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Indication of antagonistic interaction between climate change and erosion on plant species richness and soil properties in semiarid Mediterranean ecosystems

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Abstract

We analyzed the consequences of climate change and the increase in soil erosion, as well as their interaction on plant and soil properties in semiarid Mediterranean shrublands in Eastern Spain. Current models on drivers of biodiversity change predict an additive or synergistic interaction between drivers that will increase the negative effects of each one. We used a climatic gradient that reproduces the predicted climate changes in temperature and precipitation for the next 40 years of the wettest and coldest end of the gradient; we also compared flat areas with 20° steep hillslopes. We found that plant species richness and plant cover are negatively affected by climate change and soil erosion, which in turn negatively affects soil resistance to erosion, nutrient content and water holding capacity. We also found that plant species diversity correlates weakly with plant cover but strongly with soil properties related to fertility, water holding capacity and resistance to erosion. Conversely, these soil properties correlate weaker with plant species cover. The joint effect of climate change and soil erosion on plant species richness and soil characteristics is antagonistic. That is, the absolute magnitude of change is smaller than the sum of both effects. However, there is no interaction between climate change and soil erosion on plant cover and their effects fit the additive model. The differences in the interaction model between plant cover and species richness supports the view that several soil properties are more linked to the effect that particular plant species have on soil processes than to the quantity and quality of the plant cover and biomass they support. Our findings suggest that plant species richness is a better indicator than plant cover of ecosystems services related with soil development and protection to erosion in semiarid Mediterranean climates.

Keywords: climate change, interaction models, Mediterranean, plant cover, semiarid, soil erosion, soil fertility, Spain, species richness, water holding capacity

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Introduction

There is an increasing interest in the relationship between biodiversity and ecosystem functioning derived from the potential ecological consequences of the present and future loss of biodiversity caused by human activities on natural and managed ecosystems (Díaz *et al*., 2005; Hooper *et al*., 2005). As most of the evidence about the relationship between biodiversity and ecosystem functioning services derived from manipulative experiments and low altered ecosystems, an important question is whether impoverished natural ecosystems perform differently or less efficiently than the more species-rich natural systems from which they are derived (Loreau *et al*., 2001; Balvanera *et al*., 2006).

Plant diversity is essential to ecosystem processes in ways that are not yet fully understood. The sort of correlation between diversity and ecosystem functions seems to depend very much on the specific processes considered and also on the species and functional groups involved (Garnier *et al*., 2004; Berendse, 2005; Michalet *et al*., 2006). So, although the positive role of above- and below-plant biomass on soil development and protection against erosion is fully accepted (Pimen-

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tel & Kounang, 1998; Gyssels *et al*., 2005), the current evidence for the effect of plant diversity on key ecosystem functions derived from soil biological properties, such as litter decomposition, nutrient supply rates, erosion resistance, etc., is very contradictory or very limited (Gastine *et al*., 2003; Zak *et al*., 2003; Wardle *et al*., 2004; Wardle, 2006). Evidence supports that it is the degree of functional differences between species that is a driver of ecosystem processes, rather than the number of plant species (Bardgett, 2005). Changes in the dominance between herbaceous and woody species are related to the spatial and temporal heterogeneity in nutrients and water that are, in turn, mediated by resource gradients (climate and soil) and disturbance regimes (Schlesinger *et al*., 1990, 1996; Chapin, 2003; Lavorel *et al*., 2007). The replacement of herbaceous species by shrubs has been reported after grazing cessation, climate change and soil erosion, and it is correlated with soil texture coarsening and losses in soil organic content and nutrients (Archer *et al*., 1990; Hoffman *et al*., 1995; Parizek *et al*., 2002; Li *et al*., 2006; Xiao *et al*., 2006, and references herein).

Explanations about biodiversity often failed to account for patterns of species richness in ecosystems at both local and regional scales when univariate approaches were used. As a result, an increased attention has been paid on more synthetic hypotheses supported by multivariate models (Cardinale *et al*., 2006). One approach, based on the succession theory, predicts that species coexistence and diversity are the result of a dynamic equilibrium between rates of biomass production and the frequency or magnitude of disturbances (Huston, 1979). Models derived from this approach showed an interaction effect that produces a pattern that cannot simply be derived from the univariate consideration of the effects of productivity and disturbance on species richness. However, the sign and the level of how a factor shapes species richness depends on the level of the other factor (Proulx & Mazumder, 1998; Kondoh, 2001; Zhou *et al*., 2006) and also on the kind of perturbation involved (Balvanera *et al*., 2006).

In a parallel way, land use and climate change have been recognized to be the most influential drivers of biodiversity change for the year 2100 at Earth scale (Sala *et al*., 2000). As land use change is a type of ecosystem disturbance and the effect of climate on biodiversity can be viewed as the expression of energy and water balances (O'Brien *et al*., 2000), both drivers can be considered as surrogates of disturbance and productivity at the planetary scale. In their paper, Sala and colleagues considered three possible scenarios of driver interaction (see Fig. 1). In the first scenario, there is no interaction among drivers and the outcome on biodiversity change is expected to be the sum of the single effects of the drivers (additive). In the second scenario, total biodiversity change is expected to be the outcome from the driver with the largest effect (antagonistic interaction), as additional degradation by other drivers

