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A climate gradient approach toward understanding terrestrial ecosystem function

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Abstract

Recent global climate patterns demonstrate alterations in temporal and spatial rain distributions. Such alterations can potentially have very pronounced effects on water availability in Mediterranean and semi-arid regions due to characteristically high evaporation intensities. Understanding the consequences of altered water availability in Mediterranean and semi-arid regions for soil abiotic (e.g., organic matter) and biotic (e.g., soil microbial communities) components is essential, considering their crucial functions in soil fertility. The aim of the present study was to gain insight into feedback mechanisms that operate across boundaries of abiotic and biotic components, in order to expand our understanding of potential climate alterations on spatial and seasonal scales. Soil abiotic parameters (moisture, organic carbon, dissolved organic carbon, and total soluble nitrogen contents) as well as biotic parameters (microbial CO_2 evolution, biomass, qCO_2, and fungal community) were determined. Soil abiotic parameters, such as moisture, organic carbon, and dissolved organic carbon, demonstrated a great contribution to plants in semi-arid regions. The analyses of microbial activity data collected along spatial and temporal axes in different climatic regions can contribute to our ability to predict functional changes in ecosystems found under changing climatic conditions. Climate aridity level and the associated intensities of solar radiation and dry-wet cycle frequency enhance soil organic-matter liability.

Key words: Mediterranean ecosystems, climate gradient, aridity, microbial community, fungal community

Introduction

According to Houghton et al. (2001), changes in global climate associated with increased greenhouse gas emissions are expected to be among the main factors affecting temperature and hydrological cycles, resulting in more severe droughts and floods. Based on the above assumption, Ben-Gai et al. (1998), in their study on climate models for the Middle East, predict a rise in winter temperatures combined with changes in rainfall amounts and distribution. These changes may affect key soil processes, such as CO_2 evolution and net nitrogen (N) mineralization, thus affecting key ecosystem functions, such as carbon (C) storage, nutrient availability, soil biotic community and population processes, e.g., primary production, plant litter decomposition and biodiversity (Sternberg et al., 1999; Chapin et al., 2000; Sarah and Rodeh, 2004). CO_2 evolution from soils to the atmosphere depends mainly on climate and organic-matter availability and is limited by primary production and decomposing kinetics. Alvaro-Fuentes and Paustian (2011) have recently shown that soil organic-matter (SOM) turnover and decomposition processes are limited by moisture availability and temperature. According to Kurz-Besson et al. (2006), LeRoy and Marks (2006) and Liski et al. (2003), on regional scales, SOM is controlled by temperature, moisture, soil texture, plant lignin, and nitrogen inputs. According to Meentemeyer (1978), the relative importance of the above factors diverges across ecosystems.

Plant litter decomposition into SOM through biotically mediated nutrient cycling is known to be one of the most important factors sustaining ecosystem stability and productivity. It is also known that its turnover rate is determined by organic-matter transfer below-ground, the rates of SOM transformation and decomposition and that it is controlled by complex interactions between the biotic community and abiotic factors (e.g., temperature, rainfall, moisture availability) (Meentemeyer, 1978; Aerts, 1997; Swan and Palmer, 2004; Talmon et al., 2011). The interaction between the biotic and abiotic factors, along with litter-decomposition processes, on a temporal and spatial basis, was the subject of many studies conducted in different ecosystems (Whitford et al., 1986; Murphy et al., 1998; Whitford, 2002; Aneja et al., 2006). However, due to the complex nature of the interaction between temperature and moisture in regulating decomposition rates, in addition to the difficulty raised by soil physical and chemical soil composition, the challenge of modeling SOM turnover rates across climate – both geographically and seasonally – is basically unapproachable.

