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REGULAR ARTICLE

Fragmentation modulates the strong impact of habitat quality and plant cover on fertility and microbial activity of semiarid gypsum soils

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Abstract
Background and aims Plant-soil interactions are a crucial component of ecosystem functioning. However, most global change studies focus on plant communities, with information on soil properties and performance being scarce. Our goal was to assess the individual and joint effect of habitat heterogeneity and three global change drivers (fragmentation, loss of habitat quality and climate change) on nutrient availability and soil microbial activity in Mediterranean gypsum soils.

Methods We collected soil samples from an experimental field site from large/small fragments, with high/low habitat quality, subjected to two levels of water availability (dry/mesic) and from two microhabitats (under the canopy of shrubs and in the open). We analyzed nutrient concentrations (C, N and P) and enzymatic activities (ß-glucosidase, urease and acid phosphatase).
Results C, N, P content, ß-glucosidase, urease and acid phosphatase activities were higher under the canopy than in the open and in high- than in poor- habitat quality sites. These differences were exacerbated in small fragments.
Conclusions The strong interdependence between plant and soil was modulated by fragmentation in the Mediterranean gypsum soils studied. Drought did not exert a direct negative effect on soil properties, although the effect might arise under more intense drought or under drought taking place at times of the year different from those explored here. Results highlight the importance of considering several drivers simultaneously to forecast realistic ecosystem responses to global change.

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Introduction

Soil nutrient availability is one of the most important factors influencing plant growth and ecosystem

functioning (Lambers et al. 1998). The distribution of nutrients in the soil is highly heterogeneous, which in turn affects the structure and composition of plant communities (Kruger 1979; Henkin et al. 1998). Moreover, several studies have shown that soil heterogeneity can modulate the impact of global change drivers on plant communities (Maestre and Reynolds 2006; Wacker et al. 2008). Soil nutrient heterogeneity is also associated with microbial activity (Gallardo and Schlesinger 1994), which in turn are responsible for essential processes in the ecosystem such as energy transformation, mineralization of plant litter and nutrient cycling (Panikov 1999). In agreement with this, recent studies have evidenced the importance of considering the below-aboveground interactions of the biota to properly understand ecosystem functioning (van der Putten et al. 2009; Kardol and Wardle 2010; Garcia-Palacios et al. 2011).

Climatic conditions such as soil and air temperature and water availability affect enzyme activity through increased microbial growth and substrate availability (Noy-Meir 1973; Parkinson and Coleman 1991). Several studies have shown the importance of water availability for both microbial activity (Kramer and Green 2000; Li and Sarah 2003; Sardans and Penuelas 2005) and soil nutrient availability (Jensen et al. 2003; Sardans and Penuelas 2004). Consequently, changes in temperature or precipitation promoted by climate change are likely to alter nutrient cycles (Sardans and Penuelas 2007) and nutrient availability for plants (Michelsen et al. 1999). This becomes especially important in Mediterranean ecosystems, where global circulations models forecast reductions in precipitation and an increase in maximum temperatures together with heavier storms (Christensen 2007). Higher temperatures will further decrease soil water availability and exacerbate the effects of drought in these environments (Larcher 2000), while heavy storms increase nutrient loss by lixiviation (Reynolds et al. 2004), and increased runoff decreases water infiltration (Wainwright 1996).

Besides climate change, other global change drivers such as land use changes and habitat fragmentation can have dramatic effects on microbial and enzymatic activity and nutrient availability (Matias et al. 2010). Mediterranean ecosystems have been profoundly transformed over centuries due to human activities such as farming or agriculture (Valladares et al. 2008). These have caused fragmentation and reductions in habitat quality, important threats for biodiversity and natural resources conservation (Lavorel et al. 1998; Foley et al. 2005). Fragmentation decreases plant population size and increases isolation, which can lead to lower genetic variability and lower individual fitness and plant survival (Lienert 2004; Aguilar et al. 2006). As a consequence, soils in fragmented landscapes may have reduced organic inputs and thus reduced nutrient availability and cycling (Garcia et al. 2002). Reduced habitat quality has often been considered a result of habitat fragmentation (Harrison and Bruna 1999; Schleuning et al. 2008). However, in agricultural landscapes, changes in habitat quality may occur independently from fragmentation, through factors such as runoff and fertilizer drift into adjacent areas, intense ploughing, trampling or soil erosion (Boutin and Jobin 1998; Matesanz et al. 2009). Reduced habitat quality has also been associated to decreased plant cover and biological soil crust, which is translated into a meagre input of dead organic matter and a consequent decrease of microbial activities (Zak et al. 1994). However, the direct effect of habitat fragmentation and reduced habitat quality on soils attributes and performance remains largely unknown.