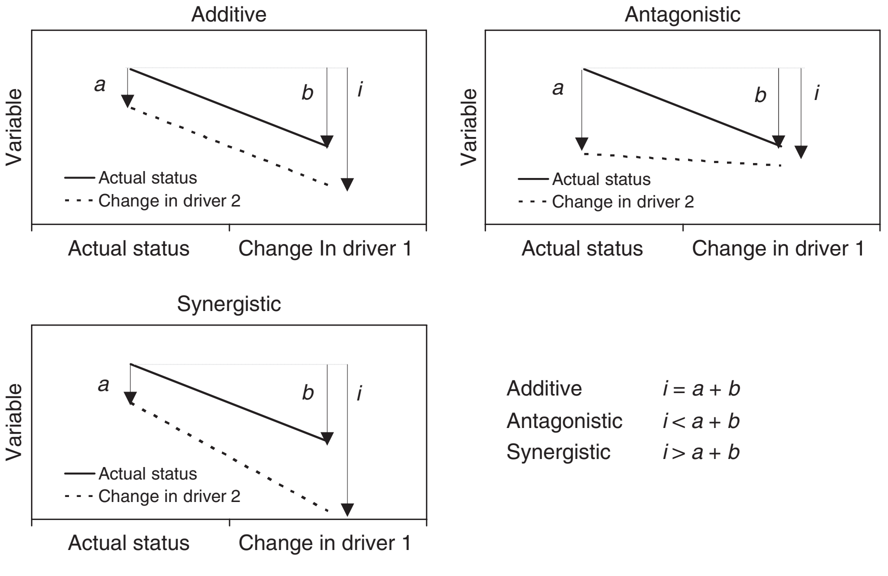

Fig. 1 Scenarios of interaction between drivers of biodiversity change (adapted from Sala *et al*., 2000). Drivers could be climate change, land use change, species invasion, etc. Variables can be expressed as number of species, diversity indexes, number of functional guilds, etc. The term *a* represents the amount of change on the variable caused by changes in driver 1 when the driver 2 does not change; the term *b* is the amount of change on the variable caused by changes in driver 2 when the driver 1 does not change and the term *i* represents the total amount of change on the variable caused by the interaction between both drivers, that is when both drivers change at the same time.

does not account for an extra in biodiversity change. In the third scenario, total change in biodiversity by the interaction of several drivers is larger than the mere sum of the individual effects of each driver (synergistic interaction). As the authors pointed out, the nature and strength of interactions among drivers is poorly known, and then there is an urgent need to obtain information about these processes and their interrelations.

Mediterranean ecosystems are reported to be one of the most vulnerable biomes on Earth in relation to future climate scenarios [Sala *et al*., 2000; Schröter *et al*., 2005; IPCC IV Assessment Report 2007 (http://www.ipcc-wg2.org/)]. Water constraint is the most characteristic limiting factor of Mediterranean-type ecosystems, affecting primary production, species richness and soil genesis (Roy *et al*., 1995; Aerts, 1997, Yaalon, 1997; Whittaker *et al*., 2007). Furthermore, the slow process of soil formation in these environments is frequently cancelled out by soil water erosion during intense rainfall events, enhanced by the lack of a continuous vegetative cover. Deforestation, cultivation, forest fires and grazing by domestic livestock have been the main perturbation agents along the human history of the Mediterranean Basin causing the loss of species and enhancing soil erosion (Grove & Rackham, 2001). Some of the consequences of deforestation on soil properties are manifested by the coarsening of the soil particle size distribution and the loss in organic carbon and nutrients (Lavee *et al*., 1998; Martínez-Mena *et al*., 2002; Xiao *et al*., 2006). Enhanced erosion also reduces soil depth, water retention, organic content, nutrients and soil biota, and therefore the soil aptitude to support plants (Pimentel & Kounang, 1998; Gómez-Plaza *et al*., 2000; Martínez-Mena *et al*., 2002) which in turn increases the risk of soil erosion giving rise to a positive feedback that underlies the desertification process (Geist & Lambin, 2004).

The population in Mediterranean areas is expected to continue to increase during the present century with an increasing impact on land use, especially in the southern rim where deforestation and cultivation will continue to the rhythm of population increase (Mazzoleni *et al*., 2004) and a increase in the recurrence and virulence of forest fires in the north rim (Schröter *et al*., 2005). As a consequence, it can be hypothesized that species loss and soil erosion will be intensified in those areas. Moreover, predictions from climate models anticipate a decrease in soil water content and an increase of air temperatures for the Mediterranean Basin (Schröter *et al*., 2005), which lead to reduced plant cover and species richness and also changes in plant growth-form proportions (Specht & Specht, 1995; Allen & Breshears, 1998). Predicted climate change could also directly and indirectly affect soil erosion rates. On the one hand, it is expected that erosion rates increase up to 10–30% even if rainfall amount declines (Nearing *et al*., 2004). On the other hand, climate change will reduce soil organic matter and nutrient cycling, therefore lowering the soil characteristics related to them such as soil water retention and stability against water erosion (Boix-Fayos *et al*., 1998; Lavee *et al*., 1998; Li *et al*., 2006), which furthermore may reduce plant cover and diversity (Ward *et al*., 2001; Guerrero-Campo & Monserrat-Martí, 2004).

