

Integrating climate change into calcareous grassland management

Jean-Paul Maalouf*, Yoann Le Bagousse-Pinguet, Lilian Marchand, Emilie Bâchelier, Blaise Touzard and Richard Michalet

UMR BIOGECO INRA 1202, Ecologie des Communautés, Université Bordeaux 1, Bât. B2 RDC Est, Avenue des facultés, 33405 Talence, France; and UMR BIOGECO INRA 1202, INRA, 69 route d'Arcachon, FR-33612 Cestas cedex, France

Summary

1. Climate change is rarely taken into consideration in conservation management strategies aimed at protecting biodiversity from other threats. We examined the implications of this perspective in European calcareous grasslands, which are among the richest herbaceous systems of the continent and are therefore of high nature conservation interest. These systems are currently undergoing species loss because of the abandonment of agro-pastoral practices. Classic ecological theory assumes that conservation management activities (such as regular mowing) and drought events should increase diversity through decreased plant competition in abandoned mesic communities. In turn, this could reduce diversity in xeric communities although positive plant interactions (facilitation) might buffer these negative effects and maintain diversity.

2. We studied the effects of regular mowing and experimentally induced drought on diversity and biotic interactions between two transplanted species in mesic and xeric calcareous grasslands. The study sites in south-western France have not been subjected to any management for the last 30 years.

3. Drought did not affect mesic systems although mowing increased plant diversity through decreased competition. By contrast, mowing had no significant effect in xeric systems although drought decreased diversity. Interestingly, transplants were subject to neither competition nor facilitation in the xeric systems.

4. *Synthesis and applications.* Regular mowing and drought events impact plant diversity of mesic and xeric calcareous grassland communities in different ways. We recommend regular mowing of mesic grasslands, even in the context of climate change. By contrast, we recommend less-frequent mowing of xeric grasslands together with specific interventions such as assisted migration for species with poor drought tolerance. Similar studies in other ecosystems on larger spatial and temporal scales should examine the dual effects of management and climate change to identify appropriate management programmes.

Key-words: biotic interactions, conservation, diversity, drought, Mesobromion, mowing, Xerobromion

Introduction

Although climate change is known to affect species diversity and range (Parmesan 2006), it is difficult to integrate into management strategies aimed at protecting biodiversity from land use change or other threats (Hobbs, Higgs & Harris 2009; Sutherland *et al.* 2010; Poiani *et al.* 2011). Few studies have so far addressed this issue (Hannah, Midgley & Millar 2002; Bierwagen, Thomas & Kane 2008; McClanahan *et al.* 2008)

even though climate change effects could be intensified by current management practices (Hulme 2005). The main goal of our work was to assess the feasibility of integrating climate change effects into management strategies of South European calcareous grasslands.

European calcareous grasslands are among the most species-rich systems on the continent (Hillier, Walton & Wells 1990; Wallisdevries, Poschlod & Willems 2002). Current management involves regular mowing or grazing to prevent species loss because of land use change (abandonment of traditional moderate grazing or hay-making practices, Bobbink &

*Correspondence author. E-mail: jeanpaul.maalouf@gmail.com

Willems 1993; Buckland *et al.* 2001) and eutrophication (Bobbink 1991). For instance, after a 25-year-long survey involving five different experimental management regimes in a German calcareous grassland, Kahmen, Poschold & Schreiber (2002) found that mowing or mulching could be efficient surrogates of traditional grazing practices. However, as management becomes increasingly expensive, it may be restricted to a limited number of grasslands in the future (Poschold & Wallisdevries 2002).