In order to be able to break this barrier – at any scale – using a natural climate-gradient platform sounds promising (Neff and Hooper, 2002; Oren and Steinberger, 2008). A continuous gradient that hosts a variety of climate gradients with large climatic variables within a relatively small area is located in the Eastern Mediterranean region, which is part of the GLOWA Jordan River project (Steinberger et al., 1990, 1999). At this transect, climatic subtypes range from humid (e.g., up to 1,300 mm mean annual rainfall) to extreme arid conditions (e.g., down to 20 mm annual rainfall), and support large plant diversity (Sternberg et al., 1999). In the present study, an attempt was made to evaluate the effects of the climate gradient (e.g., rainfall and temperature), on the one hand, and the seasonal pattern (e.g., mild, rainy winters and dry hot summers) controlled on a regional scale, on the other hand.

In the present study, the impact of climate (changes in precipitation) on a temporal basis (seasonality) and the four ecosystems along the gradient used as a spatial dimension (geographical basis) on microbial community activity, e.g., CO_2, biomass associated with soil organic matter (SOM) turnover, were studied. We hypothesized that: (1) a decrease in xeric environmental conditions will increase the microbial-community component's biomass and decrease microbial functional diversity; (2) the correlation between total rainfall and soil microbial-community activity, e.g., CO_2 evolution and biomass, will increase as we move from a humid-Mediterranean (HM) to a xeric-arid (A) ecosystem; and (3) SOM turnover dynamics will be strongly determined by the spatial, rather than the geographical, scale.

Methods

Study site

Four study sites, located along a 245-km stretch from the northern part of Israel toward the southern part, represent a climatic gradient. These sites represent different environmental and climatic conditions: humid-Mediterranean (HM), Mediterranean (M), semi-arid (SA), and arid (A) ecosystems.

The common basic climates for all four sites are characterized by rainy winters (October-April) and prolonged, dry summers (June-August). The plant-growing season commences soon after the first rains, between October and December (Fleischer and Sternberg, 2006). The sites are located at similar elevations, ranging between 470 and 620 m above sea level (a.s.l.), and are positioned on south-facing slopes. Each site overlies calcareous bedrock, giving pH values in the alkaline range (7.5-7.9). A significant decrease in yearly rainfall relative to the mean multiannual rainfall was obtained at each of the four sites.

The humid-Mediterranean (HM) site is located (N 33°0' E 35°14') in the northern Galilee Mountains, at an elevation of 500 m a.s.l., on montmorillonitic terra rossa. The average annual rainfall at this site is 780 mm and the mean annual temperature is 18.1°C. Vegetation varies from a dense-closed oak maquis cover to more open garrigues dominated by shrubs. Herbaceous vegetation, mainly composed of annuals, coexists with shrubs.

The Mediterranean (M) site is located 18 km southwest of Jerusalem (N 31°42' E 35°3') at 620 m a.s.l., on terra rossa. The average annual rainfall is 537 mm and the mean annual temperature is 17°C. Vegetation is dominated by shrubs and large numbers of herbaceous (mostly annual) plant species.

The semi-arid (SA) site is positioned between the southern Judean Mountains and the northern Negev (N 31°23' E 34°54') at 590 m a.s.l., on light brown rendzina. The average annual rainfall is 300 mm and the mean annual temperature is 18.4°C. Vegetation is dominated by dwarf shrubs associated with herbaceous (chiefly annual) plants.

The arid (A) site is situated on the Negev plateau (N 30°52' E 34°46') near Sde Boker, at an elevation of 470 m a.s.l., on desert lithosol. The average multi-annual rainfall is 90 mm, and the mean multi-annual temperature is 19.1°C. Vegetation at this site is dominated by small shrubs and sparsely growing desert annuals and geophytes (Fleischer and Sternberg, 2006).

Soil sampling

Soil from the upper 0-10 cm was randomly sampled in four replicates from the open spaces between the perennial plants. Soil samples were collected over three consecutive years on a seasonal basis. Each soil sample was placed in an individual plastic bag and transported to the laboratory, where the soil samples were sieved (< 2 mm) and kept at 4°C before chemical and biological analyses (within a four-month period).

Laboratory analysis

Soil moisture (SM) content was determined gravimetrically by drying soil samples for 24 h at 105°C.

Total organic-carbon (TOC) content was determined by oxidation with 1 N potassium dichromate in acidic medium, according to Rowell (1994).