In this paper, we aim to analyze the effect of climate change and soil erosion (as surrogate of land use change and forest fires) on vegetation and soil properties in a Mediterranean ecosystem at a regional scale and the relationships between vegetation and soil variables. We sampled data of soil and vegetation in a full crossed climate and erosion design in a single year. As Mediterranean climate is characterized as high between year variability in precipitation, which may have important consequences on vegetation variables and thus on soil properties, we checked how representative our results were before we discussed them. Because both climate change and soil erosion have a negative influence on the same vegetation and soil properties, we hypothesized that the overall effect of both drivers may fit better the antagonistic model than the additive or the synergistic ones. That is, plant species loss and soil degradation because of soil erosion or because of climate change may be so intense that further action by the other driver does not produce additional damage to these variables. Specifically, we attempt to answer the following questions: To what extent does climate change and soil erosion negatively affect vegetation and related soil properties? If any, are these effects additive, antagonistic or synergistic? Are plant species richness and plant cover related with soil properties in a similar way?

Material and methods

Study system

The study system is located at the basin of the Alfambra River (Teruel, Spain). This basin occupies 4000 km^2, with an altitude between 900 and 1300 m a.s.l. It is composed of Tertiary limestones, calcareous marls and sands, which were deeply eroded during the Quaternary by the Alfambra and Turia river systems. Soils derived from these rocks are loam to sandy–loamy, calcareous (10–40% CO_3Ca content) and nonsaline ($< 0.45\,dS\,m^{-1}$). The region suffered from intense deforestation during the last 3500 years (Stevenson, 2000), mainly by fuel, domestic livestock and dry land agriculture. A noticeable climatic contrast exists in the basin, its north and south extremes reproducing the predicted changes in temperature and precipitation for the next 40 years in the region: ca. 2 °C increment in annual average temperature and 25% reduction in annual precipitation and also the seasonal course of temperatures and precipitation (de Castro *et al.*, 2005). At the northern- and southernmost extremes of the basin, yearly average temperature and precipitation are 10.3 °C and 484 mm and 11.9 °C and 368 mm, respectively (data from the 1960–1990 period of the Bueña and Teruel meteorological stations, respectively, provided by the National Meteorology Agency, Ministerio de Medio Ambiente, http:/www.aemet.es/). The entire basin shared the same regional seasonal pattern of precipitation; therefore, we found high and significant correlations in the interannual variation in precipitation between sites in all the seasons in the 1991–2005 period (annual: $r = 0.713$, $P = 0.004$; spring: $r = 0.581$, $P = 0.029$; summer: $r = 0.790$, $P = 0.001$; autumn: $r = 0.765$, $P = 0.001$; winter: $r = 0.827$, $P < 0.001$). Associated with the climate variation, there is a change in vegetation. Mature vegetation varies from deciduous oak forest (*Quercus faginea*) at the northern extreme of the basin to juniper forest (*Juniperus thurifera*) at the southern limit. Despite the differences in climate and mature vegetation, both extremes shared 47% of their plant species (our unpublished data), indicating that long distance seed dispersal and plant species migration along the basin is ensured by local movement of sheep herds and agricultural machinery. At both climate extremes of the basin, two geomorphic forms were selected. They consisted of highlands and their associated hillslopes. Highlands are 10–100 km^2 flat forested areas with 0.03–0.7 km^2 clearings covered with herbs and shrubs, and with no signs of water erosion. Hillslopes are deforested slopes with occasional trees and a sparse layer of shrubs and herbs, 100–500 m long, 25–30° steep and with $25 \pm 1.1\%$ of the soil surface area occupied by rills ≥ 5 cm wide. There is a huge variation in erosion rate between these two treatments, 650–790% after using the standard slope factor of the Universal Soil Loss Equation (Wischmeier & Smith, 1978). However, this difference is into the range of soil erosion increase as a consequence of deforestation, cultivation and forest fires in Mediterranean areas (García-Ruiz *et al.*, 1995; Campo *et al.*, 2006; Cerdan *et al.*, 2006; and references herein).

Sampling design and analysis

A 2×2 full-crossed design was used to analyze the interaction between climate change and soil erosion on the study variables. One area at the northernmost extreme of the basin ('cool & wet' hereafter) (40°50′N and 1°9′W) and another at the southernmost extreme of the basin ('warm & dry' hereafter) (40°19′N and 1°9′W) both differing in climate characteristics were the treatment levels to test for the effects of climate change on the variables. In each climatic area, two geomorphic positions consisting of highlands ('no erosion' hereafter) and hillslopes ('high erosion' hereafter) were the treatment levels used to test for the effects of erosion on the variables within each climate. For every treatment combination, we selected 15 independent sites. Site selection criteria for the 'no erosion' treatment were forest clearings greater than 0.05 km^2 located at least 100 m apart from each other, with a slope angle lesser than 5° and south-oriented. Site selection criteria for the 'high erosion' treatment were midslope sectors of hillslopes longer than 100 m length, south oriented, 25–30° steep, separated by ravines from each other and with similar rill development ($24.5 \pm 7.2\%$ of rill cover in the 'cool & wet' and 'high erosion' site vs. $26.0 \pm 5.5\%$ in the 'warm & dry' and 'high erosion' one, see 'Material and methods' for sampling details). To avoid for the uncontrolled influence of land use on the study variables, we sampled only sites with no signs of cultivation or outcrops and with a similar grazing regime (0.60–0.70 sheeps $\text{ha}^{-1}\,\text{yr}^{-1}$ along the last 50 years (DGA, www.aragob.es/).