Interactions among global change drivers frequently generate non-additive effects, which in turn either attenuate or exacerbate ecosystem responses to individual drivers (Zavaleta et al. 2003; Matesanz et al. 2009). Several studies have addressed the interacting effects of global change drivers on ecosystems, but most of them have focussed on their influence on plant communities (Sala et al. 2000; Maestre and Reynolds 2006; Matesanz et al. 2009), while information on microbial communities and soil nutrient availability is particularly scarce (Cookson et al. 2007; Casals et al. 2009; Matias et al. 2010).

Our main goal was to assess the individual and joint effects on nutrient availability and soil microbial activity of three global change drivers that are especially important for Mediterranean ecosystems: habitat fragmentation, loss of habitat quality and water availability. Moreover, we assessed the influence of microhabitat heterogeneity (i.e. open vs. the understory of woody plants) and its interaction with these global change drivers on the same microbial and soil properties. We conducted a field experiment in a Mediterranean gypsum steppe with plots following a factorial design for the three drivers. Our working hypotheses were: (1) Habitat fragmentation, loss of habitat quality and reductions in rainfall decrease plant survival and productivity which are strongly related to soil attributes and

performance (Garcia et al. 2002; Zak et al. 2003). This in turn, will exert a negative effect on nutrient availability and microbial activity of Mediterranean gypsum soils; (2) synergistic interactions among drivers will amplify the negative impact of loss of habitat quality on soil nutrient availability (Matias et al. 2010); and (3) nutrient availability and microbial activity will increase under the canopy of shrubs in comparison with open interspaces and this microhabitat heterogeneity will modulate the influence of other global change drivers as suggested on other plant communities (Reich et al. 2001; Maestre and Reynolds 2006).

Materials and methods

Study site

The study was carried out near Belinchón in central Spain (745 m above sea level; 40° 03' N, 3° 03' O). The landscape is composed by gypsum soil hills (average slope was 11.7±0.3°) with remnants of natural vegetation interspersed in a matrix of dry-farm crops. Natural vegetation is dominated by creeping and cushion-like chamaephytes such as *Centaurea hyssopifolia* Vahl. (Compositae), *Helianthemum squamatum* (L.) Dum. Cours (Cistaceae), *Lepidium subulatum* L. (Cruciferae), *Thymus lacaitae* Pau (Labiatae) and *Teucrium pumilum* L. (Labiatae). Plant cover is usually low (<30%), and bare soil areas are often covered by a conspicuous biological soil crust, dominated by specialised lichens (Martinez et al. 2006). The area has a Mediterranean semiarid climate, with a mean annual precipitation of 433 mm, a pronounced summer drought, and a mean annual temperature of 13.8°C. The study was conducted over 2 years: 2005, which was the second driest year of the 56-year series (298 mm annual precipitation), and 2006, also a drier-than-average year, with annual precipitation of 371 mm (see detailed precipitation data of the study site in Online resource 1)

Experimental design and soil sampling

To test the effects of three global change drivers and their interactions on soil features and performance and to explore the effect of microhabitat, we conducted an experiment with four controlled factors: fragmentation, habitat quality, water availability and microhabitat. For each factor two levels were selected: large (L) and small (S) fragments, high (H) and poor (P) habitat quality, mesic (M, watered plants) and dry (D, non watered plants). Two microhabitats were considered for each combination of factors, under the understory of *C. hyssopifolia* (U, Understory) and open areas near the target plants (O, Open). We selected this plant species because it is the largest and most abundant chamaephyte in the local community.

To select the two levels of fragmentation we identified three small (area <1.5 ha) and three large (area >11 ha) fragments of natural vegetation (six fragments total) which were further characterized by measuring several vegetation attributes such as percentage of soil covered by plants, lichens and mosses, annual plants, perennial plants, litter and bare soil (see Online resource 2). Within each fragment, we randomly selected two plots of ca. 15×15 m of contrasting high- and poor-habitat quality (12 plots in total) according to plant cover as an integrative indicator of habitat suitability (see Matesanz et al. 2009 for a detailed characterisation of each habitat quality level). Each plot was further divided into two contiguous halves that were randomly assigned to one watering treatment. The irrigation experiment was conducted in the spring (May and June) of 2005 and 2006, simulating two different scenarios of water availability: non-watered plants (dry treatment) and watered plants (mesic treatment). Water was added to reach the median of the long-term series (1948–2004) in each month (Fig. 1). Plants were randomly selected within the mesic plot. Irrigation was then applied at the plant-level and consisted of adding 1 l of dechlorinated tap water per plant and application time. A 50×50 cm (0.25 m^2) rigid frame was placed around each watered plant so that the entire surface was watered and all the plants received the same amount of water, independently of their size. Each water application was equivalent to 4-mm rainfall events. Irrigation was performed at 5–6 days intervals. The non-watered (dry treatment) plants received ambient precipitation (equivalent to future drier scenarios due to the very dry spring conditions of the study years) and the irrigated plants received ambient precipitation plus the added water (equivalent to a typical year).

