partially, with the published data available. The conceptual models considered lead to predictions about specific plant trait responses to grazing. These predictions vary in the extent to which they reflect common knowledge among range managers and scientists. Our analyses enable some of the predictions (Table 1) to be tested objectively using a global dataset.

The first model of plant trait response to grazing is the range-succession model (Dyksterhuis, 1949; Arnold, 1955). The range-succession model predicts an increase in annual plant cover and a decrease of perennials with grazing, replacement of palatable plants by unpalatable ones, and replacement of tall and midheight grasses by short grasses, subshrubs, and perennial prostrate forbs. The range-succession model assumes that these patterns are universal and unaffected by differences in the characteristics of different regions.

In contrast, the generalized model of Milchunas *et al.* (1988) focuses on the idea that precipitation (proxy for productivity) and grazing history influence plant community response. This model assumes that aridity and grazing select the same plant attributes. In humid habitats, however, canopy competition and grazing select opposite attributes. As a result, changes promoted by grazing should be maximal in humid systems with a short history of grazing. With a long history of grazing, grazing response should be minimal in dry systems for some traits (e.g. life history), but maximum in humid systems for other traits (e.g. height, habit).

A third group of models are based on the idea of plant strategies (i.e. general adaptations to resource capture, use and release, and recognize disturbance, of which grazing is a particular case, within their context disturbance is simply removal of biomass) as

**Table 1** Summary of plant attributes favoured by grazing according to six models (see text for description)

Models	Traits								
	Sources	Factors	Life history	Canopy height	Habit	Architecture	Growth form	Palatability	Origin
Generalized	Milchunas <i>et al.</i> (1988), Milchunas & Lauenroth (1993)	Climate, history	Annual, more marked in humid systems	Short, more marked in systems that are humid and with long grazing history	Prostrate, more marked in systems with long herbivory history, both humid and dry, most marked in humid systems with long history	Stoloniferous, more marked in systems with long herbivory history, both humid and dry, most marked in humid with long history	Graminoid	-	Exotics in systems with short herbivory history both humid and dry, but most marked in humid systems
Range-succession	Dyksterhuis (1949), Arnold (1955)	None	Annual	Short	Prostrate	Rosette, stoloniferous	Forb, woody	Low	-
CSR	Grime (1977, 1990, 2001)	Climate*	Annual, more marked in humid systems	Short, more marked in dry systems	Prostrate, more marked in dry systems	-	-	Low in dry systems, high in humid systems	-
LHS	Westoby (1998, 1999)	None	-	Short	-	-	-	-	-
Resource availability	Coley <i>et al.</i> (1985), Herms & Mattson (1992)	Climate*	-	-	-	-	-	Low in dry systems, high in humid systems	-
Physiological	Briske & Richards (1995), Briske (1996)	None	-	Short	Prostrate	Stoloniferous	-	Low in dry systems, high in humid systems	-

\*These models do not explicitly deal with dry vs. humid climates. The equation of dry with unproductive and humid with productive is ours (see 'Methods'). Columns 3-8 refer to factors and traits that were explicitly considered by different models in their original formulation and for which we could gather enough information. For example, specific leaf area is a prominent trait in Grime's (1977, 1990, 2001) and Westoby's (1998, 1999) models, but we did not find enough case studied reporting it. The description of the predicted plant attributes refers to the *response to grazing*, rather than the abundance of that attribute under particular environmental conditions. For example, the prostrate habit may be predicted to become more abundant in response to grazing in humid systems with a long evolutionary history of herbivory, even though that habit may be generally more common in dry systems than in humid systems.

an important regulator of plant traits. The other major factor is stress, which limits biomass production. Prominent examples of this approach are the models of Grime (1977, 1990, 2001) and Westoby (1998, 1999). Grime's CSR model distinguishes three principal plant strategies: Competitor, Stress-tolerator and Ruderal. Grazing selects plants with a ruderal (short-lived, small-sized, fast-growing) strategy. However, in dry systems stress-tolerators (small, prostrate, perennial) are also favoured. Similarly, grazing should lead to shorter plants, especially in dry systems. Palatability should increase in response to grazing in humid systems (grazing tolerance, involving fast regrowth of high-quality tissue with very low structural defence), and should decrease in dry systems (grazing avoidance, involving slow-growing tissue, rich in structural defence).

Westoby's (1998) LHS (leaf-height-seed) model is based on similar considerations to Grime's CSR model, but includes only three traits, specific leaf area, canopy height and seed mass. Westoby (1999) adapted this model to grazing response by examining which plant attributes were favoured by different grazing intensities. According to this model, moderate, selective grazing favours unpalatable plants, whereas heavy, nonselective grazing favours palatable plants. Plant response to grazing is not explicitly influenced by climate or evolutionary history of grazing.

The resource availability (Coley *et al.*, 1985) and related models (e.g. growth-differentiation model, see Herms & Mattson, 1992 and references therein) include the interactive effects of productivity and herbivory, and are based on the trade-off between plant allocation to the production of new photosynthetic tissue and antiherbivore defence. Like Grime's CSR model, the resource availability model predicts that grazing will select an avoidance strategy in dry (less-productive) systems, and a tolerance strategy through increased growth in humid systems. Herms & Mattson (1992) suggest that the stronger the historical impact of grazing, the stronger the plant investment into grazing avoidance, but in general these models do not explicitly address the effects of evolutionary history of grazing.

Finally, it has been argued that predictions about trade-offs between tolerance and avoidance strategies could also be reached via detailed investigation of physiological mechanisms underlying plant response to grazing within a single system, with no need to consider the effects of climate or evolutionary history (Briske & Richards, 1995; Briske, 1996). We refer to this approach as the 'physiological' model.

The CSR and resource availability models distinguish between productive and unproductive systems without reference to the determinants of productivity (e.g. water

or nutrient availability). In this study, we draw from the generalized model, and treat dry systems as a special case of unproductive systems. We base this on evidence of the general convergence of plant attributes in floras where the proximate cause of low productivity is water or nutrient availability (Díaz *et al.*, 2004).

This paper presents a synthesis of 197 grazing studies from a wide range of biomes across all inhabited continents. In it, we compare world wide, a range of studies of plant trait responses to grazing, within a standard framework and using a common set of descriptors. The aim of this synthesis was to address the following questions:

1. Do plant traits that are commonly accepted as being associated with grazing, behave consistently as expected when examined at a global scale?
2. Are associations between plant traits and grazing dependent upon regional patterns of precipitation and/or evolutionary history of herbivory?
3. Are the most commonly used conceptual models of plant trait response to grazing supported at a global scale?
4. Is the incorporation of grazing into global or regional models of vegetation dynamics justified? If so, which plant traits should be used to enhance them?

## Methods

### *Data sources*

We compiled and analysed literature from: Africa, Australia and New Zealand, Central Asia, North America, the Eastern and Western Mediterranean region, Northern and Central Europe and South America. The studies described in this literature cover different biomes including grasslands, managed pastures, savannahs, shrublands, tundra deserts and several types of woodland (Table 2). In the analysis, and following Lavorel *et al.* (1997), we distinguished between plant traits (e.g. canopy height, habit) and their attributes (i.e. the categories of traits, such as tall, short, erect, prostrate, etc.). Our focus was on plant trait responses to grazing and so we did not consider the papers whose sole focus was changes in biogeochemical processes or those containing taxonomic composition information that could not readily be translated into individual plant attributes.