In the spring of 2006, we marked one 1 m × 20 m plot across the slope in every sampling site, measured the slope angle and aspect with an inclinometer and compass with ± 1° precision and recorded all the plant species present in the plots. We also measured the plant cover and the soil surface occupied by rills using the line-intercept method. We placed a 20 m measuring tape along the southernmost limit of the plots. The length of the measuring tape which was intercepted by a plant, divided by the total length of the line sampled, was considered an estimate of the proportion of the area covered by that species. In the same way, we estimated rill cover by measuring rills larger than 5 cm and deeper than 1 cm. We used the number of plant species per plot as a measure of species richness. All the species were assigned to a growth-form type: annual, herbaceous perennial or woody. We used this functional classification because they are broad functional types related to longevity and resource acquisition that have long been proposed and used as indicators of climate change and disturbance (Lavorel *et al.*, 2007).

At the end of the summer of 2006, we took five soil subsamples 5 cm deep and 300 cm^3 volume at regular distances in all plots where plant species were recorded. These subsamples were mixed up in a single soil sample per plot, air-dried and sieved through a 2 mm mesh before laboratory analysis. Additionally, we took three 57.73 cm^3 soil cores per plot for bulk density determination at the same depth as previous soil samples and the average value per plot was used for comparisons. Soil analysis consisted of fine sand content (0.50–0.05 mm), soil aggregate stability (percentage of water stable soil aggregates), water holding capacity [expressed as the volumetric difference between soil moisture content at field capacity (33 kPa) and wilting point (1500 kPa), determined with a pressure chamber], pH (1 : 2.5 w/v), soil organic content (potassium dichromate oxidation), total nitrogen (Kjeldalh) and soluble phosphorus (Olsen). Laboratory analyses were performed following the standard procedures for soil and water analyses (Klute, 1986; Page *et al*., 1986) but the analysis of water stable soil aggregates followed the method of Primo & Carrasco (1973). Soil data was expressed on a dry weight basis. Additionally, the water and nutrient variables were corrected to account for the rock fragment content of the samples, as proposed by Poesen & Lavee (1994). We used fine sand content as an indicator of soil degradation (Xiao *et al*., 2006). Bulk density and soil aggregate stability inform us about the susceptibility of soils to erosion. Organic matter, total nitrogen and soluble phosphorus were used as surrogates of soil fertility. The C : N relation was used as indicator of litter characteristics of the vegetation and water holding capacity was used as a surrogate of soil moisture available for plant functions (germination and development).

Statistic analyses were performed with SAS v. 9.1 (SAS Institute 2005, Cary, NC, USA). We used the GLM function to analyze the effects of the explanatory variables (climate, erosion and their interaction) on the response variables (vegetation and soil variables). From the linear models, we obtained the net balance $|i-(a+b)|$ in the change of the response variables caused by the interaction i compared with that change caused by the main effects a and b (climate and erosion). When this balance is not different to 0 we assume the additive model. When the net balance is greater than 0 we assume the synergistic model and when it is smaller than 0 we assume the antagonistic model (see Fig. 1).

The Pearson correlation coefficient was used to analyze for the relationships between vegetation and soil variables. Because multiple tests were performed simultaneously, we apply the sequential Bonferroni procedure to control for alpha inflation of *P*-values. The variables were checked for normality and homoscedascidity and transformed when necessary to fulfil these conditions. We discarded one of the sampling points of the 'cool & wet' and 'high erosion' treatment because it behaved as an outlier in the linear models for most of the plant and soil variables studied. After revisiting the sampling site, we were aware that this point was influenced by recent hillslope regularization as a consequence of the construction of a road 100 m below.

Results

All the studied vegetation and soil properties were intense and negatively affected by climate and soil erosion and their interaction (Fig. 2) except for the C : N ratio. Both climate and soil erosion caused a severe reduction in plant species richness and the reduction due to soil erosion was greater in the 'cool and wet' climate extreme than in the 'warm & dry' one (19 vs. 3 sp.). The decrease in plant species richness at the plot scale was satisfactorily explained by the linear model ($R^2 = 0.81$) (Fig. 2) and was coherent with the antagonistic model (Table 1). That is, the interaction term of the linear model was statistically significant and its size effect on species richness was lower than the sum of the size effects of the climate and soil erosion. When the effect of climate and soil erosion on plant functional groups was analyzed, we found a more detailed picture. The richness of perennial herbaceous and that of woody species were affected in the same way as total species richness and the linear models explained a similar proportion of variance (Fig. 2). However, the number of annual species per plot was higher in the 'warm & dry' plots than in the 'cool & wet' ones and was lower in the 'high erosion' than in the 'no erosion' plots. Despite these differences among functional groups, all three linear models fitted the antagonistic model (Table 1).

Plant cover was lower than 40% in all plots and it was negatively affected by the considered factors too but the linear model explained only 38% of the variation in plant cover at the plot scale. However, differently to species richness, the term interaction was not significant, thus fitting the additive model instead of the antagonistic one (Table 1 and Fig. 2) and both climate and erosion lowered plant cover by a similar amount (7.0% and 6.4%, respectively). The effect of both factors on plant cover differed among the functional groups considered. So, the cover of perennial herbaceous plants was negatively affected by both climate and soil erosion whereas cover of woody plants increased as a consequence of both factors (Fig. 2). The cover of annual plants was so negligible (<0.1%) that it was not considered in the analysis. The amount of variance explained by the linear model of each functional group was higher than that in which the total plant cover was considered. The increase in variance explained by the model was greater in the model of perennial herbaceous cover than in that of the woody cover (Fig. 2) and the interaction term was significant only for the woody plant cover model, which also held the antagonistic model. Similarly to species richness, the effect of soil erosion on the cover of woody plants was stronger in the 'cool & wet' climate than in the 'warm & dry' one.