In July 2006, we randomly selected five plants per irrigation treatment and we collected soil samples from each microhabitat. The total number of soil samples was 240 (10 plants per plot x 12 plots x 2 microhabitats). We collected four sub-samples within the perimeter where the irrigation treatment was carried

out with a 6×6×10 cm metal soil core for each subsample, which were thoroughly mixed afterwards. Once in the laboratory, soil samples were sieved (2 mm grain) and air dried.

Biochemical and microbiological analysis

Total nitrogen (N) and total phosphorous (P) contents were determined by the Kjeldahl method (Radojevic and Bashkin 1999). Each soil sample was digested in 96% sulphuric acid for 3 h at 415°C and nutrient contents were determined through colorimetry by an automatic wet chemistry analyzer (Skalar 4000 SAN System, Segmented Flow Analyzer; Skalar, Breda, The Netherlands). Total organic carbon (C) was determined by Walkley and Black method (1934) modified by Yeomans and Bremmer (1989) by oxidation with potassium dichromate in acid medium and evaluating the excess of dichromate with 0.5 N ferrous ammonium sulphate.

β-glucosidase and acid phosphatase activities were estimated using Tabatabai method (1982), which determined colorimetrically the amount of p-nitrophenol produced from p-nitrophenyl- β-D-glucopyranoside, and p-nitrophenyl-phosphate, respectively, after 1 h of incubation at 37°C. The activities are expressed as grams of p-nitrophenol per gram of soil and hour (Moreno et al. 2003). Urease activity was determined colorimetrically by Nannipieri method (1980) measuring total ammonium produced from a buffered urea solution.

Statistical analysis

The effects of the different fixed factors (fragmentation, habitat quality, water availability and microhabitat) on the dependent variables (total organic C, total N, total P, β-glucosidase, urease and acid phosphatase activity) were analyzed using a four-way nested ANOVA model. The model included fragmentation (F, 1 df), habitat quality (Q, 1 df), water availability (W, 1 df) and microhabitat (MH, 1 df) as main fixed factors. Each sampling point was considered as a random factor nested within fragmentation level (sampling point (F), 4 df). We tested main effects of these fixed factors and also included all possible interactions between them. When significant interactions between two factors were found, we performed a one-way ANOVA to test for significant effects of one factor within each level of the second factor. Normality and homogeneity of variance in the dependent variables was tested prior to analyses by means of the Kolmogorov-Smirnov and the Levene's test. All statistical analyses were performed using Statistica 6.0 (StatSoft Inc., Tulsa, OK, USA).

Results

Soil nutrients

Total organic carbon, total N and total P were significantly higher in high quality habitats and under the understory of *C. hyssopifolia* (Fig. 2, Table 1). Loss of habitat quality had the strongest impact. Fragmentation and water availability had no significant direct effects on total organic C, N and P.

We found significant interactions between factors affecting all nutrients. The interaction between habitat quality and fragmentation had a significant effect on organic C (Table 1, Fig. 4a) and total N (Table 1, Fig. 4b). Organic C was lower in small than in large fragments in poor habitat quality plots (F=8.319 p=0.005), but not in high habitat quality plots (F=0.299, p=0.586). Total N did not differ significantly between large and small fragments neither in high habitat quality (F=3.295, p=0.072), nor in poor habitat quality plots (F=3.451, p=0.066). The interaction between habitat quality and microhabitat had a significant effect on total N (Table 1, Fig. 4c): total N did not differ between open and understory in high habitat quality plots (F=3.237, p=0.075), but it was significantly lower in poor habitat quality plots (F=21.875, p< 0.001). Finally, total P was affected by a significant interaction between habitat quality and water availability (Table 1, Fig. 4d), but we did not find significant differences between watering treatments within levels of habitat quality (F=0.340, p=0.560; F= 4.248, p=0.061 for high- and low-habitat quality, respectively).