The theoretical basis for the use of mowing or grazing to maintain high levels of diversity comes primarily from the humped-back diversity-biomass model of Grime (1973). Mowing and grazing limit the competitive exclusion of ruderal species (i.e. release from competition, Grubb 1977) in productive to intermediately productive communities such as mesic calcareous grasslands. In these systems, disturbance (sensu Grime 1973, 1974) can prevent light competition induced by tall dominant species (Grime 1973; Corcket *et al.* 2003). Stress factors such as drought might also attenuate the competitive exclusion of stress-tolerant species by tall competitive species (Grime 1973; Almufti *et al.* 1977), as shown by several studies in mesic calcareous grasslands (Grime & Curtis 1976; Corcket *et al.* 2003; Stampfli & Zeiter 2004; Liancourt, Callaway & Michalet 2005; Bennie *et al.* 2006). The increase in both the magnitude and frequency of extreme events (e.g. droughts) is now considered as an important manifestation of climate change (Intergovernmental Panel on Climate Change 2007), with possible large impacts on ecosystems (Smith 2011). In this context, we predict that extreme drought events (i.e. stress factors) may have positive effects on biodiversity in abandoned mesic grasslands and could be comparable to currently recommended management strategies such as mowing or grazing.

Most studies assessing the effects of disturbance or stress on calcareous grasslands have been conducted in mesic grasslands (e.g. Mesobromion communities, Boulet 1986), in particular in the UK, Germany, Estonia, the Netherlands, Switzerland, Slovakia and Northern France. To our knowledge, we still lack similar empirical studies for xeric calcareous grasslands from Southern Europe (e.g. Xerobromion communities, Boulet 1986). In contrast to mesic grasslands, xeric communities are likely to be positioned on the high stress side of Grime's (1973) humped-back model where an increase in stress could decrease diversity. In these xeric communities, droughts could reduce diversity, especially when coupled with disturbance (Huston 1979).

The early models do not take into account positive interactions that increase diversity among plants under extreme environmental conditions (Bertness & Callaway 1994; Hacker & Gaines 1997; Bruno, Stachowicz & Bertness 2003; Michalet *et al.* 2006). For example, facilitation may buffer the negative effects of drought in extreme environments by promoting stress-intolerant species (Brooker 2006; Wipf, Rixen & Mulder 2006; Saccone *et al.* 2009). However, facilitation has also been shown to decrease in extremely stressed (Kitzberger, Steinaker & Veblen 2000) or disturbed (Vandenbergh *et al.* 2009; Forey, Touzard & Michalet 2010) conditions and may become unimportant for diversity leading to catastrophic shifts in vegetation

cover (Michalet *et al.* 2006; Kefi *et al.* 2007; Maestre *et al.* 2010).

The effects of stress and/or disturbance on the diversity of different types (mesic and xeric) of calcareous grassland communities remain unclear in the context of climate change. This is in part because of our limited knowledge of how biotic interactions mediate species' responses to the interactive effects of several global change drivers (e.g. land use change and climatic droughts). This paper addresses this knowledge gap through a field experiment in south-western France. We manipulated rainfall to simulate drought and/or mowed two calcareous grassland communities with contrasting water availability (Mesobromion and Xerobromion) for two consecutive years. We measured changes in plant diversity indices among treatments and in response to plant-plant interactions of two common target grass species, the competitive *Brachypodium pinnatum* (L.) Beauv. and the stress-tolerant *Bromus erectus* Hudson (Grime, Hodgson & Hunt 1988).

We addressed the following questions: (i) Do climatic drought and mowing both decrease competition and increase diversity of a mesic calcareous grassland community? (ii) Do the effects of drought and mowing reduce diversity in a xeric calcareous grassland community, especially when these constraints occur together? (iii) Is facilitation likely to buffer these negative effects on diversity in a xeric community but will this effect diminish when drought and mowing factors interact?