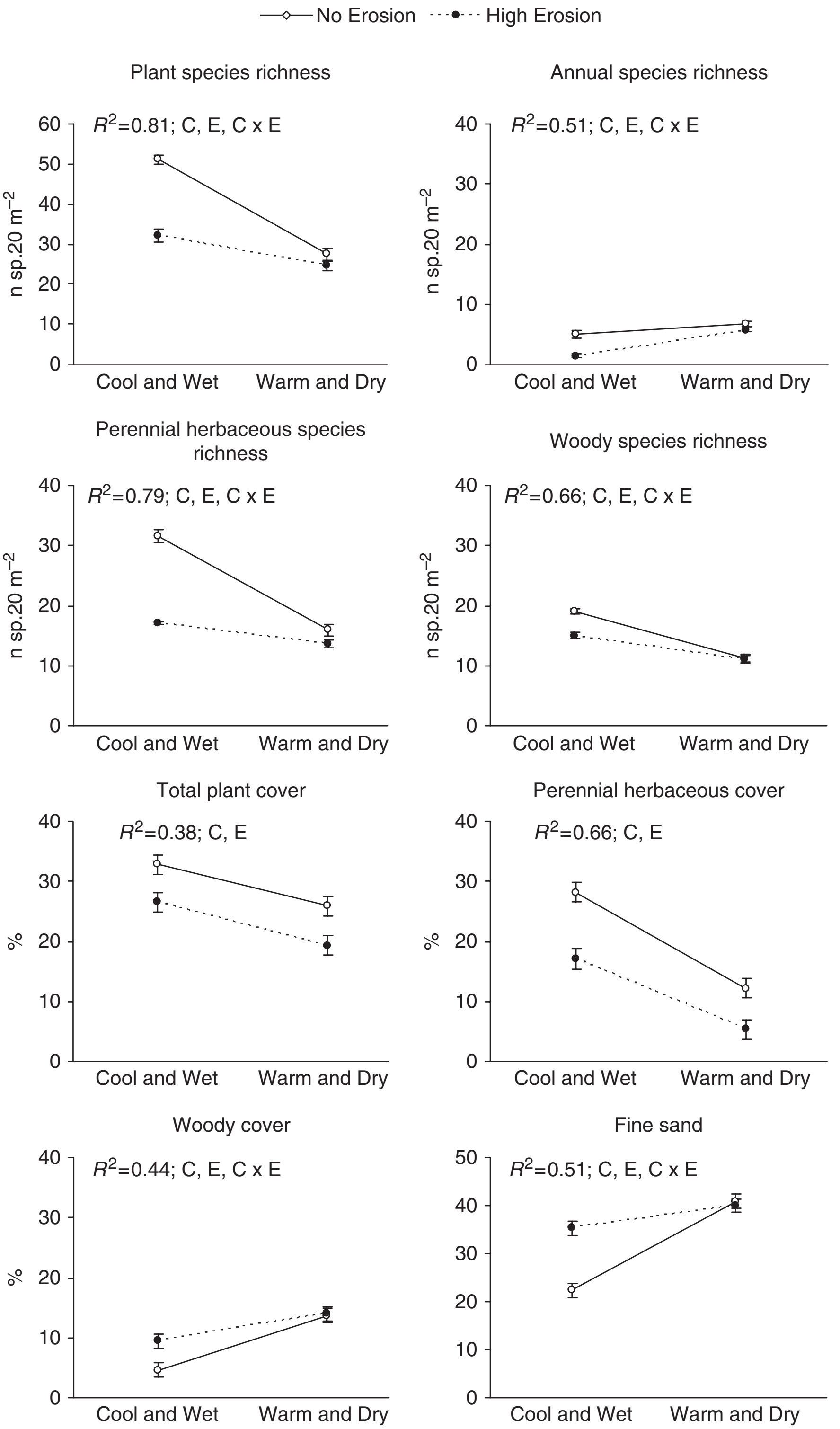

Fig. 2 Interaction plots for the effects of climate and erosion on plant and soil variables. Values are least square means ± 1 SD ($n = 15$) of untransformed variables. The text at the top of each panel indicates significant ($P < 0.05$) coefficient of determination of the linear model for the response variable and significant effects of climate (C), erosion (E) and their interaction (C × E).

Additionally, the effect of climate on perennial herbaceous cover was larger than the effect of soil erosion (a reduction of 14% and 9%, respectively).