In our data collection, we distinguished between publications, studies, and observations. Publications presented results of one or more studies of the effects of grazing (including browsing) on species richness and/or plant attributes. Some publications provided only site information so that a study or observation

**Table 2** Summary of primary sources included in the dataset

Evolutionary history of herbivory Precipitation category	Long (113; 673)		Short (45; 331)	
	Dry (58, 211)	Humid (89, 462)	Dry (27, 178)	Humid (23, 153)
Africa (21, 67)	14, 41	7, 26	–	–
Australasia (28, 292)	–	–	9, 147	19, 145
Central Asia (5, 28)	5, 28	–	–	–
Mediterranean region (30, 259)	10, 44	20, 215	–	–
North America (45, 100)	12, 38	13, 28	18, 31	2, 3
Northern and Central Europe (37, 137)	4, 14	31, 118	–	2, 5
South America (31, 121)	13, 46	18, 75	–	–

Figures indicate number of studies, observations in each category.

See 'Methods' and Appendix B for definitions of precipitation and grazing history categories.

could be supported by more than one publication. Each study was a dataset representing an independent investigation of the responses to certain traits within a certain context (e.g. a comparison between different grazing regimes at one site and/or along a certain time sequence). Each observation was an identified response (positive, neutral or negative) in species richness or abundance of an attribute to two levels of grazing. Individual publications provided one or more studies, each containing one or (generally) more observations. In total, our dataset contained 1004 observations, belonging to 197 studies, reported in 194 publications (Table 2, Appendix A). In order to standardize the information, we used a proforma that included an exhaustive list of ancillary and response variables (Appendix B).

#### *Variables used as covariates in the comparison of trait response*

Precipitation [as a proxy for aboveground net primary productivity (ANPP)] and evolutionary history of herbivory by ungulates have been considered variables of paramount importance in previous work (Milchunas *et al.*, 1988; Milchunas & Lauenroth, 1993; Díaz *et al.*, 2001). We used two categories of precipitation (dry/humid, following Köppen, 1918), and two categories of grazing history (long, short; Table 2). The different biomes were classified as having long or short evolutionary history of grazing by large mammals on the basis of the duration of occupation by wild and domestic ungulates and/or similar mammalian herbivores according to van der Hammen (1983) (Africa), Atkinson & Greenwood (1989) and Landsberg *et al.* (1999) (Australasia), Zimov *et al.* (1995) (Central Asia), Edelstein & Milevsky (1994) (Mediterranean region), Milchunas & Lauenroth (1993) (North America), Agustí & Antón (2002) (Europe) and Franklin (1982) and Borrero (1996) (South America).

Ideally, we would have used ANPP rather than precipitation as a covariate, but the latter is more readily available. Precipitation is well correlated with herbaceous ANPP up to 900–1000 mm yr<sup>-1</sup> (Lauenroth, 1979; Milchunas & Lauenroth, 1993). This relationship is weaker in more humid systems where low temperatures cause very low evapotranspiration. Only about 3.2% of the observations in our dataset were from systems that were, or were likely to be, both humid and unproductive (ANPP <300 g m<sup>-2</sup> yr<sup>-1</sup>). These cases were well spread among regions (although there was no case in Africa, Central Asia and the Mediterranean region) and so were unlikely to bias the results. Thus, we believe that using precipitation as a proxy for ANPP is justified for the purposes of our analyses. Obviously, we could not find examples of all possible combinations of grazing history and precipitation regime in every region. Because of the typically large scale of operation of these processes, most regions had only one level of grazing history, and many were characterized by a single precipitation category (Table 2). Other ancillary variables (see Appendix B) were reported in too few studies for statistical analysis.

#### *Selection of plant traits and response variables*

The selection of plant traits was based on the works of Weiher *et al.* (1999), and Díaz *et al.* (2001). The initial search comprised 20 morphological, anatomical and physiological traits, but only six of these produced enough observations for statistical analysis. These were: life history (annual, perennial), canopy height (short, tall), habit (erect, prostrate), architecture (leafy stem, rosette, stoloniferous, tussock), growth form (forb, graminoid, herbaceous legume, woody) and palatability (palatable, unpalatable). Palatability had sufficient cases for analysis only when various forms of unpalatability (tough vs. tender, nonpalatable vs. palatable, good vs. poor forage, toxic, prickly, etc.) were pooled

together in the same trait. Although not a physical plant trait, geographic origin (native vs. exotic) was also included because the spread of potentially invasive exotic plants into new habitats and its relationship to grazing is relevant for theoretical (Milchunas *et al.*, 1988; Stohlgren *et al.*, 1999) and practical (Mooney & Hobbs, 2000) reasons. Abundance data were available for all seven traits. Frequency, biomass, cover and density were all accepted forms of abundance. Species richness (the total number of species having a particular attribute) data were available for three traits (life history, growth form, origin).

Only ca. 35% of the observations contained quantitative measurements or significance tests, and they were very unevenly distributed among regions and combinations of precipitation and history of grazing. Therefore, in order to take full advantage of the literature, we included reports of responses with and without statistical testing, including qualitative reports of the direction of change. Once this dataset was compiled, we searched for changes in response to grazing in the abundance and species richness of plants bearing certain attributes. We made no attempt to separate direct (e.g. defoliation) and indirect effects (e.g. competitive release and other community-mediated mechanisms) of grazing on plants. Plant responses can vary considerably depending on grazing intensity (e.g. Naveh & Whittaker, 1979; Milchunas *et al.*, 1988; Westoby, 1989), but many authors simply describe differences between 'grazed' and 'ungrazed' situations, without defining whether grazing intensity was heavy or light. Therefore, in this study, we simply compared grazed vs. ungrazed situations. Where more than one grazing treatment was studied we used the most extreme ones (lightest vs. heaviest) for our analysis. When absolute values of abundance were recorded for a single attribute within a trait, then no information could be derived for the alternative attribute(s). When, on the other hand, the records were relative values more than one record could be derived and included in the dataset (e.g. annual increase and perennial decrease).

### Statistical analysis

We carried out a meta-analysis in the sense of applying formal statistical methods to the *post-hoc* analysis of a large collection of results from individual studies (Gurevitch & Hedges, 1999). We used a vote-counting technique because few of the compiled studies were suitable for the calculation of effect size. We constructed multiple contingency tables considering, for each trait and response variable (abundance or species richness), the different attributes (rows) and directions of response (columns). Within the cells, we considered the

frequency of positive, neutral or negative responses to grazing of plants bearing each attribute. Precipitation category and history of grazing were used as covariates to control for their effects on the association of interest (between trait and direction of response). We also used regions as a covariate to control for their effects on the association of interest (between trait and direction of response). The results were not strongly driven by any particular region, as region effects were mainly explained by precipitation and history categories.

We analysed the multiple contingency tables using the Cochran–Mantel–Haenszel General Association (CMH) test and the Maximum Likelihood  $\chi^2$  ( $G^2$ )-statistic (Agresti, 2002) for the partial tables (for each herbivory history and precipitation category combination). The CMH test was run controlling for the effects of grazing history and precipitation category to determine whether different combinations of these factors influenced the association between attributes and *direction of response to grazing*.

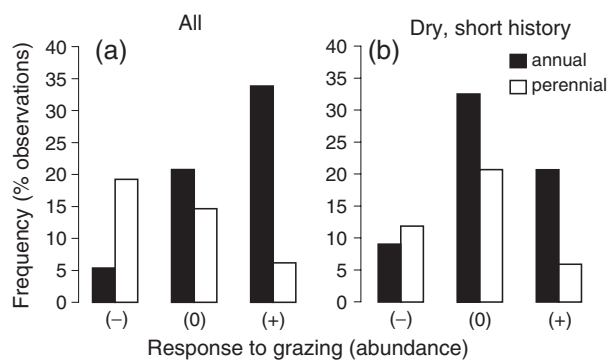
Changes in species richness were reported less frequently than changes in abundance. Only in the cases of life history and origin did we find sufficient species richness data to run meaningful tests for at least one of the combinations of precipitation and history of grazing. Frequently, the total number of cases was acceptable, but their distribution into precipitation  $\times$  history categories was markedly uneven creating empty categories and preventing us from performing tests (Appendix C).