Materials and methods

STUDY SITE AND TARGET SPECIES

We performed the experiment in abandoned species-rich, semi-natural, calcareous grasslands (Mesobromion and Xerobromion communities) located in the vicinity of Saint Sulpice de Mareuil (45°28'50"N; 0°30'22"E, 140 m above sea level) and La Rochebeaucourt (45°27'53"N; 0°23'33"E, 140 m above sea level) in the Périgord-Limousin Natural Park in south-western France. The sites are dominated by cretaceous limestone. Climate is temperate oceanic. Mean winter temperature is 6.2 °C and mean summer temperature is 19.5 °C. Mean annual precipitation is 800 mm with highest rainfall occurring in winter. During the experiment, the annual rainfall was 873 mm (2009) and 773 mm (2010, previmeteo SARL). In Europe, different grassland communities can be found close to each other depending on soil depth, slope form and degree, and exposure (Boulet 1986). The driest plant communities, usually called Xerobromion communities by European phytosociologists, are found on shallow soils located on steep convex south-facing slopes. At our Xerobromion sites, soil moisture averaged over three dates in spring 2010 was 3.4% (SD 1.4; $n = 16$, Theta probe device, ML2x, Delta-T Devices, Cambridge, England); soil depth was 5.1 cm (SD 0.8; $n = 16$); slope varied between 15° and 30° and had a south-south-western exposure. The most mesic communities, that is, Mesobromion, occur on deeper soils located on more gentle slopes. At our Mesobromion sites, soil moisture averaged over three dates in spring 2010 was 9.1% (SD 3.3; $n = 16$); soil depth was 6.7 cm (SD 0.9; $n = 16$); slope varied between 0° and 5° and had a Southern exposure. Vegetation cover was greater in the Mesobromion than in the Xerobromion sites [94% (SD 3) vs 56% (SD 5), respectively, $n = 16$], as was vegetation height [12.3 cm (SD 1.2) vs. 7.1 cm (SD 1.5), respectively, $n = 8$]. Thirty

years before the start of the experiment, both community types were subject to regular ovine grazing. Since then, there has been no conservation effort or land use, and the only grazers have been wild animals, mainly rabbits *Oryctolagus cuniculus* L. Plant nomenclature follows Tutin *et al.* (1964–1980). Dominant species are slow growing and stress tolerant (*sensu* Grime 1977), in particular the two grass species *Festuca ovina* and *Koeleria valesiana*. Other common species are *Anthyllis vulneraria*, *Teucrium chamaedrys*, *Thymus serpyllum* and *Seseli montanum*. Xerobromion-specific species are *Coronilla minima*, *Fumana procumbens* and *Helichrysum stoechas*, whereas Mesobromion-specific species are *Potentilla verna* and *Carex humilis*. The study sites support a large number of patrimonial and/or protected species (e.g. *Arenaria controversa* and *Linum austriacum* subsp. *collinum*).

We chose *Bromus erectus* and *Brachypodium pinnatum* as target species to measure biotic interactions for two reasons. First, both grass species are very frequent in poorly managed and nutrient-poor calcareous grasslands throughout Europe (Willems 1980; Royer 1987) and have been widely used in a number of experiments (Bobbink 1991; Corcket *et al.* 2003; Liancourt, Callaway & Michalet 2005; Moser *et al.* 2011). Secondly, although they are both considered stress-tolerant competitors (C-S) by Grime, Hodgson & Hunt (1988), a number of authors have shown strong functional differences among them, *B. erectus* being more tolerant to both drought stress and disturbance and *B. pinnatum* being more competitive (Corcket *et al.* 2003) and dominant in abandoned mesic grasslands (Hurst & John 1999). At our study sites, both species are rare and only dominant in small patches, in particular on deeper soils for *B. pinnatum* and in mown areas for *B. erectus*. This indicates that our plots were both drier and less disturbed than most calcareous grasslands reported in the literature. However, according to local managers, *B. pinnatum* has recently colonized the most mesic *F. ovina*-dominated communities, resulting in a decline in species richness; similar observations have been made throughout Europe (Bobbink & Willems 1987; Hillier, Walton & Wells 1990; Hurst & John 1999). Specifically, the *rupestre* subspecies was chosen for *B. pinnatum*, as it is most common at the selected sites.

EXPERIMENTAL DESIGN

The experiment lasted from December 2008 to October 2010. We established four experimental blocks (10 × 10 m) in each community type. Each block was split into four plots (3.5 × 3.5 m), in which two treatments (drought and mowing) were applied in a factorial design: control, drought, mowing, and drought and mowing. The design included a total of 32 plots (2 communities × 2 levels of drought × 2 levels of mowing × 4 blocks).