With regards to soil properties, the linear models explained a great amount of variation except for the C : N ratio (0.02%). Like the vegetation variables, all soil

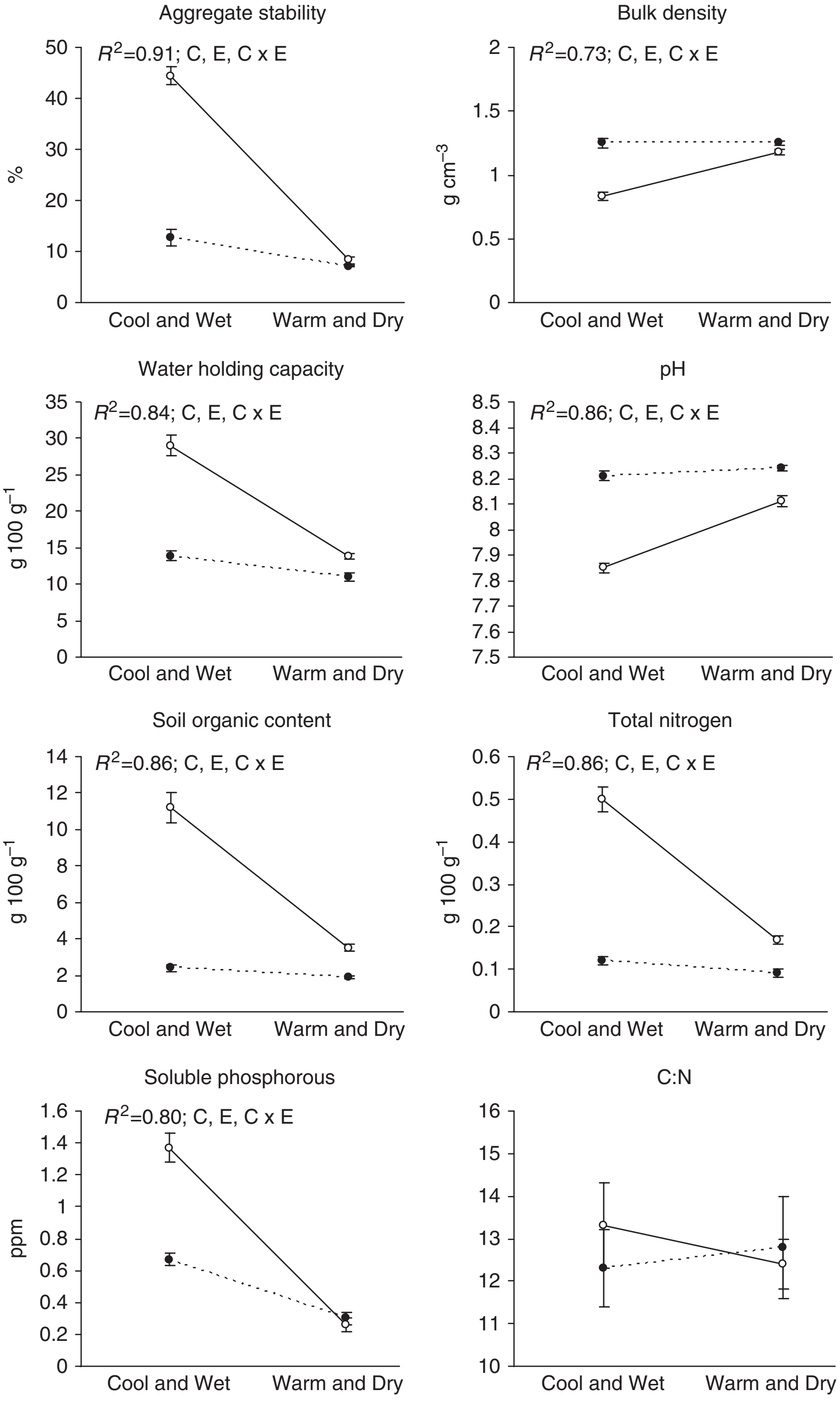

Fig. 2 Continued.

variables but the C : N ratio were negative and significantly affected by climate and soil erosion and fitted the antagonistic model (Fig. 2 and Table 1). Likewise, soil properties were more negatively affected by soil erosion in the 'cool & wet' climate extreme than in the 'warm & dry' one (Fig. 2).

Although species richness and plant cover did not differ in the signs of the coefficients of correlation with

Table 1 Net balance between the change in the response variables caused by the interaction between climate and erosion and the change caused by the main effects of both factors

	$\mid i \mid - \mid (a + b) \mid$	Model
Species richness (*n*)		
All plant species	**−16.05 ± 5.25**	Antagonistic
Annual plants	**−2.50 ± 2.04**	Antagonistic
Perennial herbaceous plants	**−12.27 ± 3.86**	Antagonistic
Woody plants	**−3.67 ± 2.49**	Antagonistic
Plant cover (%)		
All plant species	0.30 ± 6.39	Additive
Perennial herbaceous plants	−4.30 ± 6.33	Additive
Woody plants	**−4.60 ± 4.57**	Antagonistic
Soil properties		
Fine sand (%)	**−9.28 ± 4.00**	Antagonistic
Aggregate stability (%)	**−30.64 ± 4.98**	Antagonistic
Bulk density (g cm^{-3})	**−0.34 ± 0.12**	Antagonistic
Water holding capacity (g 100 g^{-1})	**−12.33 ± 3.33**	Antagonistic
pH	**−0.23 ± 0.06**	Antagonistic
*Soil organic content (g 100 g^{-1})	**−0.90 ± 0.29**	Antagonistic
*Total nitrogen (g 100 g^{-1})	**−0.81 ± 0.27**	Antagonistic
Soluble phosphorus (ppm)	**−0.73 ± 0.23**	Antagonistic

Values are absolute values of mean ± 95% confidence interval (*i*: amount of change on the variable caused by the interaction between climate and soil erosion, *a*: amount of change on the variable caused by changes in climate, *b*: amount of change on the variable caused by changes in soil erosion). The balance cannot be different to 0 (additive model), greater than 0 (synergistic model) and smaller than 0 (antagonistic model) (see also Fig. 1). Bold numbers indicate significant departure from 0 at $P < 0.05$. Only variables holding significant regression models were considered.