## Results

All associations between the direction of response to grazing and plant traits were considered at the global scale and under the different combinations of precipitation and evolutionary history of grazing. These are presented as contingency tables in Appendix C. The most ecologically significant patterns are highlighted below.

### Life history

For plant abundance, there was a significant global association between the direction of response to grazing and life history. Positive responses by annual plants to grazing, and negative responses by perennial plants, were reported more frequently than other responses under all combinations of precipitation and herbivory history (Fig. 1a). The exception to this was dry systems with a long evolutionary history of herbivory (e.g. Mediterranean semiarid grasslands, American short-grass steppe, some African systems), in which no significant pattern was detected (Fig. 1b).

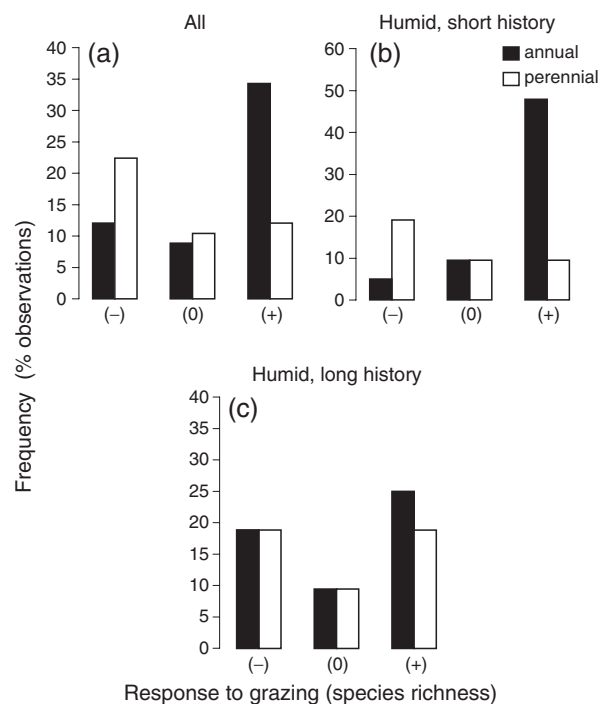


**Fig. 1** Relative frequency of observations in which the abundance of annual and perennial plants decreased (-), did not change (0) or increased (+) with grazing. (a) Considering all sites, and controlling for the effects of precipitation (dry or humid) and evolutionary history of grazing (short or long);  $P < 0.0001$ ,  $n = 130$ ; Cochran–Mantel–Haenszel Association test. (b) In dry systems with long evolutionary history of grazing;  $P = 0.353$ ,  $n = 34$ ;  $G^2$ -test.

The species richness of annuals and perennials was responsive to grazing across all sites, with observations of annuals increasing and perennials decreasing with grazing being the most frequent (Fig. 2a). Positive responses of annuals to grazing were more marked in humid systems but, within this precipitation category, the response seemed to depend on evolutionary history of herbivory. In humid systems with a short history of grazing, positive responses of annual plants to grazing and negative responses of perennial plants, were reported most frequently (Fig. 2b). In contrast, in humid systems with a long history, the pattern of responses of species richness to grazing did not differ significantly between annual and perennial plants (Fig. 2c). In the case of dry sites, there were insufficient data in either category of grazing history to calculate the  $G^2$ -statistic (Appendix C).

### Canopy height

Globally there was a significant association between the direction of response to grazing and plant height. Positive responses of short plants and negative responses of tall plants were reported most frequently in all systems (Fig. 3a), except in dry systems with a short evolutionary history (e.g. some Australian sites), where response to grazing did not differ significantly between short and tall plants (Fig. 3b). The general trend of positive response of short plants and negative response of tall plants was more marked in systems with a long history of grazing than in those with a short history (Fig. 3c and d). The trends observed in dry and humid systems were similar in direction and magnitude.



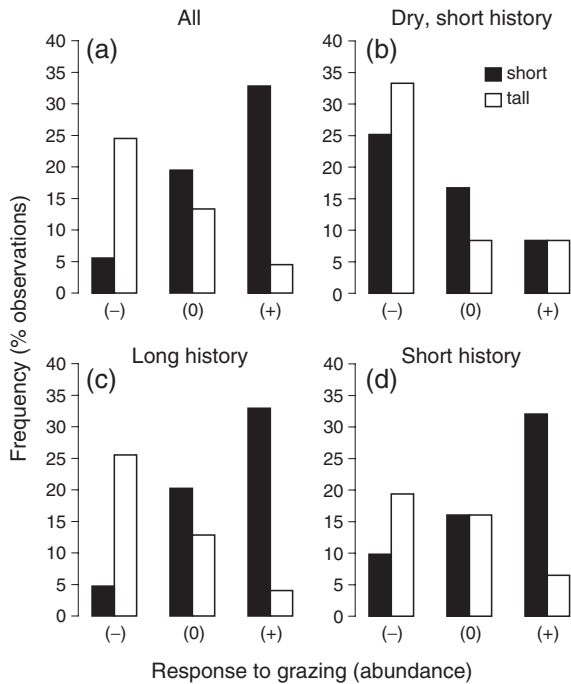
**Fig. 2** Relative frequency of observations in which the richness of annual and perennial plants decreased (-), did not change (0) or increased (+) with grazing. (a) Considering all sites, and controlling for the effects of precipitation (dry or humid) and evolutionary history of grazing (short or long);  $P = 0.013$ ,  $n = 65$ ; Cochran–Mantel–Haenszel Association test. (b) In humid systems with short evolutionary history of grazing;  $P = 0.038$ ,  $n = 21$ ;  $G^2$ -test. (c) In humid systems with long evolutionary history of grazing;  $P = 0.922$ ,  $n = 32$ ;  $G^2$ -test.

### Habit

Globally, there was a significant association between the direction of response to grazing and habit. In all systems erect plants tended to respond negatively to grazing, and prostrate plants tended to respond positively (Fig. 4). Trends observed in dry and humid systems were similar in direction, but those in dry systems were weaker and only marginally significant. Trends in short- and long-history systems were similar in direction and magnitude. There were insufficient observations to reject the null hypothesis in dry sites with a short history of herbivory or to analyse dry sites with a long history of herbivory.

### Architecture

There was a significant association between the direction of response to grazing and shoot architecture. Positive responses of rosettes and stoloniferous plants, and negative responses of tussock graminoids were reported most frequently (Fig. 5a). There was no consistent trend



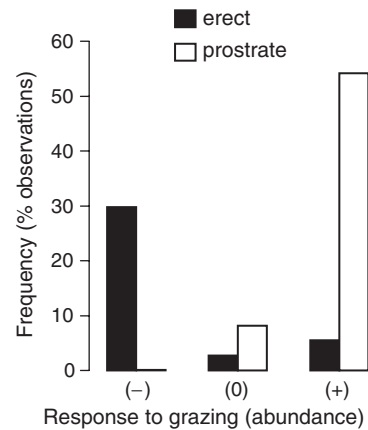
**Fig. 3** Relative frequency of observations in which the abundance of plants with different height decreased (–), did not change (0), or increased (+) with grazing. (a) Considering all observations, and controlling for the effects of precipitation (dry or humid) and evolutionary history of grazing (short or long);  $P < 0.0001$ ,  $n = 180$ ; Cochran–Mantel–Haenszel Association test. (b) In dry systems with short evolutionary history of grazing;  $P = 0.785$ ,  $n = 12$ ;  $G^2$ -test. (c) In systems with long evolutionary history of grazing;  $P < 0.0001$ ,  $n = 149$ ;  $G^2$ -test. (d) In systems with short evolutionary history of grazing;  $P = 0.049$ ,  $n = 31$ ;  $G^2$ -test.

in the response of plants with leafy stems. These global relationships were influenced mostly by sites from humid systems (crf. Fig. 5b and c) and systems with a long history of grazing (crf. Fig. 5d and e). There were insufficient data to run the analysis in the dry sites with a long history and humid sites with a short history.