We simulated drought through rainfall interception during two successive springs (from 9 April to 24 June 2009: 76 days and 31% of annual rainfall intercepted, and from 19 April to 28 June 2010: 70 days and 15% of annual rainfall intercepted). We chose spring because most plant growth occurs in this season, and both summer and spring seasons are predicted to be drier in this area in the future with climate change (IPCC 2007). We constructed roofs of transparent plastic that allowed 90% penetration of photosynthetically active radiation (CelloFlex 4TT, Prosyn Polyane; ETS Girard, Bruges, France). To avoid increases in temperature, roofs were tunnel shaped, which allowed air circulation through 2-m-high gaps at both ends [mean air temperature from April till June 2010 was not significantly different between roofed (14.8 °C) and control plots (14.6 °C)].

We applied the mowing treatment by clipping four times during the experiment, thus simulating a more intensive management than usual in calcareous grasslands, to ensure significant changes in a short-term

experiment. We clipped plots before (November 2008 and March 2010) and after (June 2009 and July 2010) the growing seasons. We removed mown biomass from the plots.

We assessed the responses of the two transplanted target species (*B. pinnatum* and *B. erectus*) to neighbours (plant–plant interactions) in all treatments using a neighbour removal procedure. We collected 500 tillers of each target species from the field outside the plots on 11 March 2010. The tillers were standardized by cutting roots and shoots (12-cm-high tillers with 3 cm of roots for *B. pinnatum* and 8-cm-high tillers with 3 cm of roots for *B. erectus*), and then grown individually in test tubes filled with tap water until transplantation. In late March 2010, we transplanted eight tillers of each species in each of the 32 plots and watered them. We replaced all dead individuals after 2 weeks to avoid bias because of transplantation shock. We hand-weeded neighbouring plants in a 10-cm-diameter circle around half of the targets, and we severed roots of neighbouring plants around each removal area. Thus, in each plot, we transplanted target individuals with and without neighbouring plants. We planted a total of 512 tillers (2 communities × 4 blocks × 2 drought levels × 2 mowing levels × 2 neighbouring levels × 2 species × 4 replicates). A schematic representation of the experimental design is provided in Appendix S1 in Supporting Information.

DATA COLLECTION AND ANALYSES

We recorded survival of the target species at the end of the experiment (mid-October 2010) to assess responses to factors (community, neighbours, drought and mowing). Survival rates were calculated per plot and per neighbouring level.

To assess community responses to environmental treatments, we visually estimated vascular plant species abundance inside 10 (25 × 25 cm) quadrats randomly distributed inside each plot. We evaluated species richness (*S*) at the quadrat scale by counting the number of vascular plant species within each quadrat. We computed Shannon (Shannon & Weaver 1949) and Pielou evenness (Pielou 1975) indices (*H'* and *J'* respectively) as follows:

$$H' = - \sum_{i=1}^S (p_i \ln p_i)$$

$$J' = H' / (\ln(S_{\text{quadrat}}))$$

where p_i is the cover ratio estimation of species *i* in the quadrat, and S_{quadrat} is the number of species in the quadrat.

We averaged quadrat richness and diversity indices per plot. We computed and averaged the quadrat abundance of graminoids (Poaceae and Cyperaceae species) and forbs (remaining vascular plant species) in each plot. We monitored quadrats at three different dates (21 May, 19 July and 31 August 2010) to encompass the phenology spectrum of all species.

We tested community, drought, mowing, neighbours, and species effects on survival rate using a split-plot mixed analysis of variance (ANOVA) model including two random effects and five fixed factors with all the possible interactions between fixed factors:

$$Y_{ijklmno} = S_i \times N_j \times M_k \times D_l \times C_n + B_m + P_{o(m)} + \varepsilon_{ijklmno}$$

where $Y_{ijklmno}$ is the survival rate of species *i* (S_i , fixed effect) undergoing the neighbouring *j* (N_j , fixed effect), the mowing *k* (M_k , fixed effect) and the drought *l* (D_l , fixed effect) treatments inside the block *m* (B_m , random effect) of community *n* (C_n , fixed effect). Plots were included as a random variable nested within blocks ($P_{o(m)}$). $\varepsilon_{ijklmno}$ is

the residual error. The (\times) signs indicate that all of the possible statistical (2-, 3-, 4- or 5-way) interactions among the fixed factors were taken into consideration. We also tested community, drought and mowing effects on species richness, Shannon index, Pielou evenness index and forb and graminoid abundance following this model:

$$Y_{klmn} = M_k \times D_l \times C_n + B_m + \varepsilon_{klmn}$$

where Y_{klmn} is the dependent variable taken into consideration, and ε_{klmn} is the residual error.