TSN and DOC content was determined by a Skalar Analytical San Plus Analyzer (Breda, The Netherlands) in soil samples extracted with a 0.01 M $CaCl_2$ solution (Houba et al., 1987).

Soil microbial community

The soil microbial community was determined by the MicroResp™ method (Campbell et al., 2003), with which we assessed the microbial biomass (MB), and CO_2 evolution (MBR). In order to determine MB, a glucose solution was added to soil samples, while no substrates were added to samples in order to determine basal CO_2 evolution (Anderson and Domsch, 1978; Carpenter-Boggs et al., 2000; Berg and Steinberger, 2010).

The dye plates were read twice in a spectrophotometer at 590 nm: just before they were placed on the deep plates containing the soil samples (Time 0) and after discerning colorimetric changes in the indicator plate (Time 1). After Time 0, the plates were incubated in the dark at 27°C. The results per well were calculated in comparison to the 16th well, which contained the same soil sample.

Isolation of microfungi

Microfungi were isolated using the soil dilution plate method (Davet and Rouxel, 2000). Three culture media with different carbon and nitrogen sources were used for cultivating microfungi: malt extract agar (MEA) with disaccharide maltose and organic nitrogen, Czapek's agar (CzA) with disaccharide sucrose and mineral nitrogen (both media of Conda Pronadisa Labs, Madrid, Spain), and carboxymethylcellulose agar (10 g polysaccharide carboxymethylcellulose, 1 g K_2HPO_4, 0.5 g KCl, 0.5 g $MgSO_47H_2O$, 0.01 g $Fe_2SO_47H_2O$, 0.5 g yeast extract, 15 g agar). Streptomycin (Sigma-Aldrich Inc., St. Louis, MO) was added to each medium (100 µg/ml) in order to suppress bacterial growth. One gram of pounded soil samples was initially diluted with 9 ml sterile water and the suspensions were agitated for 5 min. One milliliter of that dilution was transferred to a new tube containing 9 ml sterile water and the suspensions were agitated for 5 min. Two-hundred µl samples of the suspensions from the dilutions of soil were placed in 90-mm–diameter Petri dishes. After that, the agar medium (about 11 ml) at approximately 40ºC was added and mixed with the sample suspension. All plates were incubated at 27ºC (all plates) in darkness for 7-10 days.

Statistical analysis

All the data obtained in the present study were subjected to statistical analysis of variance (ANOVA) using the SAS model (Duncan's multiple range test and Pearson correlation coefficient [SAS Institute, Inc.], one-way ANOVA, and T test) for evaluating differences between separate means. Differences at the $p<0.05$ level were considered significant (Kandeler et al., 1999).

Results

Geographic variability of the soil ecosystem along the climate gradient

Soil-moisture contents were found to correspond to the spatial distribution of precipitation along the gradient: arid (A) < semi-arid (SA) < Mediterranean (M) < humid-Mediterranean (HM) (Fig. 1A). This can be attributed to the water-holding capacity (WHC) of these soils, which decreases from the HM to A, and which was found to decrease by 41% (Fig. 1B).

Soil total organic-carbon (TOC) pattern was found to follow soil moisture, producing nearly identical relations, where the mean values for the entire study period demonstrated significant differences along the climate gradient, i.e., HM > M > SA > A (Fig. 1C).

Soil dissolved organic content (DOC) followed the same trend, with values of 257, 230, 168, and 164 mg kg^{-1} soil, respectively ($P<0.0001$). Accordingly, a positive Pearson correlation ($P<0.0001$) was established between TOC and DOC for data joined from all sites. It is noteworthy that DOC was significantly greater during the dry period than during the rainy period at all sites ($P<0.0001$ for the Mediterranean sites and $P<0.05$ for the arid sites). A similar trend was generally observed for TOC, even if it was significant only for the semi-arid site ($P<0.05$).

Soil biotic properties (community-level MBR and MB) exhibited continuous decreases southward along the gradient, with some exceptions in the course between the humid and the typical-Mediterranean climate subtypes (Table 1). This trend is emphasized by positive and significant correlations between MB and SM along the geographic axis in all seasons, and between MBR and SM in spring and summer only. .Both MBR and MB correlated positively and significantly with both TOC and DOC in summer and autumn, while in winter and spring, the correlations with DOC were not significant. Contrary to the spatial trend obtained with MBR and MB levels increased steadily southward along the gradient, with the only exception being in the humid-to-typical-Mediterranean course in winter (Table 1).