Soil enzymatic activity

β-glucosidase and acid phosphatase activities were significantly affected by habitat quality and microhabitat, with habitat quality having the strongest impact (Table 1, Fig. 3a, c). Urease activity was significantly affected by microhabitat (Table 1, Fig. 3b). The

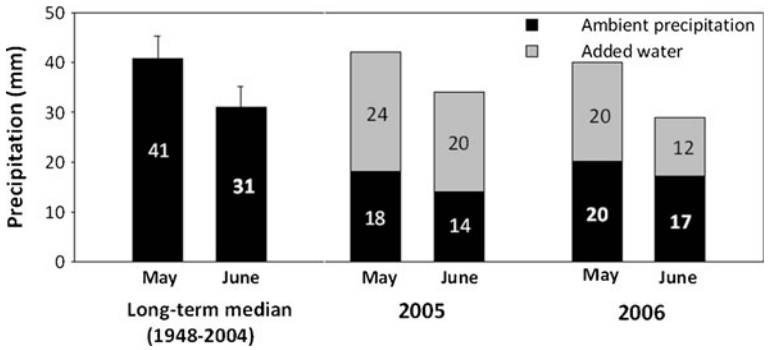

Fig. 1 Irrigation experiment. May and June precipitation medians (1948–2004 series) were used as a threshold for the irrigation treatment. Plants in the dry treatment received ambient precipitation, and plants in the mesic treatment received ambient precipitation plus added water (through 4 mm events and up to the median for the corresponding month)

activity of enzymes decreased in poor habitat quality plots, and it was lower in the open than under the understory (Table 1, Fig. 3). We found no significant main effects of fragmentation and water availability on ß- glucosidase, phosphatase and urease activity.

Phosphatase activity was significantly affected by the interaction between habitat quality and water availability (Table 1, Fig. 4e). Yet, we did not find significant differences between watering treatments within levels of habitat quality (F=1.513, p=0.221; F=4.141, p=0.064,