When only graminoids were considered, the tendencies described above were maintained. Positive response of stoloniferous graminoids, and negative response of tussock graminoids to grazing were reported most frequently (Fig. 5f). Again, these results were driven mostly by humid systems and systems with a long history of grazing. There was no significant trend in dry systems and there were insufficient short-history cases for analysis. When only forbs were considered, no significant trend of response of rosettes vs. plants with leafy stem was detected.

#### Growth form

Globally, there was a significant association between the direction of response to grazing and growth form

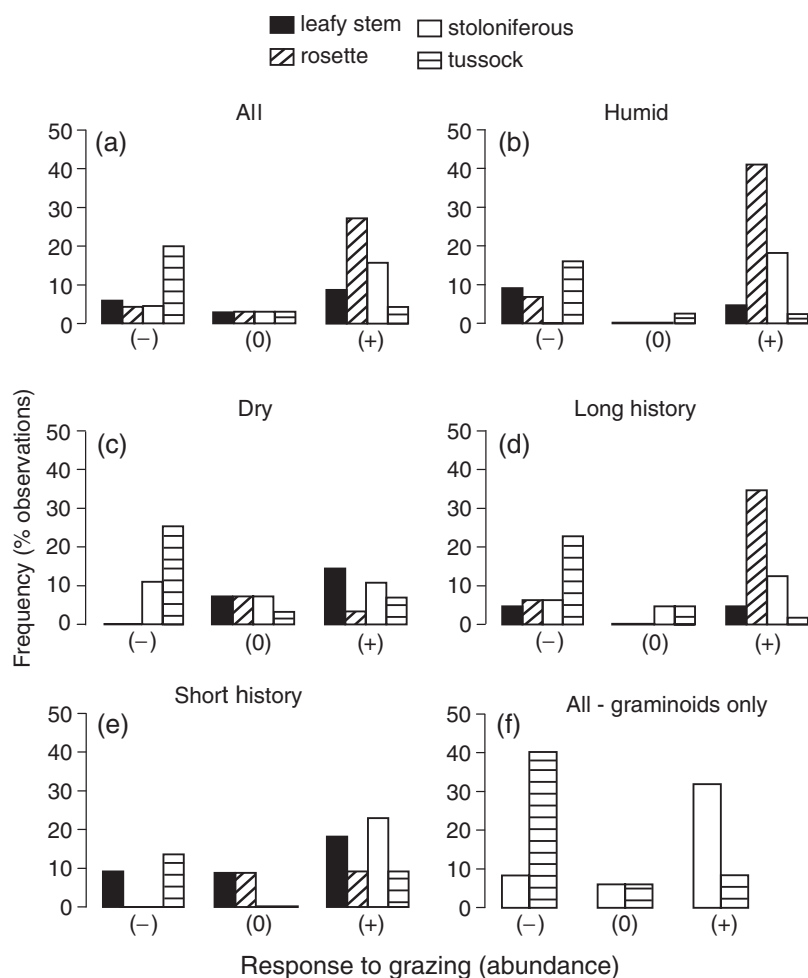


**Fig. 4** Relative frequency of observations in which the abundance of plants with different habit decreased (–), did not change (0), or increased (+) with grazing, considering all observations, and controlling for the effects of precipitation and evolutionary history of grazing;  $P < 0.0001$ ,  $n = 37$ ; Cochran–Mantel–Haenszel Association test.

(Fig. 6). Forbs and woody species most frequently showed neutral responses to grazing, whereas graminoids had predominantly neutral or negative responses. There was insufficient information to draw conclusions on the response of herbaceous legumes. The association between response to grazing and growth form remained significant among different combinations of precipitation and grazing history, except for humid systems with short herbivory history that displayed no significant trend. The direction of the response of the woody growth form was the least consistent across climate and history combinations. However, the most common response of woody plants to grazing was a neutral response, both at the level of the entire dataset (Fig. 6) or under different combinations of precipitation and evolutionary herbivory history.

#### Palatability

We detected a significant association between the direction of response to grazing and palatability, with an increase in unpalatable plants being most frequently reported ( $P = 0.005$ , Appendix C). However, most observations came from systems with a long grazing history and so we cannot say whether this relationship holds under other conditions. In addition, when examining individual combinations of precipitation and grazing history, this result appeared to be accounted for by the bias of the data towards dry systems with a long herbivory history (mainly African). In regions with a long history and humid climate the relationship was not significant.



**Fig. 5** Relative frequency of observations in which the abundance of plants with different architecture (leafy stem, stoloniferous, tussock) decreased (-), did not change (0), or increased (+) with grazing. (a) Considering all observations, and controlling for the effects of precipitation (dry or humid) and evolutionary history of grazing (short or long);  $P = 0.002$ ,  $n = 71$ ; Cochran-Mantel-Haenszel Association test. (b) In humid systems;  $P < 0.001$ ,  $n = 44$ ;  $G^2$ -statistic. (c) In dry systems;  $P = 0.032$ ,  $n = 27$ . (d) In systems with long evolutionary history of grazing;  $P < 0.001$ ,  $n = 49$ . (e) In systems with short evolutionary history of grazing;  $P = 0.040$ ,  $n = 22$ . (f) Considering only graminoids with different architecture (stoloniferous, tussock), taking into account all observations, and controlling for the effects of precipitation and evolutionary history of grazing;  $P = 0.002$ ,  $n = 35$ ; Cochran-Mantel-Haenszel Association test.

### Origin

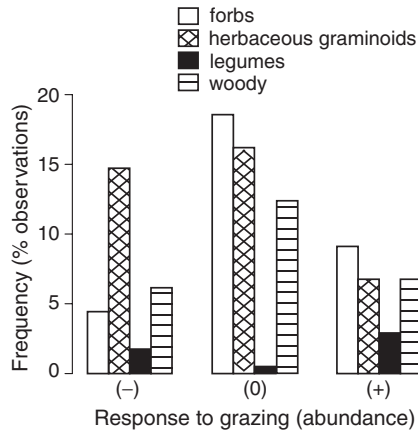
The association between origin and the direction of grazing response was not significant. The most common response to grazing was no change in the richness of both native and exotic species. In the case of abundance, however, there was a weak trend for a positive response of exotic plants and a negative response of native plants to grazing. The lack of clear trends may result from the low number of observations (23). These observations were strongly biased towards humid systems with short history of grazing (mostly Australasian systems), and even in this subset of observations the trend was not significant. No test could be run for

the other combinations of precipitation and grazing history.

### Discussion

#### Data and publication biases

Our knowledge of the effect of grazing at a global scale is restricted to a surprisingly small number of plant traits. Even for these basic traits, there were insufficient data to adequately test all combinations of precipitation and history of herbivory. Data availability varied markedly across regions for several reasons. Regional studies



**Fig. 6** Relative frequency of observations in which the abundance of plants with different growth forms (forbs, graminoids, legumes, and woody plants) decreased (–), did not change (0), or increased (+) with grazing, considering all observations and controlling for the effects of precipitation (dry or humid) and evolutionary history of grazing (short or long);  $P < 0.0001$ ,  $n = 341$ ; Cochran–Mantel–Haenszel Association test.