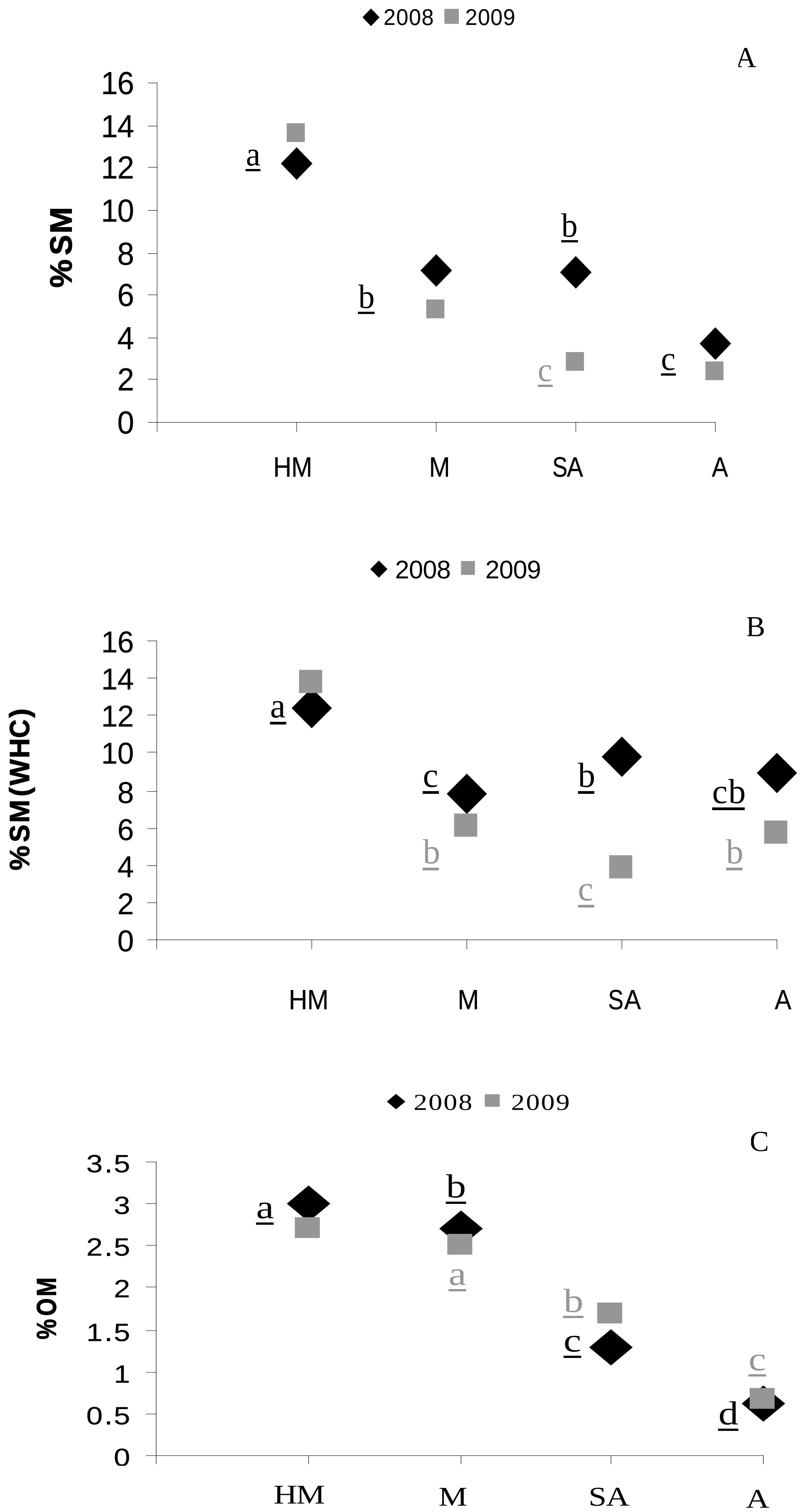

Figure 1. Changes in mean values of soil moisture (SM) (A), soil moisture based on water holding capacity (WHC) (B) and percent organic matter (OM) (C) during the study period at different locations along the climatic gradient. HM = humid-Mediterranean; M = Mediterranean;SA=semi-arid;A=arid.

