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ORIGINAL PAPER

Long-term response of plant communities to herbivore exclusion at high elevation grasslands

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Abstract Understanding the effects of herbivores on plant communities is needed for anticipating how variation in grazing regimes will impact natural and semi-natural ecosystems. Prominent ecological hypotheses predict that drastic reductions of herbivory, as have occurred in many European mountains, will trigger fast diversity loss and structural changes in grasslands, because grazing tolerant species are expected to be rapidly replaced by taller and more competitive species. The aims of this study were to test generalizations of herbivory effects (mostly from lowlands) in high elevation grasslands over ecological relevant times scales, and to unravel the contribution of climatic conditions to observed changes. Species richness, canopy height, plant community structure, and transition probabilities among ecological groups were monitored throughout 19 years in herbivore exclusions and control plots in the Central Pyrenees. We used ordination analyses to track the long-term community response to herbivore exclusion, and generalized additive models

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to assess the non-linear effects of herbivore exclusion and climatic conditions on measured variables. Contrary to expectations, herbivore exclusion did not significantly affect species richness, and although canopy height increased, it was not drastic enough to suppress shade intolerant species. The strongest shifts in plant community structure and transition probabilities between ecological groups occurred during a sequence of warm and dry growing seasons, whereas in control plots, these changes were smaller, and largely reversed after cooler and wetter climatic conditions returned. Our results suggest that long-term effects of grazing cessation in high elevation grasslands can be weaker and slower than predicted. However, these effects can act synergistically with dry and warm events. Therefore, the maintenance of past grazing activities can be key in the face of ongoing climatic warming.

Keywords Alpine · Community monitoring · Generalized Grazing Model · Grassland management · Land abandonment · Land-use change

Introduction

Understanding the community effects of herbivory is a pivotal issue for the management of healthy plant communities. Many human activities shift the pattern of herbivore effects in both natural and semi-natural ecosystems worldwide. Therefore, these effects are of particular concern for understanding the optimal management of domestic herbivores as well as for defining conservation policies (Noy-Meir et al. 1989; Westoby et al. 1989; Hobbs and Huenneke 1992). In some areas, the main management question is how to lessen grazing pressure (e.g. Zhao and Zhou 1999), while in others, economic shifts have resulted in rapid reduction of herbivory that may have equally negative effects on plant diversity and foraging value of grasslands (e.g. Wells 1969; Stohlgren 1999; Tasser and Tappeiner 2002).

While herbivory has been one of the most intensively studied ecological interactions (McNaughton 1985; Milchunas et al. 1988; Huntly 1991), ecologists have crafted a wide range of sometimes opposing generalities about herbivore effects on plant communities and when and why these effects will be strong or weak (Milchunas et al. 1988; Westoby et al. 1989; Olff and Ritchie 1998; Proulx and Mazumder 1998). During the last decades, the Generalized Grazing Model (GGM) has provided the most prominent theoretical framework for understanding the variable impact of herbivory across different plant communities (Oesterheld and Semmartin 2011). The GGM is largely based on the hump shaped response of plant richness to disturbance (i.e. grazing) predicted by the 'Intermediate Disturbance Hypothesis' (Grime 1973). However, the GGM suggests that the strength of the response of plant communities to grazing will be different across gradients of precipitation and evolutionarily history of grasslands. In particular, the GGM predicts that competition between plant species shifts from soil resources to light along gradients of humidity (Milchunas et al. 1988), and primary productivity (Cingolani et al. 2005). Therefore, largest effects of herbivory on plant richness are expected in sub-humid and/or productive areas (Milchunas et al. 1988; Milchunas and Lauenroth 1993). The model also predicts that plant communities with long grazing histories will rapidly shift in response to large changes in grazing intensity, because they have evolved under divergent selection for grazing and canopy dominance, and developed pools of native species adapted to different levels of herbivory. Given that non-resilient species were eliminated from the initial species pool long ago, the predicted structural changes are likely to be more reversible than those occurring in communities with a short grazing history (Cingolani et al. 2005).

Empirical support for the GGM is mostly from low elevation grasslands and shrublands (Milchunas and Lauenroth 1993), whereas the herbivore impact on high elevation grasslands remains relatively less thoroughly studied (Erschbamer et al. 2003). This fact contrasts with the key role that wild and domestic herbivores play on the maintenance of highly valuable ecological and cultural landscapes at high elevations (Austrheim and Eriksson 2001; Chemini and Rizzoli 2014; Fillat et al. 2008), which in some cases are alarmingly endangered (Habel et al. 2013). In European mountains, the shift in socio-economic conditions of rural societies has weakened seasonal grazing to historical minimums, including the complete abandonment of many pastures (García-Ruiz et al. 1996; Luick 1998; MacDonald et al. 2000, Zervas 1998). As a result, forest and shrubs have encroached into semi-natural grasslands (Welch and Scott 1995; Gehrig-Fasel et al. 2007; Améztegui et al. 2010; Pajunen et al. 2012), and even more drastic changes to these ecosystems have been predicted (Sala et al. 2000).