*Data log-transformed

soil variables they differed in the strength of their correlations (Table 2). Plant species richness was more strongly correlated with all the soil variables than plant cover and this also occurred when the functional groups were considered separately (Table 2). All the correlations were significant except that of the annual plant richness and that of the C : N ratio. Plant species richness and plant cover correlated positively with all the soil variables but with fine sand content, bulk density and pH. When the plant functional groups were considered, the strength and the sign of the correlation remained for perennial herbaceous and woody species richness and also for the cover of perennial herbaceous (Table 2) but the cover of woody plants correlated weaker with soil variables and the sign of the correlation was inverse to that of the cover of herbaceous plants (Table 2).

Discussion

As expected, we found a strong correlation between most plant and soil variables and a negative impact of increasing soil erosion (as surrogate of land use change) and the predicted changes of temperature and precipitation for the next 40 years on most of the studied plant and soil variables.

The joint effect of both drivers on the studied variables did not accommodate the synergistic model predicted by Sala *et al*. (2000). Most of the variables fitted the antagonistic model. That is, the single effect of climate change or soil erosion on plant species richness and soil properties is so negative that when the other driver is acting on the same system there is no further effect on species loss or deterioration of soil properties. However, this was not the case for most variables

Table 2 Pearson's correlation coefficients between plant and soil variables

	FS	AS	BD	WHC	SOC*	N*	P	pH	C : N
Species richness (*n*)									
All plant species	**−0.7840**	**0.8647**	**−0.7699**	**0.8176**	**0.8102**	**0.7852**	**0.7964**	**−0.7817**	0.1570
Annual plants	−0.0980	0.0033	−0.1835	0.0199	0.1524	0.1600	−0.2141	−0.1871	−0.0199
Perennial herbaceous plants	**−0.7931**	**0.8714**	**−0.7943**	**0.8237**	**0.8013**	**0.8097**	**0.7665**	**−0.8166**	0.0557
Woody plants	**−0.6290**	**0.7050**	**−0.5993**	**0.6713**	**0.6734**	**0.5882**	**0.7074**	**−0.5794**	**0.3241**
Plant cover (%)									
All plant species	**−0.3750**	**0.5894**	**−0.5558**	**0.5149**	**0.5971**	**0.5506**	**0.5172**	**−0.5856**	0.2255
Perennial herbaceous plants	**−0.5790**	**0.7543**	**−0.7154**	**0.7310**	**0.7272**	**0.7074**	**0.6969**	**−0.7484**	0.1359
Woody plants	**0.5320**	**−0.5583**	**0.5336**	**−0.6157**	**−0.4998**	**−0.5264**	**−0.5519**	**0.5528**	0.0580

Bold coefficients indicate correlations significant at $P < 0.05$.

FS, fine sand; AS, aggregate stability; BD, bulk density; WHC, water holding capacity; SOC, soil organic content; N, total Nitrogen; P, soluble phosphorous.

*Data log-transformed

related to plant cover. Total plant cover and cover provided only by perennial herbaceous species fitted the additive model, thus they suffered from additional deterioration when the other driver also affected the system.

Our sampling work was performed under the relative drought conditions prevailing during the spring of 2006 (61.5 mm for the 'cool & wet' site and 80.4 mm for the 'warm & dry' site), after a 3-year period wetter than the average (211.3 mm for the 2002–2004 period vs. 150.6 mm for the 1960–1990 period in the 'cool & wet' site and 174.0 vs. 106.7 mm in the 'warm & dry' site). This wet period might have generated good conditions for plant reproduction and establishment. As variation in the amount and rhythm of precipitation influences seed production, germination and the establishment of annual plants in the semiarid Mediterranean (Sher *et al*., 2004, Tielborger & Valleriani, 2005), it may affect the ability to detect annual plant species. Therefore, model performances of annual species richness would vary in years with different precipitation. However, perennial plants and physical and chemical soil properties are reported to be less responsive in the short-term to between year variability in annual precipitation in semiarid ecosystems (Boix-Fayos *et al*., 1998, Kieft *et al*., 1998, Adler & Levine, 2007, Meyer *et al*., 2007, Sardans & Peñuelas, 2007, Singh *et al*., 2007) except after multiyear drought periods or after catastrophic drought events with a long time recurrence (Bardgett, 2005, Lloret *et al*., 2007, Miriti, 2007). In consequence, we consider that the data obtained in the spring of 2006 make model performance for perennial species and soil variables reliable.

In our system, the 'warm & dry' and 'high erosion' sites had more species and also had better soil properties than we had expected under the scenarios of synergistic or additive interaction between climate change and soil erosion. This extra species may thus be responsible for the improved soil properties we found, despite the fact that plant cover was similarly reduced by soil erosion at both extremes of the climate gradient (Table 1). Alternatively, these improved soil properties could be the consequence of the structure or the functional properties of the species in the 'warm & dry' and 'high erosion' site.