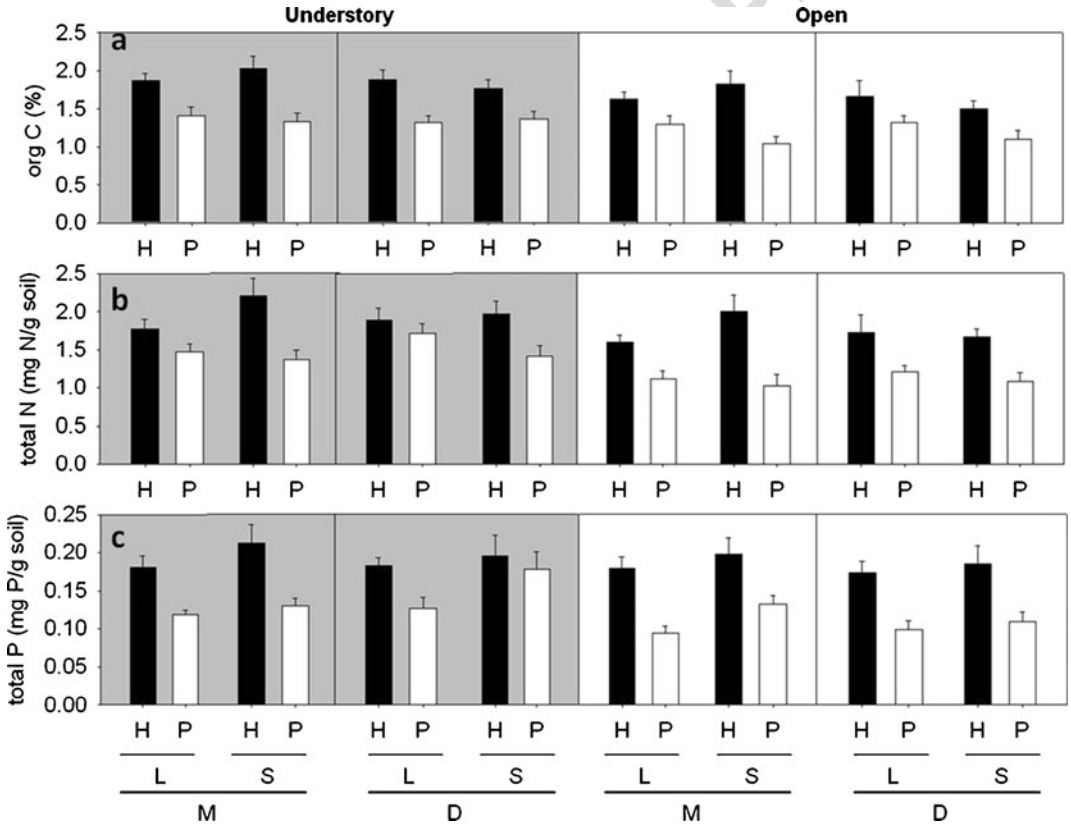

Fig. 2 Soil nutrient content across treatments. **a** Total organic C; **b** total N; **c** total P. Each half of a panel corresponds to data from understory (*left*) and open (*right*) microhabitats. Values are mean ± SE in each treatment. Different colours indicate significant differences between microhabitats (background color) and between high and poor habitat quality (bar colours). Abbreviations are: H, high-habitat quality; P, poor-habitat quality; L, large fragment; S small fragment; M, mesic treatment (watered plants); D, dry treatment (non-watered treatments)

t1.1 **Table 1** ANOVA results (F and *p*-values) for the soil nutrient contents and soil enzymatic activity. *N*=240 soil samples. NS: not significant. See results section for direction of the effects. Significant effects ($p<0.05$ are indicated in bold)

t1.2		Total organic C		Total N		Total P		β- glucosidase		Phosphatase		Urease	
t1.3		F	*p*	F	*p*	F	*p*	F	*p*	F	*p*	F	*p*
t1.4	Fragmentation (F)	0.561	NS	0.002	NS	0.324	NS	0.642	NS	3.214	NS	2.850	NS
t1.5	Habitat quality (Q)	**56.560**	**0.000**	**70.872**	**0.000**	**92.861**	**0.000**	**20.160**	**0.000**	**4.575**	**0.034**	0.045	NS
t1.6	Water availability (W)	0.045	NS	0.259	NS	1.257	NS	1.005	NS	0.668	NS	2.482	NS
t1.7	Microhabitat (MH)	**19.750**	**0.000**	**23.658**	**0.000**	**7.870**	**0.005**	**65.711**	**0.000**	**26.369**	**0.000**	**20.809**	**0.000**
t1.8	Q × F	**6.056**	**0.015**	**9.393**	**0.002**	0.347	NS	3.505	NS	2.554	NS	**4.214**	**0.041**
t1.9	F × W	2.121	NS	1.865	NS	0.576	NS	3.260	NS	1.642	NS	1.085	NS
t1.10	Q × W	3.315	NS	2.902	NS	**4.735**	**0.031**	0.251	NS	**6.214**	**0.013**	0.169	NS
t1.11	F × MH	0.109	NS	0.000	NS	0.290	NS	0.011	NS	0.361	NS	0.286	NS
t1.12	Q × MH	0.008	NS	**4.024**	**0.046**	2.216	NS	0.597	NS	0.122	NS	0.153	NS
t1.13	W × MH	0.949	NS	0.098	NS	0.284	NS	0.610	NS	0.462	NS	2.436	NS
t1.14	F × Q × W	0.214	NS	0.596	NS	3.195	NS	0.664	NS	0.594	NS	0.431	NS
t1.15	F × Q × MH	0.132	NS	0.088	NS	0.000	NS	0.342	NS	2.435	NS	1.796	NS
t1.16	F × W × MH	0.048	NS	0.175	NS	0.032	NS	0.048	NS	0.102	NS	0.003	NS
t1.17	Q × W × MH	0.075	NS	0.039	NS	0.238	NS	0.017	NS	0.176	NS	0.158	NS
t1.18	F × Q × W × MH	1.467	NS	0.071	NS	0.354	NS	0.005	NS	0.099	NS	0.262	NS
t1.19	Sampling point(F)	**4.291**	**0.002**	**10.440**	**0.000**	85.840	NS	**13.757**	**0.000**	1.622	NS	**14.997**	**0.000**

for high- and low-habitat quality, respectively). Urease activity was also affected by the interaction between habitat quality and fragmentation (Table 1, Fig. 4f): the difference between large and small fragments was greatest in poor habitat quality plots. Urease activity was greater in small fragments, both under poor ($F=7.227$, $p=0.008$) and under high habitat quality ($F=28.861$, $p<0.001$).