naturally focus on locally important traits and attributes and so do not record less important traits in a systematic way. Traits or attributes that are absent, or do not vary much, are ignored. For example, 74% of our data on exotics came from humid regions with a short evolutionary history of herbivory where exotic invasions are a conservation issue. Similarly, data on unpalatable plants are collected where they are a problem, for example in Africa and Australia. Such failures to report on specific traits represent a serious obstacle for literature-based syntheses in general (Díaz *et al.*, 2002). In addition, because of biogeographical reasons, some combinations of grazing history and climate are more frequent than others in the planet. This is an unavoidable constraint in most global-scale studies, and available statistical techniques can overcome it only to a certain degree. However, the consistency among independent studies is encouraging. For example, for dry areas with short herbivory history the findings of Milchunas & Lauenroth (1993) and those of this study are in agreement, despite the fact that the former is biased towards North American sites, and the latter towards Australian sites. We conclude that more investigations of plant trait responses to grazing are needed that follow a common framework and are conducted in a variety of locations (Díaz *et al.*, 2002). Using common lists of traits across research groups would ensure standardization of trait measurement in different systems of the world. This would alleviate the problem of unreported responses, or lack of response because species with the relevant attribute are simply absent. Publications describing consensus trait lists (e.g. Weiher

*et al.*, 1999), and standard methods of measurement are available (Cornelissen *et al.*, 2003; Knevel *et al.*, 2005). Shortlists of traits that should be favoured or disfavoured by grazing under different environmental contexts, with implications for ecosystem functioning, have also been proposed (Coley *et al.*, 1985; Grime *et al.*, 1996), and validated in a small number of studies (Pérez-Harguindeguy *et al.*, 2003; Duru *et al.*, 2004). Chief among these traits are leaf nitrogen content, toughness and specific area. These traits are also implicated in primary productivity, nutrient cycling and trophic transfer (e.g. Lavorel & Garnier, 2002; Díaz *et al.*, 2004; Garnier *et al.*, 2004), and are applicable from the local to the transcontinental scale (Díaz *et al.*, 2004; Wright *et al.*, 2004). Substantial progress can also be made by reanalysing existing species-based studies. For example, the abundant phytosociological data on responses of plant communities to grazing available from Europe could be reanalysed incorporating information from the trait datasets available (e.g. Fitter & Peat, 1994; Hodgson *et al.*, 1995; Knevel *et al.*, 2003).

#### *Global and context-specific patterns of trait response to grazing*

Despite the inherent limitations of the data our results show that there are traits that exhibit consistent response to grazing, provided that the general context (e.g. climate and evolutionary history of herbivory) is taken into account. We can, therefore, use these results to assess whether predictions of the different conceptual models of plant trait response to grazing (Table 1) are supported at the global scale (Table 3).

*Life history.* In general, annuals are favoured by grazing and perennials are disadvantaged. This is consistent with the predictions of the range-succession, generalized, and CSR models. Although dry regions with a short evolutionary history of grazing conformed to this pattern, dry regions with a long history showed no consistent pattern in annuals and perennials. The prediction of the CSR and generalized models that the increased abundance of annuals should be more marked in humid systems is confirmed by our results.

*Canopy height.* Grazing favours short plants irrespective of climate and grazing history. This is consistent with the predictions of all the models. There is no evidence that short plants are more favoured by grazing in dry systems, as suggested by the CSR model. Rather, the response to grazing appeared more marked in humid systems and in systems with a long herbivory history, as predicted by the generalized model.

**Table 3** Summary of plant trait responses to grazing under different combinations of precipitation and herbivory history

Trait	Is there any overall effect of grazing on the trait, controlling for precipitation and history?	Does precipitation by itself influence the direction of the response to grazing?	Does history of herbivory by itself influence the direction of the response to grazing?	Do different combinations of history and precipitation influence the direction of response to grazing?
Life history (abundance)	Yes	No	No	Yes (neutral response most frequent in dry + long history)
Life history (sp. richness)	Yes	Uncertain	Yes	Yes (ns difference in humid + long history)
Canopy height (abundance)	Yes	No	Uncertain	Yes (ns difference in dry + short history)
Habit (abundance)	Yes	No	No	Uncertain
Architecture (abundance)	Yes	Uncertain	Uncertain	na
Growth form (abundance)	Yes	No	Yes	Yes (ns difference in humid + short history)
Growth form (sp. richness)	No	na	na	na
Palatability (abundance)	Yes	Yes	Uncertain	na
Origin (abundance)	Uncertain	na	na	na
Origin (sp. richness)	No	na	na	na

'Uncertain' denotes that a trend existed, but it may have been nonsignificant due to small sample size, or that changes under different situations occurred in the same direction, but were much stronger in one case than in the other; na, not assessed due to lack of data. See text and Appendix C for details.

*Habit.* Grazing promotes increases in prostrate plant abundance and decreases in erect plants. This supports the predictions of the range-succession, generalized, CSR and physiological models. There is no indication that responses are stronger in dry systems, as predicted by the CSR model. Again, the response seems marginally stronger in humid systems and in systems with long herbivory history, as predicted by the generalized model. The low significance values obtained for dry and short-history systems may reflect small sample sizes.

*Architecture.* Grazing increases the abundance of stoloniferous and rosette plants. The increase in stoloniferous plants is a prediction of all the models that dealt with architecture (Table 1). The results also support the prediction of the generalized model that this effect is stronger in humid sites with long herbivory history.

*Growth form.* According to our results, grazing does not uniformly favour forbs, graminoids or woody species. Only two models provide explicit predictions of the impact of grazing on growth form. Neither the prediction of the range-succession model that forb and woody species abundance increases with grazing nor the prediction of the generalized model (Milchunas & Lauenroth, 1993) that graminoids increase with grazing is supported by this study. Instead, our results suggest that neutral responses of both groups are widespread. It is evident from the conflicting predictions that this is a complex issue, and while we have detected different responses in different systems, it appears that 'graminoids' as a functional group is too general. The analysis of architecture within graminoids shows negative responses of tussocks and positive responses of stoloniferous grasses, suggesting a wide range of grazing responses within this broad group.

The fact that grazing does not favour woody species, with neutrality being the most common response in our study, seems surprising considering the extensive literature on woody encroachment (e.g. Milchunas & Lauenroth, 1993; Scholes & Archer, 1997; Skarpe, 2000; but see Vesk *et al.*, 2004). Grazing did not increase shrub abundance even in dry rangelands for which the prediction is most commonly made (e.g. Milton *et al.*, 1994), perhaps because cases of grazing-induced shrub encroachment are balanced by cases where grazing-sensitive shrubs are reduced by grazing. Other explanations may be irreversible shrub increases (Westoby *et al.*, 1989), or the alternation of positive and negative interactions between herbaceous and woody plants at different life cycle stages in a mosaic landscape (Olff *et al.*, 1999). Finally, changes in grazing

and woody vegetation are intimately linked with changes in fire regimes, so that it may not be possible to distinguish the separate rather than synergistic effects of climate, fire and grazing (Bond *et al.*, 2003).

*Palatability.* Grazing leads to increases in unpalatable plants, and the effect is stronger in dry systems than in humid systems. This is consistent with the predictions of all four conceptual models that included palatability. This trend however seems to be driven mostly by dry systems with long herbivory history. Fewer studies in dry regions with short herbivory history (e.g. Landsberg *et al.*, 2002; Vesk *et al.*, 2004) have analysed palatability. The evidence from studies in humid regions with long herbivory history was inconclusive. This seems to disagree with the theory and observations that in productive areas with a long herbivory history, grazing increases the abundance of palatable plants (e.g. McNaughton, 1984). However, this discrepancy may partly result from the pooling together of palatability traits and so our results do not provide clear-cut evidence of the effect of grazing history on palatability.

*Origin.* There were too few studies available to obtain solid conclusions on the impact of grazing on exotic plant invasion. However, as predicted by the generalized model exotics tended to increase under grazing in regions with a short history of herbivory, particularly in humid climates. The model predicts relatively less invasion by exotics under grazing where there has been a long herbivory history, but there were insufficient data to test this.