Several studies conducted to address the specific impact of cessation of grazing on mountains have reported a decline in species richness (Rawes 1981; Tasser and Tappeiner 2002; Niedrist et al. 2008; Speed et al. 2013), whereas a few others have shown no changes in species richness, but rapid changes in the community composition and structure (Hill et al. 1992; Hope et al. 1996; Krahulec et al. 2001; Mayer et al. 2009). The lack of consistent results along with the particularly slow response of alpine plant species (Evju et al. 2009) limit our current understanding of the long-term effects of grazing reductions. To further complicate matters, the land-use change is coincident with climate warming in mountains (Dessens and Bücher 1997; Beniston 2006). As disentangling their separate effects is not easy under natural conditions, the interaction between these two drivers of change is still understudied at high elevation. However, this gap needs to be addressed to forecast the biological consequences of grazing reduction and to guide successful management of high elevation grasslands, particularly in the face of ongoing climate change.

In this study, we experimentally assess the long-term impacts of herbivore exclusion on plant species richness, canopy height, and relative abundance of species in some of the most common grassland communities of the Pyrenees (Fillat et al. 2008). The studied grasslands can be defined as sub-humid (annual precipitation $\sim$1700) and long grazing history systems (Chocarro et al. 1990) following the classification criteria used in Milchunas and Lauenroth (1993). For this sort of grasslands, the GGM predicts a rapid shift in community structure towards taller and more competitive species in response to grazing cessation, and in some cases, a decline in species richness via competitive exclusion (Milchunas et al. 1988). If a few dominant grasses increase at the expense of forbs and shade intolerant grasses, we would also expect a decline in species richness (Milchunas et al. 1988; Hobbs and Huenneke 1992) and pasture value for livestock (Crawley 1983). We also expect that structural and diversity impacts of herbivore exclusion will be faster and more dramatic if climate-induced migration of high competitive lowland species (e.g. shrubs) alters the pool of available species (Olofsson et al. 2009; Speed et al. 2012). In contrast, whether climate-driven impacts would alter the equilibrium composition of grazed grasslands is more uncertain (Vittoz et al. 2009), and will depend on whether climate can override the effects of herbivory (Post and Pedersen 2008).

Methods

Study site

The study sites were located in the Ordesa-Monte Perdido National Park, Central Pyrenees, Spain (42°40′18″N, 0°3′20″E). This mountain park extends along five valleys radiating from the highest calcareous summit in Europe (3355 m a.s.l.), covering an elevational gradient of ~2400 m. Subalpine and alpine grasslands cover more than one third of the total area of the National Park (15608 Ha.), and have been used as summer pastures for livestock since at least the fifteenth century (Fillat et al. 2008), and probably into ancient pre-history. However, this traditional land-use has been dramatically modified owing to socio-economic shifts in the Pyrenean region during the last century, with the total number of domestic herbivores (mainly sheep) drastically diminished since the 1950s (García-Ruiz et al. 1996; Aldezabal 1997).

In 1992, two exclosures of 144 m^2 each were established to assess the effect of grazing abandonment on plant diversity and community composition and structure in high elevation grasslands. They were selected to represent the two most abundant types of grasslands along the Pyrenees (Fillat et al. 2008): *Bromion erecti* (henceforth Bromion) and *Nardion strictae* (henceforth Nardion). The former harbors high species richness (>40 sps) and plants of high fodder value (e.g. *Lotus corniculatus, Medicago suffruticosa and Trifolium* spp.) whereas the latter has lower species richness (<20), is usually dominated by the tussock-forming grass *Nardus stricta,* and poorer in terms of nutrient quality (Gómez 2008). In both communities *Festuca nigrescens* was the most abundant species at the beginning of the study. For Bromion communities, the mean aboveground net primary production was 483 g of dry matter per m^{-2} $year^{-1}$, and 378 for Nardion (García-González et al. 2002). Such values correspond to productive grasslands following the classification criteria of the GGM in Milchunas and Lauenroth (1993). Exclosures are located in a flat area (1930 m a.s.l.) 600 and 450 m distant from the nearest subalpine forest limit and shrubland, respectively, and separated each other by 125 m. The area was frequently visited by domestic herbivores (mostly cattle) for summer pasturing (from July to October) and a very few wild ungulates. Activity of other small herbivores (e.g., marmots and moles) was negligible in study area. The stocking rate was relative high throughout the study: 0.79 LU ha^{-1} (1LU = 1.25 cow = eight sheep) (Aldezabal et al. 1992).