Discussion

Effects of habitat quality and habitat heterogeneity

As expected, total organic carbon, N and P, β-glucosidase and acid phosphatase activities were significantly reduced in open interspaces and in low quality habitat sites. The relative influence of fragmentation, water availability and habitat quality was different with a maximum impact associated with habitat degradation. The reduction of aboveground plant productivity in poor quality habitats underlies reduced organic C inputs, the main energy source for heterotrophic microbial communities (Zak et al. 2003; Allen and Schlesinger 2004). This result agrees with previous studies showing that microbial community composition and function depend directly on plant cover and soil organic matter content (Zak et al. 1994; Garcia et al. 2002). Limited nutrient input also explains the decrease in N and P content and consequent decrease in β-glucosidase and phosphatase activities. These results suggest that plant abundance significantly affects soil microorganisms and the ecosystem processes they mediate, like nutrient cycling (Schlesinger and Pilmanis 1998; Stephan et al. 2000; Tilman et al. 2001; Zak et al. 2003). Given that soil nutrient deficiencies limit plant growth (Henkin et al. 1998; Fenner 2001; Sardans and Penuelas 2004), we can expect reduced enzymatic activity to indirectly affect plant growth, highlighting the strong interdependence between plant and microbe soil communities, which involves positive feedbacks.

Microhabitat heterogeneity played an important role for soil properties, affecting both nutrient content and soil enzymatic activities. Higher enzymatic activity underneath the canopy of *C. hyssopifolia* and in high-quality sites may be due to the larger microbial and root biomass densities beneath the plants, which entails a faster nutrient intake and stimulates the synthesis and excretion of enzymes (Garcia et al. 2002;

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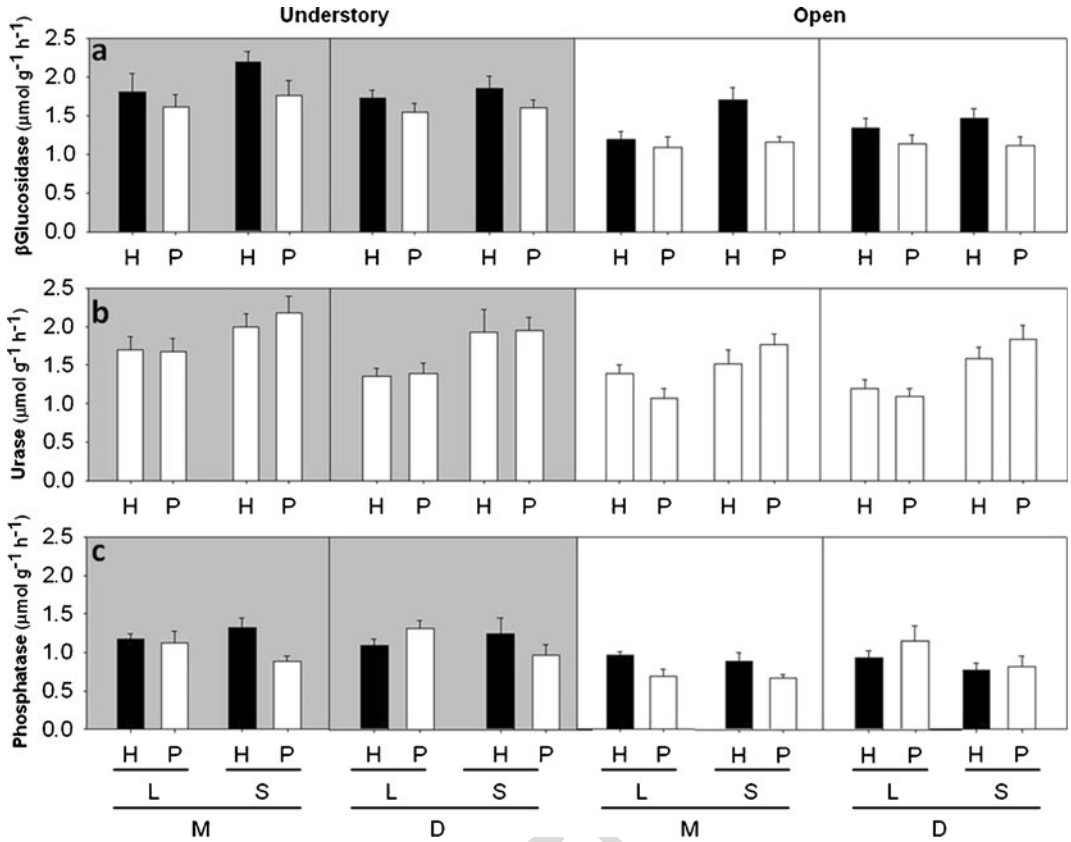