We found that 35% of the species were present in less than four out of fifteen plots in the 'cool & wet' and 'no erosion' site, and 16% of these species were annuals, but the number of rare species increased up to 44% in the 'warm & dry' and 'high erosion' site and up to 30% of these species were annuals that have a negligible contribution to plant cover. Several authors have also found an increase in the contribution of ephemeral annual plants to species diversity with increasing soil erosion and climate drought (Osem *et al*., 2002; Li *et al*., 2006; Zhou *et al*., 2006). We propose that the contribution to certain ecosystem processes of that extra species we found in the 'warm & dry' and 'high erosion' extreme of the gradient may explain these differences. It is now widely accepted that certain plant species, independently of their functional traits, can promote particular mycorrhiza and microbe associations that can eventually modify the rate of decomposition and nutrient availability for plants (Niklaus *et al*., 2001; Wardle *et al*., 2003; Johnson *et al*., 2004). This, in turn, has direct and indirect consequences for seedling recruitment and survival (van der Heijden, 2004).

The different behaviors of plant cover and plant species richness in relation to soil properties can also aid to explain these differences. Although both variables were significantly correlated ($r_P = 0.5637$; $n = 59$; $P < 0.0001$) and also similarly related to soil properties, plant species richness correlated with soil properties more strongly than plant cover did. The positive relationships between plant cover and soil properties are considered to be mainly due to litter accumulation onto soils and their subsequent decomposition and nutrient liberation, the accretion of soil aggregates and the increase of water infiltration. But the effect of litter quality should also be taken into account (Wardle *et al*., 2006). Litter of herbaceous species usually decomposes to higher rates than that of woody species because of differences in their content of lignin, hemicellulose and secondary chemical compounds (Cornelissen *et al*., 1999). Thus, the higher the proportion of herbaceous species living in a community, the higher would be the incorporation of organic matter into the soil. As the differences in plant cover among treatments in our study were mainly due to variations in perennial herbaceous cover ($r_{P(\text{plant cover} \times \text{perennial herbaceous cover})} = 0.8311$, $P < 0.0001$) the positive correlation between plant cover and soil organic, nitrogen and phosphorous content and aggregate stability can be attributed mostly to the cover of perennial herbaceous plants. This interpretation is also supported by the lack of relationship between plant cover and woody cover ($r_P = -0.1493$ $P = 0.2592$), the inverse correlation between woody cover and soil properties and the positive and significant correlation between woody species richness and the C : N ratio, an indicator of litter decomposition (Table 2).

There is solid evidence that plant–soil feedbacks are strongest in water and in nutrient limited ecosystems (Ehrenfeld *et al*., 2005). In these systems, there is a strong correlation between species richness and soil properties that can be attributed to the increase in nutrient cycling and water infiltration with the increase in the number of species living in, thus leading to an increase in the availability of soil resources (Ward *et al*., 2001; Maestre & Cortina, 2004; Li *et al*., 2006). Furthermore, increasing plant species richness could positively affect soils through the increased probability of including plants with different tissue structures and chemical properties that promote available niches for soil biota, thus enhancing litter decomposition, nutrient mineralization and soil aggregation in a plant–soil feedback process (Oades, 1993; Tisdall, 1994; Bezemer *et al*., 2006). Accordingly, in our study case, perennial herbaceous richness, woody richness and total species richness were strong and positively correlated with soil nutrient stocks, soil aggregate stability and water holding capacity (Table 2).

The evidence that soil erosion affected more negatively plant species richness and soil properties at the ‘cool & wet’ extreme than those at the ‘warm & dry’ extreme indicates that a threshold may exist between the two extremes of our climatic gradient. Alternatively, we can interpret the findings to suggest that the ‘warm and dry’ area represents the threshold itself and has buffer capacity to reduce dramatic changes due to disturbance. Annual rainfall between 350 and 400 mm has been defined as a threshold in rangelands that separates subhumid systems, which are relatively rich in species and are controlled by biotic factors such as plant interactions, microbial activity and organic matter production and decomposition, from poorer arid systems that are controlled by abiotic factors such as lithology and climatic interactions (Lavee *et al*., 1998; Puigdefábregas, 1998). Above the threshold, perturbations like overgrazing are buffered by a more diverse community (both in species and functional groups) and cause vegetation to change asymptotically around a particular point, which structure and composition are in equilibrium with perturbation regime and environmental conditions. Below this threshold, reduced numbers in species and functional groups do not lead to the recovery of the previous plant community after cessation of grazing or other disturbances (Didham *et al*., 2005).

The results presented here may be considered as an indication of the output of the joint effect of climate change and soil erosion. Although our results are coherent with those from previous experimental and observational studies, the correlative approach we used precludes inferring causal relations between the studied factors and variables. Past uses, perturbations and geomorphic processes could have differentially affected the study plots thus accounting for some of the patterns we attributed to the effects of climate change and soil erosion.

Our results also have important implications for resource management. On the one hand, our finding that the species richer communities suffered from higher species loss and heavier soil deterioration by erosion than poorer communities cautioned us against the generalization of the view that climate warming will have worse consequences on low diverse ecosystems than on richer ones (Proulx & Mazumder, 1998; Wilson & Tilman, 2002; Harrison *et al*., 2003; Martínez-Fernández & Esteve, 2005). On the other hand, our results reinforce the role that the increase in fine sand fraction, the decrease in soil organic content and nutrients, and the change in dominance from perennial herbaceous plants to woody shrubs have played as indicators of land desertification (Schlesinger *et al*., 1996, Lavee *et al*., 1998, Sarah, 2006; Xiao *et al*., 2006). However, plant cover, which has been extensively used in satellite desertification monitoring, would be a poorer indicator of ecosystem health than plant species richness, at least in semiarid ecosystems.

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