The monitored grasslands share most topographic and environmental features, such as N aspect, length of vegetative period (Del Barrio et al. 1990), mean annual temperature (5 °C) and precipitation (~1700 mm). However, edaphic conditions were different: the soil of Bromion was basic, high permeable and with moderate levels of organic matter, whereas that of Nardion was acidic (pH 4), humic, with high levels of organic matter and water retaining capacity (Badía et al. 2002).

Climatic data

We gathered daily temperature, precipitation, and snow depth records between 1982 and 2012 from the nearby Góriz Meteorological Station (42°39’49′’N, 00°00′50′’E; 2215 m a.s.l.). In 2006, we also set up a Station at the Nardion site, which was used to validate the temperature records from Góriz, and to fill the gaps in the temperature series. We calculated the mean, maximum and minimum temperature, and the mean thermal sum (measured in degree days) for each year, summer (from June to September), snow free period, and growing season, defined as the span between the snow melt-out and the exact date of vegetation sampling (between July 28th and August 1st). For each of these periods, we also calculated the accumulated precipitation.

Vegetation sampling

Between 1993 and 2012 (with the exception of 1999), we annually monitored the vegetation community within the exclosures by using the point intercept method along two perpendicular transects (10 m long each) at each site. At each semi-permanent sample point ($n = 200$, spaced every 10 cm along the transects), we recorded the height and species of the tallest plant. When the point was not covered (e.g. bare soil, dung, or litter), it was registered as a 'non-plant'. Control transects were also established outside the exclosure, where the same sampling procedure was applied. This yielded a total of 400 sample points per site. The abundance of each species was calculated as the number of points covered by the species out of the total number of points per treatment (exclosure *vs* control). The sum of the heights of all recorded plant individuals was used as a surrogate of canopy height. Community structure was defined according to the composition and abundance of species.

Although the beginning and end of transects were permanently marked with sticks, we could not assume that each sample point was exactly relocated every year. Even if we did, it is unlike that the same plant individuals were always recorded, due to the small size of plants, their architecture, microtopography, and simple inaccuracy. While inaccuracy does not influence the relative abundance estimates, it might result in serious sampling error for analyses that track transitions between plants at each point (Conway-Cranos and Doak 2011). To account for such potential bias, we estimated the sampling error in point relocation, following Conway-Cranos and Doak (2011). One of the two transects at each control site was successively resampled three times in a single day in 2011. Each time, we removed and replaced the transects to reproduce the alignment process in annual resampling. Using the resulting data in combination with the annual sampling allowed us to correct transition estimates for sampling uncertainty (Conway-Cranos and Doak 2011).

Data analyses

Climate trends in annual mean temperature and precipitation were tested with the Mann–Kendall test (Mann 1945; Kendall 1975). For vegetation analyses, we first analyzed the effect of grazing exclusion on species richness, canopy height and abundance of dominant species over the 19 years by using the following Generalized Additive Model (GAM; Wood 2006; Hastie and Tibshirani 1990):

$$y_i = \alpha + \beta \text{ treatment } + f(x_i)\text{treatment} + \varepsilon_i \qquad ([1])$$

where y is the response variable in year i, α the intercept, β the factor indicating the treatment (control *vs* herbivore exclusion), $f(x_i)$ the smooth function of time, and ε_i the random error. Species richness and the abundance of dominant species were initially modeled using Poisson distribution, whereas data on canopy height was log transformed to fit into a Gaussian distribution. The effect of the grazing exclusion was evaluated as a smooth function of time by using cubic splines (Wood 2006) and the number of knots were selected from three to a maximum of five, iteratively. When we observed that an increase in the number of knots did not lead to a better explanation of the residuals, we selected the lowest number to minimize model overfitting (Wood 2006). Given that annual data within each plot is used as an independent sample, clearly, our sampling design is pseudo-replicated (with one single plot per treatment in each site), so *P* values may be inaccurate. For such reason, *P* values higher than 0.01 were not considered as significant. We used the same approach for testing the interactive effect of climate and herbivore exclusion by substituting the 'time' variable in Eq. (1) with temperature and/or precipitation variables. Inclusion of interaction effects between climatic variables was infeasible because of limited sample size. From the set of candidate climatic variables (see above), we selected thermal sum and accumulated precipitation during the growing season based upon their explanatory power (i.e. the proportion of deviance explained by the model).