When statistical interactions including the community factor occurred, we ran Tukey multiple comparison contrasts adapted to mixed models. We logit-transformed survival data prior to analysis to meet homoscedasticity and residual normality assumptions following Warton & Hui (2011): $Y_i = \log[(y_i + \varepsilon)/(1 - y_i + \varepsilon)]$, where Y_i is the transformed survival of the i th observation, y_i is the untransformed survival of the i th observation and $\varepsilon = 0.0001$ is a small value which allows avoiding 'zero' occurrences in the denominator. Parametric model assumptions were met for all the remaining models. Data analysis was performed using the R software for statistical computing version 2.10.1 (R Development Core Team, Vienna, Austria).

Results

The full split-plot mixed ANOVA table of effects of the five crossed factors (community, drought, mowing, neighbours and species) on tiller survival is given in Table S1 in Supporting Information. There was a highly significant species effect because *B. pinnatum* survived less than *B. erectus* overall ($F_{1,72} = 18.48$; $P < 0.001$). Drought had an important significant effect on the survival of targets ($F_{1,18} = 26.53$; $P < 0.001$), and this negative effect was stronger for *B. erectus* than for *B. pinnatum* (drought \times species treatments interaction, $F_{1,72} = 5.08$; $P < 0.05$). A significant community \times mowing \times neighbours interaction also occurred ($F_{1,72} = 4.10$; $P < 0.05$), because in the Mesobromion community, neighbours had a negative effect on the survival of both targets in the unmown plots but not in the mown plots; this difference was not observed in the Xerobromion community where the effects of neighbours were not significant (Fig. 1). In addition, a 4-way significant statistical interaction occurred (community \times drought \times mowing \times species, $P < 0.05$, $F_{1,72} = 5.59$; $P < 0.05$). This statistical interaction was complex but likely to be due to a decrease in *B. erectus* survival with mowing in dried Mesobromion plots and in control Xerobromion plots (data not shown).

The Shannon diversity index significantly increased with mowing in the Mesobromion community but not in the Xerobromion community, as shown by the significant community \times mowing interaction ($P < 0.05$, Table 1, Fig. 2). Shannon diversity as well as species richness significantly decreased with drought in the Xerobromion community but not in the Mesobromion community, as shown by the significant community \times drought interactions ($P < 0.05$ for both variables, Table 1, Fig. 2). In addition, in the Xerobromion community, the lowest values of both of these diversity variables were observed when drought and mowing were applied together, although the interactive effect of these two constraints was not significant. Pielou's evenness index was

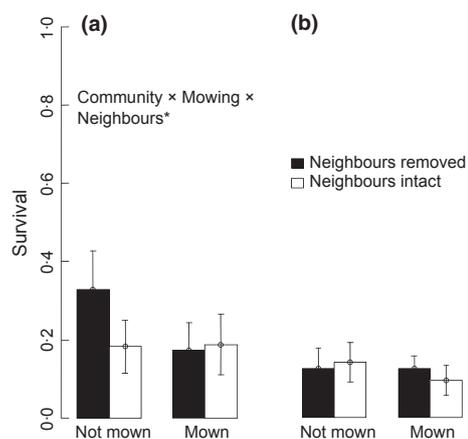


Fig. 1. Survival of pooled *Bromus erectus* and *Brachypodium pinnatum* tillers in the Mesobromion (a) and Xerobromion (b) communities, in absence/presence of neighbouring plants, and according to the mowing treatment. Data are presented this way to highlight the significant statistical interaction shown on the top left of the chart. Bars indicate means (SE). * $P < 0.05$.

slightly higher in the Xerobromion community than in the Mesobromion ($P < 0.05$ for the community effect, Table 1, Fig. 2) and increased with mowing in the latter but not the former community ($P < 0.05$ for the community \times mowing interaction, Table 1, Fig. 2). Graminoid cover was twice as high in the Mesobromion community than in the Xerobromion community ($P < 0.05$, Table 1, Fig. 2) and declined with mowing and drought in both communities ($P < 0.001$ and $P < 0.01$, respectively, Table 1, Fig. 2). However, the negative effect of mowing was much stronger in the Mesobromion community than in the Xerobromion community, as shown by the significant community \times mowing interaction ($P < 0.01$, Table 1). In the Mesobromion community, graminoid cover in the mown plots was half that in the unmown plots (Fig. 2). Forb cover was not significantly affected by any treatment (33% SD 8; Table 1).