Our results supported all five conceptual models of plant trait response to grazing at the global scale. However, the generalized model was the one which best explained the patterns observed under different combinations of climate and herbivory history. There was no case where the direction of the response was changed, but response strength varied depending on climate and herbivory history. In total, our results suggest that response to grazing is modulated by these two interacting factors. Although the influence of productivity on plant grazing response has been widely recognized (e.g. Proulx & Mazumder, 1998; Milchunas & Noy-Meir, 2002), that of herbivory history has been largely ignored and very few empirical studies have taken it into consideration (e.g. Naveh & Whittaker, 1979; Milchunas & Lauenroth, 1993; Díaz *et al.*, 2001; Milchunas & Noy-Meir, 2002; Adler *et al.*, 2004; Cingolani *et al.*, 2005). Our results indicate that a conceptual framework for the investigation of plant trait response to grazing, both

under specific regional situations and as part of transregional comparisons, should incorporate both climatic and historical contexts.

#### *Implications for plant functional classifications for large-scale vegetation models*

Our study, the first meta-analysis to assess plant trait responses to grazing at a worldwide scale, suggests that (1) plant trait responses to grazing could improve the ability of current large-scale vegetation models; and (2) care should be taken when attempting to project vegetation response to climate in grazed ecosystems, as these two factors interact in driving the functional composition of vegetation.

What would be the minimum set of traits that would allow us to incorporate plant responses to grazing in predictions of climate change impacts? On the basis of Table 3, we confirm that the distinction between woody and herbaceous plants made by current large-scale models is useful and that a minimum set of easily accessible traits for herbaceous plants should include life history and height or habit. The distinction between woody and herbaceous plants is included in DGVMs, but the models generally do not subdivide herbaceous plants on the basis of life histories or height (see e.g. Prentice *et al.*, 2007). Leaf traits of shrubs, such as leaf size, specific area and toughness are important to capture climatic response (Barboni *et al.*, 2004), and possibly for grazing response and effects on biogeochemistry. However no leaf trait could be analysed in this study due to the paucity of data. Among herbaceous plants, grasses are often classified in global models as C3 vs. C4 (e.g. Cramer *et al.*, 2001). Subgroups should distinguish within these two main climatically and biogeochemically relevant groups to account for grazing response. A minimal classification would divide the C3 and C4 groups into annual vs. perennial, and then within each of these subgroups, distinguish between tussock vs. stoloniferous grasses.

Our study also indicates that to incorporate grazing impacts in climate change predictions it seems necessary to develop rules for specific climate regimes (e.g. dry vs. humid climates). Given that differences in response between dry and humid climates are thought to reflect ANPP (Milchunas *et al.*, 1988; Milchunas & Lauenroth, 1993), it would also be possible to formulate rules as functions of model-simulated ANPP in the absence of grazing (potential vegetation). Our analyses indicate that it will also be necessary to map grazing histories globally in order to predict the correct response to grazing. This seems feasible provided broad categories are applied. However, more detailed information on grazing regime (e.g. frequency, intensity)

**Table 4** Plant functional types proposed for inclusion in DGVMs that take grazing into consideration

Humid – long grazing history*	Humid – short grazing history*†	Dry – long grazing history*	Dry – short grazing history*†
Woody evergreen	Woody evergreen	Woody evergreen	Woody evergreen
Woody deciduous	Woody deciduous	Woody deciduous	Woody deciduous
Graminoid short C <sub>3</sub> annual prostrate	Graminoid short C <sub>3</sub> annual prostrate	Graminoid short C <sub>3</sub>	Graminoid C <sub>3</sub> annual prostrate
Graminoid short C <sub>3</sub> annual erect	Graminoid short C <sub>3</sub> annual erect	Graminoid short C <sub>4</sub>	Graminoid C <sub>3</sub> annual erect
Graminoid short C <sub>3</sub> perennial prostrate	Graminoid short C <sub>3</sub> perennial prostrate	Graminoid tall C <sub>3</sub>	Graminoid C <sub>3</sub> perennial prostrate
Graminoid short C <sub>3</sub> perennial erect	Graminoid short C <sub>3</sub> perennial erect	Graminoid tall C <sub>4</sub>	Graminoid C <sub>3</sub> perennial erect
Graminoid short C <sub>4</sub> annual prostrate	Graminoid short C <sub>4</sub> annual prostrate	Forb short prostrate	Graminoid C <sub>4</sub> annual prostrate
Graminoid short C <sub>4</sub> annual erect	Graminoid short C <sub>4</sub> annual erect	Forb short erect	Graminoid C <sub>4</sub> annual erect
Graminoid short C <sub>4</sub> perennial prostrate	Graminoid short C <sub>4</sub> perennial prostrate	Forb tall	Graminoid C <sub>4</sub> perennial prostrate
Graminoid short C <sub>4</sub> perennial erect	Graminoid short C <sub>4</sub> perennial erect		Graminoid C <sub>4</sub> perennial erect
Graminoid tall C <sub>3</sub> annual	Graminoid tall C <sub>3</sub> annual		Forb annual prostrate
Graminoid tall C <sub>3</sub> perennial	Graminoid tall C <sub>3</sub> perennial		Forb annual erect
Graminoid tall C <sub>4</sub> annual	Graminoid tall C <sub>4</sub> annual		Forb perennial prostrate
Graminoid tall C <sub>4</sub> perennial	Graminoid tall C <sub>4</sub> perennial		Forb perennial erect
Forb short annual prostrate	Forb short annual prostrate		
Forb short annual erect	Forb short annual erect		
Forb short perennial prostrate	Forb short perennial prostrate		
Forb short perennial erect	Forb short perennial erect		
Forb tall annual	Forb tall annual		
Forb tall perennial	Forb tall perennial		

Relevant functional types are listed for each climate × grazing history category. See text for further explanation.

\*There was not sufficient data in our database to assess whether the distinction between erect and prostrate forbs was relevant in any of the combinations of climate and grazing history.

†There was no significant difference in the grazing responses of erect and prostrate graminoids, but the number of cases was low. Therefore, and taking a conservative approach, their inclusion is suggested until more information is available.  
 DGVM, Dynamic global vegetation model.

may be needed for finer-scale regional assessments (Cingolani *et al.*, 2005).

In practice, we propose a three-step approach to refining plant functional type (PFT) classifications of DGVMs in order to account for grazing response and effects. First, ANPP needs to be simulated using classical life form and phenology/metabolism based classifications, yielding a global or regional map of ANPP. This could then be reclassified into two productivity categories using an agreed threshold (e.g. Milchunas *et al.*, 1988; Milchunas & Lauenroth, 1993). Second, a four category map of productivity  $\times$  grazing history would be obtained by combining this productivity map with a map of grazing history (short and long). As a third and final step, a different set of relevant PFTs could be applied to each climate  $\times$  grazing history combination, on the basis of our results (Table 4). The relevant PFTs listed in Table 4 were obtained by subdividing, for each category of regional climate  $\times$  grazing history, the PFTs based on combinations of life form and phenology that are commonly used by DGVMs. The traits used for subdivision within each PFT were those shown as significant by our analyses for each climate  $\times$  grazing history category. The additional traits for herbaceous plants were: life form, life history, plant height, and architecture. Under dry climates the number of relevant traits, and therefore of PFTs, was reduced, especially with a long grazing history. Region-specific PFTs have already been implemented in some DGVMs (e.g. Barboni *et al.*, 2004), suggesting that the incorporation of these refinements in future developments should not pose serious technical challenges.

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## Appendix A

List of publications used as primary sources of data.

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## Appendix B

Proforma utilized in data gathering, standardization and codification.

*Region:* Africa, Australasia, Central Asia, Mediterranean, North America, Northern and Central Europe, South America.

#### *Latitude and longitude*

*Latitudinal category:* tropical, temperate, austral, boreal. Tropical-temperate boundary, 25°; temperate-boreal, 60°; temperate-austral, 45°.

#### *Annual precipitation (mm)*

*Precipitation category* according to Köppen (1918): Dry, humid.

*Seasonality of rainfall:* summer, winter, rainfall evenly distributed throughout the year.