To assess the effect of herbivory on the community structure over our 19 years of data, we performed a non-multidimensional scaling ordination based on the species abundances and the Bray-Curtis dissimilarity measure (Bray and Curtis 1957), comparing the trajectories of community structure in exclusion and control plots. Although the Bray-Curtis is a robust measure of plant community response (Faith et al. 1987), the use of any other

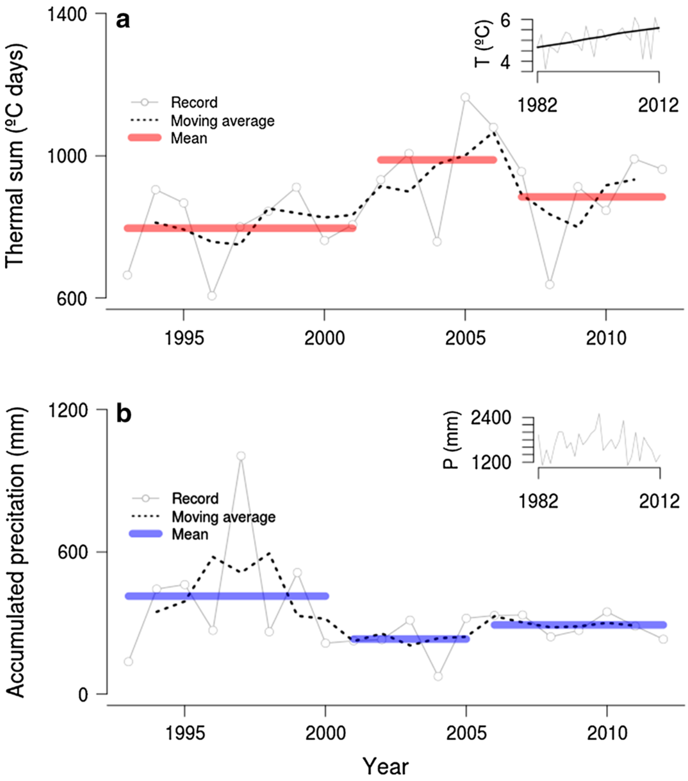

Fig. 1 Trends of thermal sum (**a**) and accumulated precipitation (**b**) in the growing season in the Ordesa-Monte Perdido National Park for the last decades. Moving averages (3-years fixed interval) of these variables indicate a warmer period between 2002 and 2006, and a dry period between 2001 and 2005. On average, corresponding bracketing time periods were cooler and more humid, respectively (*horizontal lines*). Embedded subplots show records of mean annual temperature (**a**) and precipitation (**b**) between 1983 and 2012. The *black line* indicates a significantly increasing trend in annual temperature ($P < 0.05$) according to the Mann–Kendall trend test

dissimilarity measures would lead to different ordination results (Anderson et al. 2006), and thus, to different interpretations. To assess the robustness of the observed trajectories of communities, we repeated ordination analyses with (i) two other dissimilarity measures (Euclidean and Horn-Morisita; Horn 1966), (ii) only common species, and (iii) incidence data (see Online Resource 1).

To further characterize the dynamics of grazed and ungrazed communities we used community transition models (Horn 1975; Hill et al. 2004). Because of the high number of species and specific functional groups (geophytes, rosette forbs) with low values at both sites, model construction with individual species or specific functional groups was problematic. Therefore, we decided to parameterize models using four ecological classes: (1) the dominant grass *F. nigrescens,* which was the only tall species (>35 cm based on field averaged field records); (2) other non-dominant grasses; (3) forbs; and (4) non-plants (i.e. bare soil, dung and litter). Non-dominant grasses were long-lived hemicriptophytes with similar leaf morphology, plant propagation and dispersal syndromes, whereas forbs were mostly dominated by highly palatable and small size hemicriptophytes. Nevertheless, and given the existent heterogeneity mostly within forbs (e.g. legumes, rosette forbs, thistles, all of which appeared in very low abundance), transition analyses were only used to identify broad effects of herbivory exclusion, such as gap creation or colonization (Non-plants ↔ other plants), competition relaxation (Dominant grass → other plants), stability (transition within groups) and ecological changes (Forbs ↔ Grasses). Transition probabilities between each set of groups were estimated using the approach of Conway-Cranos

Table 1 Summary of generalized additive models used to test the effect of herbivore exclusion and climate on species richness and log-transformed canopy height across 19-years

Response variable	Site	Predictor variable	Treatment parameter	Smooth term				Deviance explained (%)
				Control		Exclusion		
				Edf	Statistic	Edf	Statistic	
Species richness	Bromion	Year	−0.12	1	0.02	1	1.28*	40.7
		T_{sum}	−0.12	1	0.21	1	0.88	38.5
		P_{acc}	−0.12	1	0.06	1	0.63	35.0
	Nardion	Year	−0.14	1	1.07	1	0.72	48.6
		T_{sum}	−0.14	1	0.01	1	1.05	40.3
		P_{acc}	−0.14	1	0.98	1	0.10	41.2
Canopy height	Bromion	Year	0.69***	1.95	1.63	2.85	5.65**	78.6
		T_{sum}	0.69***	1.70	6.92**	1.77	1.23	75.7
		P_{acc}	0.69***	1	0.77	2.69	0.88	66.3
	Nardion	Year	0.32***	2.47	1.73	1	6.78*	50.4
		T_{sum}	0.32***	1.86	3.07	1.82	0.43	45.2
		P_{acc}	0.32***	1	2.06	1	1.50	35.7