Table 1: Soil parameters determined in the various study sites along a Mediterranean climate gradient in the various seasons. Variation among study sites is denoted by Duncan's multiple range test groupings (*n* = 2 years * 4 replicates = 8).

Winter	HM	M	SA	A
SM (%)	29.6 (±4.8)^{a}	22.3 (±7.7)^{b}	17.6 (±2.9)^{c}	9.0 (±1.9)^{d}
TOC (%)	1.84 (±0.26)^{a}	1.56 (±0.12)^{b}	0.81 (±0.24)^{c}	0.31 (±0.13)^{d}
DOC (mg kg^{-1})	231 (±220)^{a}	186 (±142)^{a}	126 (±101)^{a}	116 (±75)^{a}
MBR (µg CO_2 -C g^{-1} h^{-1})	0.130 (±0.058)^{a}	0.122 (±0.074) ^{a}	0.104 (±0.062)^{a}	0.098 (±0.062)^{a}
MB (µg C g^{-1})	46.8 (±14.9)^{ab}	71.5 (±48.7)^{a}	22.3 (±10.6)^{bc}	11.2 (±7.4)^{c}
Spring	HM	M	SA	A
SM (%)	14.9 (±10.2)^{a}	9.9 (±4.2)^{b}	4.4 (±1.6)^{c}	2.8 (±1.9)^{d}
TOC (%)	1.75 (±0.11)^{a}	1.53 (±0.29)^{b}	0.95 (±0.28)^{c}	0.42 (±0.10)^{d}
DOC (mg kg^{-1})	158 (±92)^{a}	142 (±42)^{a}	160 (±164)^{a}	126 (±156)^{a}
MBR (µg CO_2 -C g^{-1} h^{-1})	0.154 (±0.055)^{a}	0.150 (±0.050)^{a}	0.137 (±0.036)^{a}	0.074 (±0.031)^{b}
MB (µg C g^{-1})	109.8 (±58.5)^{a}	115.1 (±128.8)^{a}	28.4 (±9.7)^{b}	9.1 (±5.7)^{b}
Summer	HM	M	SA	A
SM (%)	8.0 (±1.6)^{a}	5.8 (±1.1)^{b}	3.0 (±0.7)^{c}	1.3 (±0.3)^{d}
TOC (%)	1.92 (±0.21)^{a}	1.65 (±0.19)^{b}	0.62 (±0.21)^{c}	0.43 (±0.10)^{d}
DOC (mg kg^{-1})	227 (±150)^{a}	232 (±96)^{a}	146 (±70)^{ab}	132 (±92)^{b}
MBR (µg CO_2 -C g^{-1} h^{-1})	0.173 (±0.042)^{ab}	0.193 (±0.060)^{a}	0.126 (±0.083)^{bc}	0.097 (±0.071)^{c}
MB (µg C g^{-1})	75.2 (±32.9)^{a}	59.4 (±29.8)^{a}	19.4 (±12.6)^{b}	11.8 (±8.8)^{b}
Autumn	HM	M	SA	A
SM (%)	20.0 (±10.5)^{a}	17.8 (±8.9)^{a}	6.2 (±2.3)^{b}	1.8 (±0.2)^{b}
TOC (%)	1.64 (±0.13)^{a}	1.40 (±0.27)^{b}	0.83 (±0.34)^{c}	0.33 (±0.12)^{d}
DOC (mg kg^{-1})	320 (±192)^{a}	230 (±114)^{ab}	137 (±91)^{b}	151 (±122)^{b}
MBR (µg CO_2 -C g^{-1} h^{-1})	0.278 (±0.162)^{a}	0.181 (±0.087)^{ab}	0.221 (±0.046)^{ab}	0.122 (±0.069)^{b}
MB (µg C g^{-1})	124.5 (±69.1)^{a}	60.6 (±38.0)^{b}	42.1 (±13.4)^{bc}	16.1 (±8.9)^{c}