#### *Evolutionary history of herbivory*

*Long history:* continuous occupation by ungulates and/or similar large (>25 kg) mammalian herbivores since at least the Pleistocene (ca. 10 000 years ago), including the presence of domestic or semidomestic ungulates since at least ca. 4000 years ago (e.g. Africa, Mediterranean, Andean South America), and the presence of wild herbivores (e.g. North America east of the Rocky Mountains, non-Andean South America).

*Short history:* wild ungulates absent since before the Pleistocene; or their presence discontinued in the Pleistocene; occupation by large (wild or domestic) mammalian herbivores occurred for the first time less than 4000 years ago (e.g. Australasia, North America west of the Rockies).

*Soil type:* sandy, clayey, gravelly, loamy, organic.

*Soil nutrient content:* nitrogen and phosphorus content.

*Productivity:* aboveground net primary productivity or standing biomass.

*Stocking rate:* number of animals per ha.

*% consumption:* what proportion of the ANPP is consumed by the herbivores.

*Grazing frequency:* frequency and duration of grazing at the site.

*Grazing pressure:* no grazing; light/moderate (selective); heavy (mostly nonselective).

*Type of grazer:* cattle, goats, Camelidae, etc.

*Response variable:* variable on which the effects of grazing are measured (e.g. cover of annual vs. perennial plants, richness of prostrate vs. erect species).

*Response direction:* increase (+) or a decrease (–) in the response variable in the face of grazing.

*Response mean:* % change of the mean as a response of grazing (e.g. grazing is associated with 20% reduction of plant height).

*Response variance:* variance (or other estimator of dispersion, such as standard deviation or standard error) for the response variable.

*P-value:* corresponding to test performed to assess differences in response value as a result of grazing.

*Degrees of freedom:* Corresponding to test performed to assess differences in response value as a result of grazing.

## Appendix C

*Contingency tables.* The values in the response columns correspond to relative frequency of observations documenting a negative (–), neutral (0) or positive (+) response to grazing of the abundance or richness of plants bearing the attribute listed in each row (with 100% being N, or the total number of observations in each contingency table). *P* corresponds to the Cochran–Mantel–Haenszel Association test (CMH) in the case of comparisons involving all sites (and controlling for precipitation and grazing history), and to the Likelihood Ratio  $\chi^2$  test ( $G^2$ ) in the case of comparisons, which involve particular categories of precipitation and/or evolutionary history of grazing. In both CMH and  $G^2$  tests, the null hypothesis was that the direction of response to grazing was not associated with a specific trait. Rejection of the null hypothesis meant that plant species with some attributes were more abundant or more common than plants with other attributes within the trait. Being unable to reject the null hypothesis meant that directions of response to grazing were not significantly different between the trait attributes. In all cases df, (number of possible grazing responses – 1)  $\times$  (number of attributes in a trait – 1); the degrees of freedom are the same for the comparisons involving all sites or individual combinations corresponding to each trait, NC, not computable, either because there were too few observations or the sum of one or more rows or columns in the table was zero. Table A1

Table A1

	Response				P	df
	N	(-)	(0)	(+)		
<i>Life History – abundance</i>						
All Sites	130				<.00001	2
Annual		5.38	20.77	33.85		
Perennial		19.23	14.62	6.15		
Dry	78				0.005	
Annual		5.13	26.92	24.36		
Perennial		15.38	20.51	7.69		
Humid	52				<.00001	
Annual		5.77	11.54	48.08		
Perennial		25	5.77	3.85		
Short history	63				<.00001	
Annual		1.59	19.05	36.51		
Perennial		22.22	14.29	6.35		
Long History	67				0.004	
Annual		8.96	22.39	31.34		
Perennial		16.42	14.93	5.97		
Dry + short History	44				0.006	
Annual		2.27	22.73	27.27		
Perennial		18.18	20.45	9.09		
Dry + long history	34				0.353	
Annual		8.82	32.35	20.59		
Perennial		11.76	20.59	5.88		
Humid + short history	19				<.00001	
Annual		0	10.53	57.89		
Perennial		31.58	0	0		
Humid + long history	33				0.009	
Annual		9.09	12.12	42.42		
Perennial		21.21	9.09	6.06		
<i>Life History – spp. Richness</i>						
All sites	65				0.019	2
Annual		11.94	8.96	34.33		
Perennial		22.39	10.45	11.94		
Dry	12				0.002	
Annual		0	8.33	41.67		
Perennial		33.33	16.67	0		
Humid	53				0.169	
Annual		13.21	9.43	33.96		
Perennial		18.87	9.43	15.09		
Short history	26				0.009	
Annual		3.85	11.54	42.31		
Perennial		19.23	15.38	7.69		
Long history	41				0.309	
Annual		17.07	7.32	29.27		
Perennial		24.39	7.32	14.63		
Dry + short history	5				NC	
Dry + long history	7				NC	
Humid + short history	21				0.038	
Annual		4.76	9.52	47.62		
Perennial		19.05	9.52	9.52		
Humid + long history	32				0.922	
Annual		18.75	9.38	25		
Perennial		18.75	9.38	18.75		

(contd.)

Table A1. (Contd.)

	Response				P	df
	N	(-)	(0)	(+)		
<i>Canopy Height – abundance</i>						
All Sites	180				<0.0001	2
Short		5.56	19.44	32.78		
Tall		24.44	13.33	4.44		
Dry	62				0.008	
Short		11.29	16.13	27.42		
Tall		25.81	9.68	9.68		
Humid	118				<.00001	
Short		2.54	21.19	35.59		
Tall		23.73	15.25	1.69		
Short history	31				0.05	
Short		9.68	16.13	32.26		
Tall		19.35	16.13	6.45		
Long history	149				<.00001	
Short		4.7	20.13	32.89		
Tall		25.5	12.75	4.03		
Dry + short history	12				0.785	
Short		25	16.67	8.33		
Tall		33.33	8.33	8.33		
Dry + long history	50				0.006	
Short		8	16	32		
Tall		24	10	10		
Humid + short history	19				0.011	
Short		0	15.79	47.37		
Tall		10.53	21.05	5.26		
Humid + long history	99				<.00001	
Short		3.03	22.22	33.33		
Tall		26.26	14.14	1.01		
<i>HABIT – abundance</i>						
All Sites	37				<.00001	2
Erect		29.73	2.7	5.41		
Prostrate		0	8.11	54.05		
Dry	6				0.088	
Erect		16.67	16.67	0		
Prostrate		0	16.67	50		
Humid	31				<.00001	
Erect		32.26	0	6.45		
Prostrate		0	6.45	54.84		
Short history	10				0.005	
Erect		30	10	0		
Prostrate		0	10	50		
Long History	27				<.00001	
Erect		29.63	0	7.41		
Prostrate		0	7.41	55.56		
Dry + Short History	5				0.138	
Erect		20	20	0		
Prostrate		0	20	40		
Dry + Long History	1				NC	
Humid + Short History	5				<.00001	
Erect		40	0	0		
Prostrate		0	0	60		
Humid + long history	26				<.00001	
Erect		30.77	0	7.69		

(contd.)

Table A1. (Contd.)