Models were formulated using herbivore exclusion as a treatment, and time, growing thermal sum (T_{sum}) and accumulated precipitation (P_{acc}) as predictor variables. Cubic splines were used to account for potential non-linear relationships, with a maximum degrees of freedom of the model (edf) set to five to avoid overfitting. Note that test statistics of the smooth terms are *F* and Chi squared statistics for species richness' and canopy height's models, respectively

***$P < 0.001$; **$P < 0.01$; *$P < 0.05$

and Doak (2011). Estimation of error-corrected transition rates were conducted using Matlab programs modified from Conway-Cranos and Doak (2011). All other analyses were conducted using R 2.14.1 (R Development Core Team 2011), and ‘kendall’ (http://www.stats.uwo.ca/faculty/aim/), ‘mgcv’ (Wood 2006) and ‘vegan’ (Oksanen et al. 2013) R-packages.

Results

Meteorological records from Góriz Station indicated a significant increasing trend in annual mean temperature since 1981 ($\tau = 0.32$; $P < 0.05$) (Fig. 1). The period between 2001 and 2012 was on average warmer (+0.3 °C) than the previous decade. Most notably, the average (3-years fixed interval) of the thermal sum during the growing season evidenced a warm period between 2002 and 2006 (Fig. 1), whereas the prior and subsequent periods were markedly cooler. The pattern in annual mean precipitation over the last decades was less clear, with no linear trend in precipitation ($\tau = 0{,}06$; $P < 0{,}67$). However the driest growing seasons were concentrated in early 2000s (Fig. 1).

We did not find any significant ($P < 0.01$) effect of herbivore exclusion on species richness at any of the grasslands between 1993 and 2012 (Table 1). Temporal fluctuations in species richness were also unrelated to temperature and precipitation regimes in both cases. In contrast, canopy height increased significantly in response to herbivore exclusion (Table 1). In the Bromion exclusion, a significant decrease in canopy height was observed during the warm and dry period, which was reversed at the end of the study (Fig. 2). In the Nardion exclusion, on the contrary, canopy height gradually increased throughout the study (Table 1; Fig. 2), although in this case, the effect was not statistically significant ($P > 0.01$). The separate effects of thermal sum and accumulated precipitations on canopy height were significant ($P < 0.001$) in both grasslands, but only in the case of Bromion explained a reasonable amount of the observed variability (Table 1). In this case, the highest temperatures decreased canopy height only in the control plot.

Exclusion of herbivores affected the community structure at both sites, but the differences between control and exclusion plots after 19 years were stronger at Nardion (Fig. 3).

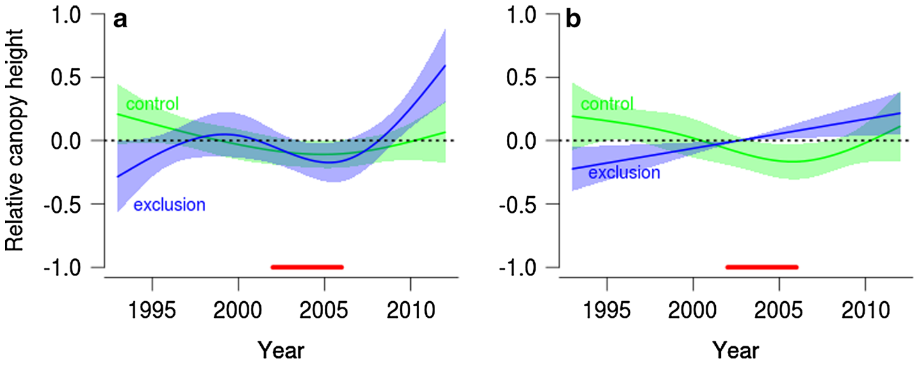

Fig. 2 Effect of herbivore exclusion on log-transformed canopy height in the Bromion (**a**) and Nardion (**b**) grasslands across 19-years. *Shaded area* represents 95 % confidence intervals for control and exclusion plots. Canopy height values are centered on 0 to facilitate comparison between sites and plots. *Red line* highlights an exceptionally warm and dry period detected between 2002 and 2006