Fig. 3 Soil enzyme activity across treatments. **a** β-Glucosidase; **b** Urease; **c** Phosphatase. Values are mean ± SE in each treatment. Each half of a panel corresponds to data from understory and open microhabitats. Different colours indicate significant differences between microhabitats (background color) and between high and poor habitat quality (bar color). Abbreviations are: H, high-habitat quality; P, poor-habitat quality; L, large fragment; S small fragment; M, mesic treatment (watered plants); D, dry treatment (non-watered treatments). See text for details

Allen and Schlesinger 2004). Moreover, greater levels of plant production (e.g. litter production) also stimulate microbial enzymatic activity (Zak et al. 2003; Allen and Schlesinger 2004). ß-glucosidase, urease and acid phosphatase are hydrolases involved in the decomposition of complex compounds. In particular, ß-glucosidase has a key role in the C cycle, it is responsible for the transformation of large chains of carbohydrates into assimilable sugars (Eivazi and Zakaria 1993). Thus a decrease in ß-glucosidase activity has negative effects on the activity of other enzymes (Sardans and Penuelas 2005). These findings together with the patchy distribution of plants in Mediterranean gypsum soils support the idea that plant cover clumps in dry ecosystems function as resource islands with milder living conditions arranged in a barren matrix of bare soil (Maestre and Cortina 2002; Goberna et al. 2007).

The lack of direct effect of water availability could be explained by the different time scale at which this driver can impact on ecosystem properties. For example, in our study case, the 2 years of manipulative changes in water availability contrasts with the long term processes associated with loss of habitat quality. Nutrient availability usually shows a lagged response to climatic variations, sometimes taking even decades to respond to environmental variation in the case of so-called slow variables (Reynolds et al. 2007). However, enzymatic activities are rapid soil functional surrogates and therefore short-term effects of our water treatment can be expected. We did not detect these effects for the different water treatments due to our experiment mimicking either a mild or too short drought or a drought not affecting soils at the most responsive time of the year; it must be noted, however, that our drought simulation was guided both in extent

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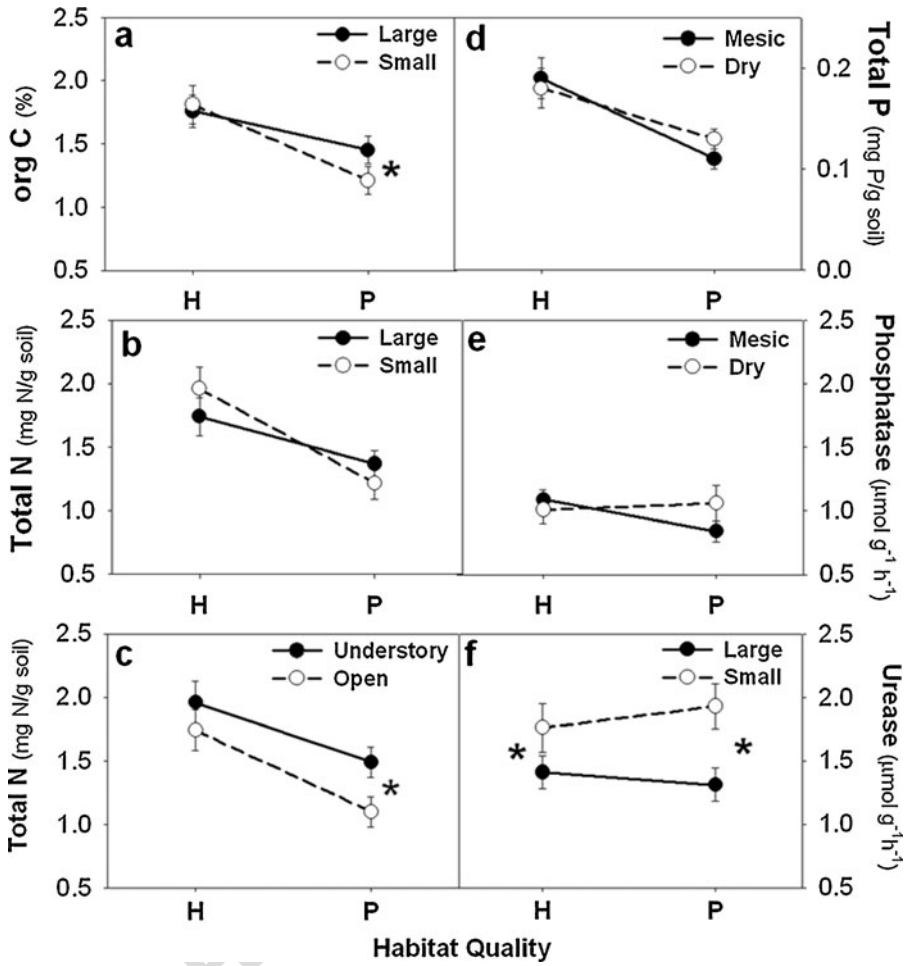