Discussion

Our results highlight the importance of accounting for community type and response to specific environmental constraints when establishing management plans for calcareous grassland conservation in the face of climate change. Drought and mowing affected the diversity of calcareous grasslands differently. Mowing increased the diversity of the Mesobromion community, whereas drought decreased the diversity of the Xerobromion community. The effect of mowing was likely to be due to decreased competition of dominant graminoids, whereas the effect of drought did not appear to be related to variations in biotic interactions. Competition was only observed in the most mesic and undisturbed conditions of our design, whereas facilitation never occurred for the two target species.

Consistent with classic ecological theory and management practices in other mesic calcareous grasslands, even within the

Table 1. Split-plot mixed ANOVA effects of three crossed factors (community, drought and mowing) on species richness, Shannon and Pielou indices and forbs and graminoids cover. numDF and denDF represent the numerator and the denominator degrees of freedom respectively

Source of variation	numDF	denDF	Species richness	Shannon index	Pielou evenness	Forbs cover	Graminoids cover
			<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>
Community	1	6	2.38	5.57	8.51*	2.42	6.69*
Drought	1	18	3.69	4.24	0.53	4.39	11.18**
Mowing	1	18	0.11	1.33	1.59	1.74	30.37***
Community × Drought	1	18	6.21*	7.48*	3.36	0.37	0.99
Community × Mowing	1	18	4.68*	10.34**	7.06*	3.26	17.24**
Drought × Mowing	1	18	0.61	1.51	1.24	1.19	0.01
Community × Drought × Mowing	1	18	0.07	0.44	0.18	0.65	0.28
Error (model)	24						