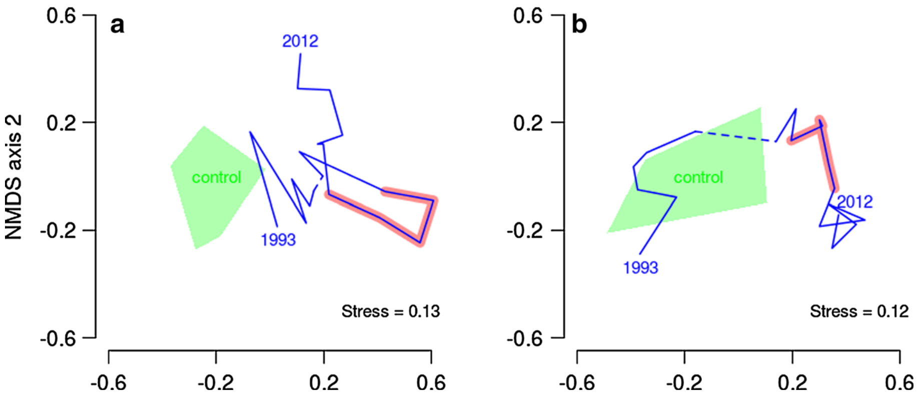

Fig. 3 Long-term trajectory of plant community structure in response to herbivore exclusion in the Bromion (**a**) and Nardion (**b**) grasslands. Ordination is based on non-metric multidimensional scaling (NMDS), and shows plant community dynamics in controls (convex hull) and exclusion plots (*solid line*) between 1993 and 2012 (no data was recorded in 1999; *dashed lines*). *Shade line* stresses the exceptionally warm and dry period between 2002 and 2006

The community structure of Bromion diverged considerably from the control in 2001, but it was partially reversed after 2006 (Fig. 3). In Nardion, changes in the community structure after herbivore exclusion were only noticeable after the 8th year (Fig. 3). At the end of the study, control plots approached initial community structures in both cases. Interestingly, interpretation of ordination analyses was consistent regardless of the dissimilarity measure used, and consideration or not of rare species, but not when incidence data was used (see Online Resource 1).

The dominant grass *Festuca nigrescens* underwent a markedly different shift in abundance in the different sites and treatments (Fig. 4). At the Bromion site, herbivore exclusion led to declining *F. nigrescens* during the warm and dry period, but that trend was reversed afterwards (Fig. 4). At the Nardion site, the decreasing trend of dominant *F. nigrescens* was gradual and significant since the first years of herbivore exclusion, and mirrored the increase of *Nardus stricta*. As a result, *N. stricta* became the most dominant species at the end of the study. In control plots, temporal fluctuations of the dominant

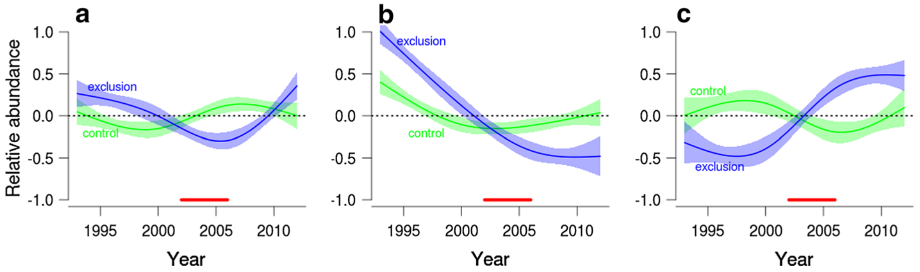

Fig. 4 Long-term dynamics of the most dominant species in response to herbivore exclusion. **a** Relative abundance of *Festuca nigrescens* at Bromion site. **b** Relative abundance of *F. nigrescens* at Nardion site. **c** Relative abundance of *Nardus stricta* at Nardion site. *Shaded areas* represent 95 % confidence intervals. Abundance values are re-scaled to 0 to ease visual comparison between sites and plots. *Red line* highlights an exceptionally warm and dry period detected between 2002 and 2006

species were less intense that in exclusion plots, and neither of these grasses showed substantial changes in abundance after 19-years.