Fig. 4 Significant interactions between Habitat Quality and global change drivers (Fragmentation, Water availability and Microhabitat). Values are mean ± SE in each treatment. Graphs only show significant interactions between factors. An *asterisk* indicates significant differences (at $p<0.05$) between levels of a factor. Abbreviations are: H, high-habitat quality; P, poor-habitat quality

and timing by climate change scenarios and not by the responsiveness of soil biota. This explanation is supported by results from other studies showing that drought significantly decreased soil enzymatic activity when more intense rainfall reductions were simulated (Sardans and Penuelas 2005) or when long-term rainfall variations were explored (Li and Sarah 2003). Likewise, fragmentation did not have a significant direct effect on any of the response variables. According to the literature, microbial communities are, in general, not sensitive to habitat fragmentation and habitat size (Rantalainen et al. 2005 and 2008). However, this does not mean that fragmentation is irrelevant for soil functioning. We found that fragmentation indirectly affected soil performance (e.g. the effects of loss of habitat quality on nutrient availability were exacerbated in small fragments). Therefore, studying the effect of habitat fragmentation on soil features and performance is critical, especially in combination with other global change drivers.

Interactive effects of global change drivers

As hypothesised, habitat quality, fragmentation and water availability interactively affected nutrient availability and microbial activity of Mediterranean gypsum soils (Sala et al. 2000; Brook et al. 2008; Matesanz et al. 2009; Pias et al. 2010). First of all, we found that the negative impact of habitat quality loss on total organic C and total N was exacerbated in small fragments, which is relevant to predict the final outcome of land degradation on ecosystem functioning since, both drivers usually act together (Schleuning et al. 2008). Second, we found that the reduction of total N from high- to poor- habitat quality sites was greater in open areas than under the

understory of *C. hyssopifolia*. This result agrees with other studies showing that microhabitat heterogeneity modulates the impact of global change drivers such as loss of habitat quality (Maestre and Reynolds 2006). Furthermore, given that soil nutrient heterogeneity exerts a strong influence on the development of plant individuals and communities (Hodge et al. 2000; Day et al. 2003), we can expect ecological processes mediated by environmental heterogeneity (such as plant distribution or plant-plant interactions) to be indirectly affected by habitat quality loss. Finally, we found an interaction between habitat quality and water availability. Contrary to our expectations, we did not find significant differences in total P and phosphatase activity between watering treatments. Our results contrast with other studies showing that enzymatic activity is correlated with soil water availability in semiarid (Kramer and Green 2000) and dry Mediterranean soils (Li and Sarah 2003; Sardans and Penuelas 2004, 2005).

Fragmentation affects plant survival due to decreased genetic variation and increased inbreeding (Ellstrand and Elam 1993; Fischer et al. 2003). This has been also suggested by Matesanz et al. (2009) in a previous study in the same system, where the interaction between habitat quality and fragmentation affected survival and relative growth of *C. hyssopifolia*. This reduction in plant survival, and therefore in plant cover, reduces organic matter content in the soil and could, in turn, affects soil microbial activity, in small fragments. According to these results, fragmentation did not have a significant direct effect on soils features and performance, but it modulated the effect of habitat quality through synergistic interactions having an indirect effect on soil properties mediated by plant cover decline.

Conclusions

Our results highlight the importance of considering several drivers simultaneously to forecast realistic ecosystem responses to global change impacts (Sala et al. 2000; Matesanz et al. 2009). Each driver operates on different time scales: year to year change for water availability versus decades for habitat quality loss and fragmentation. This different time scale of the drivers could explain the greater effect of habitat quality on soils properties, which could be exacerbated by the interactive effect of habitat fragmentation over a long time scale. Moreover, there are feedbacks between plant and microbial activity so cumulative effects of drivers affecting plant productivity and microbial activity and interactions among them can be expected in the long-term and could accelerate the degradation of Mediterranean gypsum habitats.

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AUTHOR QUERIES

AUTHOR PLEASE ANSWER ALL QUERIES.

Q1. Please check capturing of Affiliations 1–3 if appropriate.
Q2. The citation “Garcia et al. 2000” (original) has been changed to “Garcia et al. 2002”. Please check if appropriate.