Notes: Abbreviations of study sites: HM – humid-Mediterranean; M – typical Mediterranean; SA – semi-arid; and A – arid. Abbreviations of soil parameters: SM- soil moisture; TOC – total organic carbon; DOC – dissolved organic carbon; MBR – microbial basal respiration; MB – microbial biomass. All soil parameters are expressed on a soil dry-weight basis.

Soil fungal biomass (FB) increased along the gradient with increasing climate moisture availability, excluding the semi-arid site. At the semi-arid site, FB values reached the highest value of 112 mg C*g^{-1} soil in the HM and 104 mg C*g^{-1} soil in the arid soil, while significantly ($p<0.05$) lower values (by 25%) were obtained at the two remaining sites. Fungal CO_2 evolution was significantly higher ($P<0.05$) in the semi-arid and arid soils (0.54 and 0.35 mg CO_2 C g $soil^{-1}$*h^{-1}, respectively) on the geographical gradient compared to the Mediterranean and humid-Mediterranean soils (0.26 mg CO_2 C g $soil^{-1}$*h^{-1}).

The ratio between the CFU of fungi and the number of species at each site along the gradient was found to be relatively higher at the HM and arid sites compared to the other two sites (M and SA).

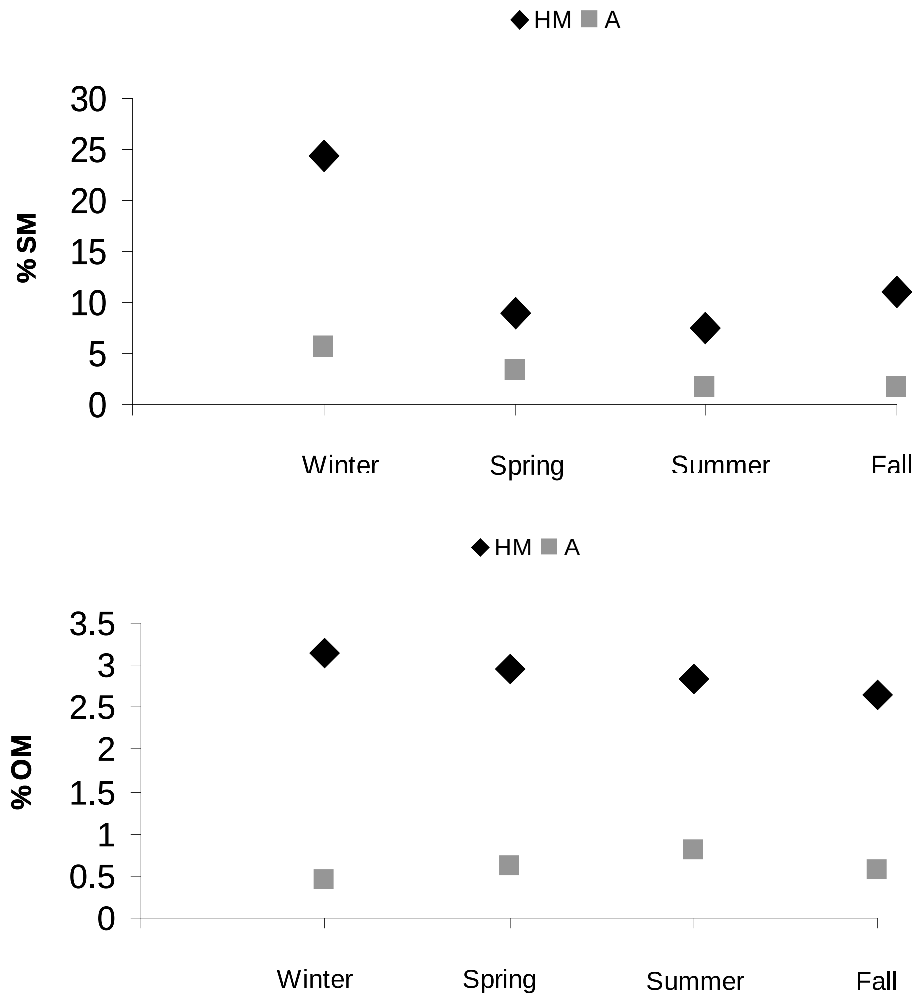

Figure 2. Changes in mean values of soil moisture (SM) (A and percent organic matter (OM) (B) during the study period at HM and A sites along the seasons. (HM = humid-Mediterranean; A = arid)

Seasonal variability of the soil ecosystem

The seasonal changes in soil moisture at the two extremes sites, the humid Mediterranean and the arid site, demonstrated sharp and significant ($p<0.05$) differences in the winter season (Figure 2) as a result of differences in total rainfall. The decrease in moisture along the seasons was strongly related to moisture availability and site location. The amounts of OM were similar along the seasons for each site, showing six-fold higher values for the HM than the A site (Figure 2).

Regarding soil biotic activity, both MBR and MB generally decreased on a seasonal scale, with increasing SM at all sites (although significant only for MBR in the typical-Mediterranean site). In contradistinction, MBR and MB were positively and significantly correlated with organic carbon at all study sites.

The CFU fungi at the HM decreased sharply with the decrease in SM along the seasons (Figure 3), where the changes at the A site demonstrated a significantly different trend. A sharp 4-fold increase toward the spring season compared to the winter season and again a relatively significant increase in the autumn relative to the summer, triggered by dewfall, are known as important moisture sources in A systems (Figure 3). No significant differences were found in the number of fungal species between the sites.