Despite the permanent location of transects, our spatial sampling error rates were estimated as 0.64 and 0.33 at the Bromion and Nardion sites, respectively. For the sake of simplicity, and given the importance of the warm and dry period between 2002 and 2006 for community changes, transition probabilities were calculated separately for the warm period and the bracketing cooler time periods (1992–2001 and 2007–2012, respectively), and for each of the two treatments. The main difference in the transition probabilities of the two grasslands was related to grasses, whose probability to be replaced by forbs was higher than that of any other ecological groups in Bromion. In contrast, grasses were the most persistent group in Nardion. Regardless of the climatic period, we found more stable transitions (i.e. less transitions between groups) in presence of herbivores at both sites (Fig. 5). At the Bromion site, largest changes in transition probabilities in response to herbivore exclusion took place between 2002 and 2006, when the transition from the dominant grass and other grasses to forbs increased, as did the persistence of forbs relative to preceding time period. Conversely, there was a decrease in the transition from all groups towards *F. nigrescens* (Fig. 5). These changes were detectable at both control and exclusion plots, being higher in the latter case (Fig. 5). After 19-years of herbivore exclusion, however, only the persistence of forbs remained higher than initially seen. In Nardion, the clearest changes during the 2002–2006 period were the reduction of transition probabilities from all groups to the dominant grass, and the increasing persistence of grasses and forbs relative to that observed in previous time period. After 2006, the transition between ecological groups approached initial values in presence of herbivory (Fig. 5). Unlike in Bromion, the shifts in transition probabilities observed (except that between dominant and non-plants) during the warm and dry period continued afterwards in the exclusion plot (Fig. 5).

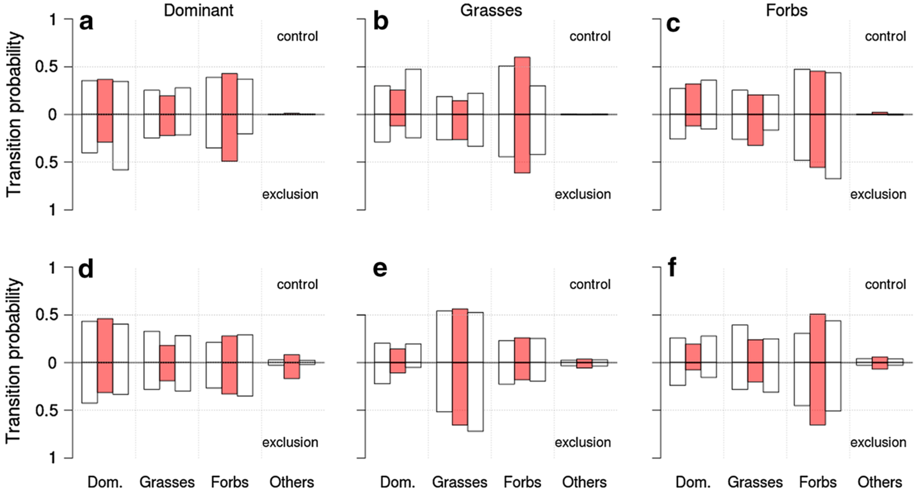

Fig. 5 Corrected mean transition probabilities between main ecological groups (dominant species, non-dominant grasses, forbs and other non-plants) in Bromion (**a**, **b**, **c**) and Nardion (**d**, **e**, **f**) grasslands. Each plot shows the averaged transition probabilities between a given group and the others for an exceptionally warm period (2002–2006; *bar* in *red*) and bracketing cooler time periods (1993–2000 and 2007–2012, respectively; *bars* in *white*)

Discussion

Contrary to expectations, we found that two decades of herbivore exclusion did not trigger large changes in community structure and diversity losses. Although the canopy height increased significantly within exclosures over 19 years as predicted by the GGM, this change was not drastic enough to modify competition for light and thereby, to suppress shade intolerant species. The lack of effect of herbivore exclusion on species richness may also be related to stronger effects of rates of local colonization and extinction on grassland structure (Glenn and Collins 1992; Olff and Ritchie 1998), or to the fact that herbivores were not selecting the most competitive species (Crawley 1983), and hence that their relative importance in altering interspecific competition was minor.

For productive subhumid grasslands, the GGM predicts rapid community shifts in response to changes in grazing regimes (Milchunas and Lauenroth 1993). However, we found that high-elevation grasslands responded slowly to the most extreme reduction of grazing possible. In fact, the response was mostly related to the shift in abundance of species, and marked divergences in community structure between control and exclusion plots did not happen before the ninth year of exclusion. This result is in disagreement with theoretical expectations, but also contrasts with previous findings from exclusion experiments in other mountain regions, where community changes (including those in composition) were stronger soon after excluding herbivores (Rawes 1981; Hill et al. 1992; Krahulec et al. 2001; Tasser and Tappeiner 2002; Mayer et al. 2009; Speed et al. 2013). Importantly, our results were irrespective to the dissimilarity measure used to characterize grasslands trajectories, and potential bias related to the detection of rare species.