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

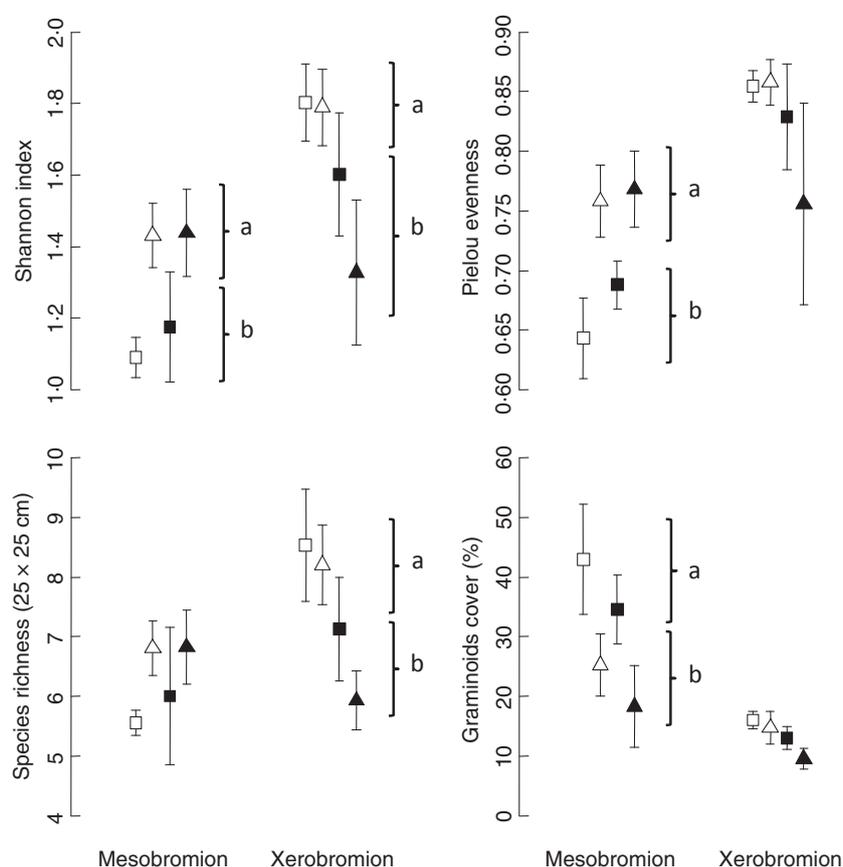


Fig. 2. Shannon and Pielou evenness indices, species richness and graminoids cover measured on the Mesobromion and Xerobromion communities, according to control (empty squares), mowing (empty triangles), drought (filled squares) and drought and mowing (filled triangles) treatments. For each parameter and within each community, different letters show significant differences between groups of treatments according to Tukey contrasts, which were performed when significant statistical interactions occurred (Table 1). Bars indicate means (SE).

short time-scale of the experiment mowing had a positive effect on diversity in the Mesobromion community (Grime 1973; Huston 1979; Bobbink & Willems 1993). The Shannon–Wiener diversity index increased with mowing as a result of an increase in community evenness. This effect was clearly associated with a strong decrease in graminoid cover in this mesic community. Furthermore, our transplant experiment showed that competition occurred in the unknown plots of the Mesobromion community but disappeared with mowing.

Mowing is known to increase diversity in grasslands by limiting competitive exclusion (Grime 1973; Grubb 1977; Hobbs & Huenneke 1992; Bobbink & Willems 1993). The lack of a significant increase of species number with mowing was probably due to recruitment limitations common in these systems (Zeiter, Stampfli & Newbery 2006).

By contrast, the experimental drought did not significantly affect any diversity variable in the Mesobromion community. Although graminoid cover was slightly negatively affected,

biotic interactions did not vary with drought. At least at the scale of our experiment, the response of the Mesobromion community subjected to experimental drought was not consistent with Grime's (1973) model proposing that drought stress should alleviate the competitive effect of dominant species and increase diversity at high to intermediate productivity levels. This result also differs from several experiments showing a decrease in competition with increasing drought in mesic calcareous grasslands (Corcket *et al.* 2003; Liancourt, Callaway & Michalet 2005). However, in those studies, the calcareous grasslands under consideration were traditionally mown or grazed and thus dominated by *B. erectus*, a stress-tolerant species that is known to also tolerate a certain level of disturbance and to be a poor competitor (Corcket *et al.* 2003; Liancourt, Callaway & Michalet 2005). In contrast, our mesic calcareous grasslands were abandoned for at least 30 years during which they became progressively dominated by *Festuca ovina*, a stress-tolerant species known to be very intolerant to disturbance (Grime, Hodgson & Hunt 1988). Therefore, our results are in agreement with the model of Taylor, Aarssen & Loehle (1990); competition was unrelated to the level of stress in the Mesobromion community but was driven by the level of disturbance. In other words, in the absence of long-term disturbance, the dominant stress-tolerant bunch grass *F. ovina* may remain highly competitive with other species even with increasing climatic drought. However, the very low survival rate of transplanted *B. pinnatum* tillers in the drought treatment plots suggests that, at least in the short term, drought may impede the invasion of this highly competitive species and should contribute to the maintenance of diversity in the Mesobromion community.

In contrast to the response of the Mesobromion community, the Shannon–Wiener diversity index did not change in the Xerobromion community subject to mowing but decreased under drought conditions. This effect was driven by a decrease in species richness with no significant change in evenness. Evenness was already high in the xeric community control plots where graminoid cover was half that of the Mesobromion community. The decrease in species richness with drought in this dry community is consistent with the humped-back model of Grime (1973), which predicts that increasing stress at intermediate to low productivity levels should decrease diversity. However, the absence of any negative effects of mowing is not consistent with Huston's (1979) model which predicts that disturbance should reduce diversity in low-productive communities. There was a tendency for diversity to decline when mowing was carried out in combination with experimental drought. This suggests that more frequent and severe drought events coupled with a more aggressive disturbance regime may interact to induce a collapse of diversity, as proposed by several modelling and empirical studies conducted in arid and overgrazed ecosystems (Kefi *et al.* 2007). Such an interaction of severe constraints is unlikely to occur in European calcareous grasslands considering the current trend towards dereliction of these low-productive ecosystems (Poschloed & Wallisdeivries 2002).