	Response				P	df
	N	(-)	(0)	(+)		
Prostrate		0	7.69	53.85		
<i>Architecture – abundance</i>						
All sites	71				0.002	6
Leafy stem		5.63	2.82	8.45		
Rosette		4.23	2.82	26.76		
Stoloniferous		4.23	2.82	15.49		
Tussock		19.72	2.82	4.23		
Dry	27				0.032	
Leafy stem		0	7.41	14.81		
Rosette		0	7.41	3.7		
Stoloniferous		11.11	7.41	11.11		
Tussock		25.93	3.7	7.41		
Humid	44				<0.001	
Leafy stem		9.09	0	4.55		
Rosette		6.82	0	40.91		
Stoloniferous		0	0	18.18		
Tussock		15.91	2.27	2.27		
Short history	22				0.040	
Leafy stem		9.09	9.09	18.18		
Rosette		0	9.09	9.09		
Stoloniferous		0	0	22.73		
Tussock		13.64	0	9.09		
Long history	49				<0.001	
Leafy stem		4.08	0	4.08		
Rosette		6.12	0	34.70		
Stoloniferous		6.12	4.08	12.24		
Tussock		22.45	4.08	2.04		
Dry + short history	15				0.006	
Leafy stem		0	13.33	26.67		
Rosette		0	13.33	0		
Stoloniferous		0	0	20		
Tussock		20	0	6.67		
Dry + long history	12				NC	
Humid + short history	7				NC	
Humid + long history	37				<0.001	
Leafy stem		5.41	0	5.41		
Rosette		8.11	0	43.24		
Stoloniferous		0	0	16.22		
Tussock		18.92	2.7	0		
<i>Architecture – graminoids only, abundance</i>						
All sites	35				0.002	
Stoloniferous		8.57	5.71	31.43		
Tussock		40.00	5.71	8.57		
Dry	18				0.374	
Stoloniferous		16.67	11.11	16.67		
Tussock		38.89	5.56	11.11		
Humid	17				<0.001	
Stoloniferous		0	0	47.06		
Tussock		41.18	5.88	5.88		
Short history	10				NC	
Long history	25				0.014	
Stoloniferous		12.00	8.00	24.00		
Tussock		44.00	8.00	4		

(contd.)

Table A1. (Contd.)

	Response				P	df
	N	(-)	(0)	(+)		
Dry + short history	7				NC	
Dry + long history	11				0.411	
Stoloniferous		27.27	18.18	0		
Tussock		36.36	9.09	9.09		
Humid + short history	3				NC	
Humid + long history	14				<0.0001	
Stoloniferous		0	0	42.86		
Tussock		50.00	7.14	0		
<i>Architecture – forbs only, abundance</i>						
All sites	36				0.204	
Rosette		8.33	5.56	52.78		
leafy stem		11.11	5.56	16.67		
Dry	9				NC	
Humid	27				NC	
Short history	12				0.351	
Rosette		0	16.67	16.67		
Leafy stem		16.67	16.67	33.33		
Long history	24				NC	
Dry + short history	8				NC	
Dry + long history	1				NC	
Humid + short history	4				NC	
Humid + long history	23				NC	
<i>Growth form – abundance</i>						
All Sites	341				<0.0001	6
Forb		4.4	18.48	9.09		
Graminoid		14.66	16.13	6.74		
Herbaceous legume		1.76	0.59	2.93		
Woody		6.16	12.32	6.74		
Dry	200				<0.0001	
Forb		3.5	19	7		
Graminoid		15.5	21	4		
Herbaceous legume		1.5	0	2		
Woody		4	15.5	7		
Humid	141				0.048	
Forb		5.67	17.73	12.06		
Graminoid		13.48	9.22	10.64		
Herbaceous legume		2.13	1.42	4.26		
Woody		9.22	7.8	6.38		
Short history	120				0.180	
Forb		3.33	21.67	5.83		
Graminoid		6.67	28.33	4.17		
Herbaceous legume		1.67	0.83	1.67		
Woody		4.17	20	1.67		
Long history	221				<0.0001	
Forb		4.98	16.74	10.86		
Graminoid		19	9.5	8.14		
Herbaceous legume		1.81	0.45	3.62		
Woody		7.24	8.14	9.5		
Dry + short history	81				0.016	
Forb		1.23	27.16	2.47		
Graminoid		6.17	37.04	0		
Herbaceous legume		0	0	1.23		
Woody		0	22.22	2.47		

(contd.)

Table A1. (Contd.)

	N	Response			P	df
		(-)	(0)	(+)		
Dry + long history	119				0.002	
Forb		5.04	13.45	10.08		
Graminoid		21.85	10.08	6.72		
Herbaceous legume		2.52	0	2.52		
Woody		6.72	10.92	10.09		
Humid + short history	39				0.130	
Forb		7.69	10.26	12.82		
Graminoid		7.69	10.26	12.82		
Herbaceous legume		5.13	2.56	2.56		
Woody		12.82	15.38	0		
Humid + long history	102				0.007	
Forb		4.9	20.59	11.76		
Graminoid		15.69	8.82	9.8		
Herbaceous legume		0.98	0.98	4.9		
Woody		7.84	4.9	8.82		
<i>Growth form – spp. richness</i>						
All sites	64				0.094	6
Forb		10.94	14.06	15.63		
Graminoid		17.19	20.31	3.13		
Herbaceous legume		0	0	1.56		
Woody		6.25	6.25	4.69		
Dry	19				NC	
Humid	45				0.056	
Forb		8.89	15.56	15.56		
Graminoid		15.56	24.44	4.44		
Herbaceous legume		0	0	2.22		
Woody		8.89	4.44	0		
Short history	22				NC	
Long History	42				0.002	
Forb		9.52	16.67	16.67		
Graminoid		16.67	26.19	0		
Herbaceous legume		0	0	2.38		
Woody		4.76	0	7.14		
Dry + short history	6				NC	
Dry + long history	13				NC	
Humid + short history	16				NC	
Humid + long history	29				0.007	
Forb		3.45	24.14	13.79		
Graminoid		10.34	37.93	0		
Herbaceous legume		0	0	3.45		
Woody		6.9	0	0		
<i>Palatability – abundance</i>						
All sites	52				0.005	2
Palatable		28.85	13.46	5.78		
Unpalatable		11.54	13.46	26.93		
Dry	29				<.00001	
Palatable		24.14	24.14	0		
UnPalatable		0	20.69	31.03		
Humid	23				0.344	
Palatable		34.78	0	13.04		
Unpalatable		26.09	4.35	21.74		
Short history	8				0.062	
Palatable		25	25	0		

(contd.)

Table A1. (Contd.)

	Response				P	df
	N	(-)	(0)	(+)		
Unpalatable		0	25	25		
Long History	44				0.015	
Palatable		29.55	11.36	6.82		
Unpalatable		13.64	11.36	27.27		
Dry + short history	8				0.062	
Palatable		25	25	0		
Unpalatable		0	25	25		
Dry + long history	21				<0.001	
Palatable		23.81	23.81	0		
Unpalatable		0	19.05	33.33		
Humid + short history	0				NC	
Humid + long history	23				0.344	
Palatable		34.78	0	13.04		
Unpalatable		26.09	4.35	21.74		
<i>Origin – abundance</i>						
All sites	22				0.156	2
Exotic		8.7	21.74	47.83		
Native		17.39	4.35	0		
Dry	8				NC	
Humid	14				0.016	
Exotic		7.14	28.57	28.57		
Native		28.57	7.14	0		
Short history	14				0.013	
Exotic		7.14	21.43	35.71		
Native		28.57	7.14	0		
Long history	8				NC	
Dry + short history	3				NC	
Dry + long history	5				NC	
Humid + short history	10				0.080	
Exotic		10	20	20		
Native		40	10	0		
Humid + long history	4				NC	
<i>Origin – spp. richness</i>						
All sites	48				0.524	2
Exotic		6.12	28.57	22.45		
Native		8.16	22.45	12.24		
Dry	2				NC	
Humid	46				0.470	
Exotic		4.35	28.26	21.74		
Native		8.7	23.91	13.04		
Short history	43				0.522	
Exotic		4.65	30.23	18.6		
Native		9.3	25.58	11.63		
Long history	5				NC	
Dry + short history	0				NC	
Dry + long history	2				NC	
Humid + short history	43				0.513	
Exotic		4.65	30.23	18.6		
Native		9.3	25.58	11.63		
Humid + long history	3				NC	