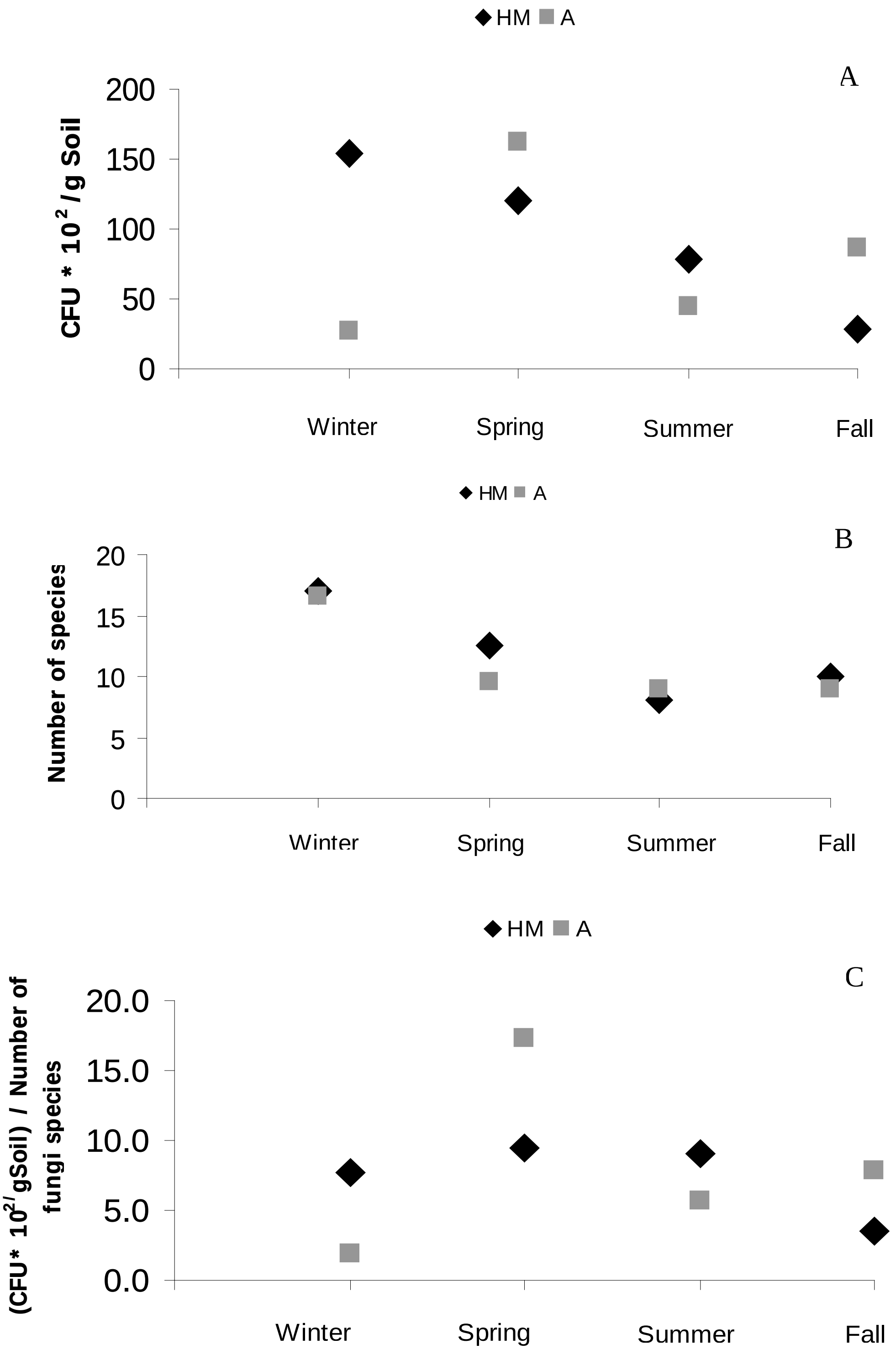

Figure 3 Changes in mean values of soil fungi colony forming units (CFU)(A), number of species (B) and the ratio between them (C) during the study period at HM and A sites along the seasons. (HM = humid-Mediterranean; A = arid)

Discussion

The relationships between abiotic and biotic soil ecosystem properties obtained in the current study are in good agreement with accepted ecological perceptions. The observation that moisture and organic matter availability account for a significant proportion of the substrate for microbial activity, is well-known (Jandl and Sollins, 1997; Bengtson and Bengtsson, 2007; Jones et al., 2008; Ghani et al., 2010). The significant positive correlations between microbial CO_2 evolution and dissolved organic matter along the geographic axis of the engaged climatic gradient are analogous to results obtained by the direct measurement of soil CO_2 efflux in the field, obtained at the same study sites by Talmon et al. (2011). They reported that the variation in soil organic-carbon content along this climatic gradient accounted for 77% of the variation in annual soil respiration. While no dissolved organic carbon was measured in that field study, total organic carbon and dissolved organic carbon were found to be correlated along the geographic climate transect. Raich and Schlesinger (1992) obtained similar results: in reviewing soil respiration data from a wide range of vegetation biomes, they reported positive correlations between annual net primary productivity and annual soil respiration rates.

On the seasonal axis, only the typical-Mediterranean site exhibited a significant positive correlation between microbial CO_2 evolution and total organic carbon, similar to results obtained by Korschens et al. (1998). However, at all the other sites, the microbial CO_2 evolution-organic carbon was persistent, and complemented a similar correlation every season along the geographical axis. This spatio-temporal correspondence emphasizes the fundamental role of soil organic C availability in regulating soil metabolic activity.

Based on the present study, we can emphasize that climatic gradients with different environmental components, such as altitude, topography, temperature, and precipitation, provide a useful framework for studying the effects of climate change, as discussed by Diaz and Cabido (1997) and Dunne et al. (2003). In the gradient studied in the present study, with four different natural environments, a diverse microbial-community level was found. In the arid ecosystem, the low levels of organic matter might be the reason for relatively high utilization of organic matter without any inconsistency in its composition. At the humid-Mediterranean site, the frequency of high amounts of organic matter that may be easily decomposed is relatively high and can maintain a relatively high microbial community compared to the other locations along the transect.

The present study elucidated the complex interplay between microbial-community litter decomposition and climatic features. However, further studies should be conducted in order to understand the partial contribution of organic-matter composition and the interaction between precipitation, volatilization, litter quality, and microbial community function.

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