Although the absence of significant plant–plant interactions in the Xerobromion community was only related to two species, we suggest that the reduction in diversity with drought is in accordance with classic ecological theory predicting that diversity is only driven by species tolerance to stress and disturbance in severe environmental conditions (Grime 1973; Huston 1979). In contrast, this result does not support facilitation theory predicting that positive interactions are frequent in highly stressed and/or disturbed conditions and may contribute to increasing diversity in severe environmental conditions (Bertness & Callaway 1994; Hacker & Gaines 1997; Bruno, Stachowicz & Bertness 2003). The absence of significant facilitative effects for the target species in the Xerobromion community is probably due to its structure and to the morphology and functional strategy of the dominant species (Michalet 2007; Gross *et al.* 2009; Maestre *et al.* 2009). This community has a very low biomass and appears more like a mat dominated by several short forbs than a grassland dominated by bunchgrasses. Following Michalet *et al.* (2006), when stress-tolerant benefactors are too 'weak' to mitigate environmental conditions for other species in extremely severe conditions, facilitation does not occur. However, many authors have shown the occurrence of positive interactions in semi-arid ecosystems dominated by bunchgrasses or shrubs (Pugnaire *et al.* 1996; Maestre & Cortina 2004). The low abundance and size of bunchgrass benefactors in the Xerobromion community may be explained by the high physical disturbance induced by the steepness and convexity of the calcareous slopes.

We emphasize that these conclusions are linked to the survival of transplanted tillers of only two species, and therefore, our conclusions must be considered cautiously. Additional studies are needed in other Xerobromion communities and for other species before robust generalisations can be made about the absence of facilitation in the dry and physically disturbed ecosystems of southern Europe.

Integrating climate change into South European calcareous grassland management strategies

Our results highlight the difficulty of integrating climate change into grassland management strategies. In South European calcareous grasslands, mowing disturbance and climatic drought appeared to have very different effects on diversity, which were highly community-specific. In the Mesobromion community, mowing increased diversity through decreased competition but drought had no effect. This was probably due to dominance of the highly competitive, stress-tolerant bunch grass *F. ovina*, given the absence of any disturbance over 30 years. Although drought is unlikely to restore plant diversity in this community, long-term drought may indirectly prevent diversity loss through limiting the invasion of undesirable competitive species such as *B. pinnatum*.

The two target species were not subject to any significant biotic interaction in the Xerobromion community, probably because of a low abundance and size of bunchgrasses because of a high physical disturbance induced by the steepness and

convexity of the slope. We suggest that the absence of facilitation in this community may partly explain why drought but not mowing had a negative effect on diversity. However, this conclusion was only related to the survival of two transplanted species. Further experiments are needed in xeric communities to really evaluate the potential of facilitation as a buffer against the negative effect of drought. We observed short-term stability in the diversity of Xerobromion communities that were mown regularly, but we do not know whether this effect persists in the long term. If that were the case, we would recommend less-frequent mowing of xeric communities together with specific interventions such as assisted migration to more benign Mesobromion communities for species with poor drought tolerance.

We emphasize that our conclusions and management recommendations should be considered with caution because they are based on two target species and a short-term experiment. It is known that community composition may sometimes not reach an equilibrium state even after several years of management (Kahmen, Poschlod & Schreiber 2002). Additionally, we cannot exclude the possibility that our results were community specific. Another study comparing the effect of management on species composition of dry and wet calcareous grassland communities over 5 years showed that the dry community responded faster than the wet community (Galvanek & Lepš 2009).

In conclusion, our work highlights the relevance of combining climatic effects and conventional management interventions in field experiments to investigate how conservation management strategies could be adapted to changing climate scenarios. Similar studies in other ecosystems on larger spatial and temporal scales are needed to identify appropriate management programmes.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Schematic representation of the experimental design.

Table S1. ANOVA table of treatment effects on target survival.

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