Why was the community response to the exclusion of large herbivores so weak in this study? We speculate about four different possibilities, not mutually exclusive. First, the lack of response might be due to the absence of life forms such as dwarf-shrubs, which have been shown to fast modify community physiognomy and structure (e.g. De Bello et al. 2005; Olofsson et al. 2009). Second, the reduced growing period and predominance of long-lived species at high elevations might have slowed down the response of communities to herbivore exclusion (Tasser and Tappeiner 2002; Mayer et al. 2009). Third, given that the studied plots were surrounded by large grassland areas, immigration of species from lower elevations (including shrubs) might be reduced compared to grasslands close to the forest limit and/or shrublands (e.g. Speed et al. 2013). Likewise, the colonization of more competitive lowlands species (including shrubs) may also be limited in the absence of grazing (Austrheim and Eriksson 2003), because above ground biomass and species colonization and seedling emergence are negatively related (Eskelinen and Virtanen 2005). The fact that all the new species detected within the exclosure across the 19-years were also present in the surrounding grasslands support this explanation. Finally, continued intensive grazing throughout the last centuries might have depleted the pool of strictly non-tolerant species from the system, thus limiting the resilience mechanisms proposed by the GGM that allow for reversible floristic changes in response to grazing intensity (Cingolani et al. 2005).

A striking finding of this study was that hervibory played an important role in modulating the effect of climate in community structure and turnover between ecological groups. In both grasslands, plant assemblages become more vulnerable to a period of unusually warm and dry conditions in absence of herbivory. This was evidenced by higher changes in both the plant community structure and transition probabilities of ecological groups within exclosures between 2002 and 2006. The exceptionally warm and dry growing seasons affected negatively the dominant *Festuca nigrescens* in both sites, although it trigger different plant community responses. *Festuca nigrescens* was mostly replaced by forbs in Bromion, which explains the temporal shift in the community structure found in this grassland. Importantly, the initial community structure and group replacements were partially recovered once the exceptional climatic conditions reverted at this site, indicating a high resilience of this grasslands.

In Nardion site, *F. nigrescens* was mostly replaced by the *Nardus stricta,* which became the most dominant since the 2002. The replacement of one dominant species from another suggests a lower competitive release, and may explain why transition from grasses to forbs between 2002 and 2006 was lower than in Bromion. In this case the dominance of *N. stricta* continued after the end of the warm and dry event. This trend may constitute a potential risk from a management perspective, because *N. stricta* can spread in absence of herbivores up to form dense tussocks (Chadwick 1960; Hulme 1996; Tasser and Tappeiner 2002), which can be difficult to control even by restoring past grazing regimes (Rosef et al. 2004). As the low foraging value *N. stricta* spreads at the expense of more nutritive grasses and legumes, it can also result in an impoverishment of the quality of grassland for livestock production, and in some cases, in a diversity loss (Cernusca et al. 1996; Fillat et al. 2008). Our result do not corroborate such extremes, but they do warn about the potential influence of exceptional climatic conditions in favouring the spread of *N. stricta.*

As the community structure in all control plots was relatively stable across the 19-yr, we suggest that herbivory buffered changes of plant community in response to exceptional climatic events (Post and Pedersen 2008; Olofsson et al. 2009; Speed et al. 2012; Kaarlejärvi et al. 2013). A straightforward implication of this result is that the maintenance of past grazing stocking rates (or restoration in case of recent loss) may not only be valuable for the conservation of current biological diversity (Austrheim and Eriksson 2001), and productive communities (e.g. in the case of Nardion grasslands), but an efficient strategy to slow down some of the detrimental effects expected under ongoing climate warming (Theurillat and Guisan 2001).

Taken together, our results do not support the application of the GGM for guiding successful management of high elevation grasslands. As the GGM was mainly based on studies from low-elevation grasslands and shrubslands (Milchunas et al. 1988; Milchunas and Lauenroth 1993) it does not contemplate some particular aspects of high elevation grasslands (i.e. predominance of long-lived species, short growing periods) that may be critical in modulating the response of grasslands to grazing. At first glance, the weak long-term impact of the herbivory exclusion on grasslands may be perceived as good news for managers. However, caution is recommended when interpreting these results, because as we have shown, the relative slow response of plant communities to exclusion treatment would accelerate under climatic conditions, similar to those predicted for many European mountain (Engler et al. 2011).

Summarizing, we have shown that the long-term effect of herbivore exclusion on high elevation plant communities can be more moderate than expected, but also that they are modulated by the climatic conditions. Importantly, our results demonstrate that the strength of the response of grasslands to herbivory exclusion is likely to be enhanced under exceptional warm and dry periods, such as those expected under ongoing climate warming. Unfortunately, as in many other long-term experiments, the lack of replication limits our ability to generalize these results. However, we must be aware that the huge variability of grassland communities will make it difficult to establish accurate generalizations even if we had triplicated the number of grasslands. In absence of further detailed studies, our study provides novel insights into the long-term response of particular ecological communities under climate and land-use change. Grassland management should consider not only the direct effect of herbivore activity or climate warming, but also their combined effect across a variety of communities over ecological relevant times scales.

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