Microbial degradation at night, abiotic degradation at day – litter decomposition in dryland ecosystems

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ABSTRACT [up to 150 words]

Decomposition in drylands is not well understood and predictions often underestimate decay rates. Recently identified abiotic decay mechanisms operating at day-time (photodegradation, thermal degradation) only partly explain litter decomposition under dry conditions, suggesting contribution of additional processes. To disentangle and quantify the litter-decay mechanisms in semi-arid ecosystems we manipulated irradiance and litter-moisture in a field experiment during the dry season. The study revealed that microbial activity was enabled at night by dew formation and high relative humidity. Microbial, photochemical and thermal degradation contributed 56, 35 and 9% to seasonal litter CO_2 fluxes. These decay mechanisms were validated by litter-CO_2 measurements in a transect across the Mediterranean Basin. Our results imply that night-time microbial activity facilitated day-time photodegradation which in turn stimulated further night-time microbial degradation. This characterization of the complex interplay of decay mechanisms in drylands can improve projections of the terrestrial carbon cycle.

INTRODUCTION

Global carbon (C) cycling is sensitive to the decomposition dynamics of organic matter, which, in addition to NPP, determines the size of soil C stores in ecosystems and fluxes of CO_2 to the atmosphere (Schmidt *et al.* 2011). Semi-arid biomes may play a crucial role as drivers of the balance and the interannual variability in the global C cycle (Wohlfahrt *et al.* 2008), and their importance might increase in coming decades (Poulter *et al.* 2014). However, decomposition and turnover of carbon in dryland systems is not still well understood (Throop & Archer 2009; Carvalhais *et al.* 2014; Poulter *et al.* 2014), especially as it relates to plant litter decomposition on the soil surface and during long, largely precipitation free periods (Dirks *et al.* 2010; King *et al.* 2012). Consequently, soil carbon models inadequately simulate and usually underestimate litter decomposition rates in semi-arid ecosystems (Parton *et al.* 2007; Adair *et al.* 2008; Bonan *et al.* 2013). To improve our understanding of litter decay in drylands, recent research has largely focused on the study of abiotic mechanisms and, in particular, on photochemical degradation (photodegradation) of dead plant material by solar radiation occurring mostly through mineralization of photo-reactive compounds and photo-oxidation of chemical bonds (Moorhead & Callaghan 1994; King *et al.* 2012; Barnes *et al.* 2015).

Photodegradation can mineralize 14% (Foereid *et al.* 2011) of net primary production and 19-36% of net ecosystem production, can be responsible for 60% of the dry season CO_2 fluxes (Rutledge *et al.* 2010) and be accountable for 60% of annual litter-mass loss (Austin & Vivanco 2006). It also contributes to the emission of trace gases, such as CO_2, CO and CH_4 (King *et al.* 2012), and alters litter quality, thus indirectly affecting microbial decomposition in subsequent wet periods (Gallo *et al.* 2009; Austin & Ballaré 2010; Barnes *et al.* 2015). However, photodegradation is only able to partially explain litter

decomposition in drylands (Verhoef *et al.* 2000; Hoorens *et al.* 2004; Gallo *et al.* 2006; Brandt *et al.* 2009; Kirschbaum *et al.* 2011; Song *et al.* 2011; Uselman *et al.* 2011; Lambie *et al.* 2014; Liu *et al.* 2014; see meta-analyses: King *et al.* 2012; Song *et al.* 2013) and it cannot explain decomposition in the shade (Grünzweig *et al.* 2007; Henry *et al.* 2008; Dirks *et al.* 2010). In addition, our knowledge of the quantitative contribution of photodegradation to CO_2 emissions is insufficient, and relies mostly on laboratory experiments (King *et al.* 2012; but see Brandt *et al.* 2009, Rutledge *et al.* 2010).

Thermal degradation is an additional abiotic decay mechanism whereby organic matter is degraded by chemically reactive processes upon excitation by high temperatures (<100°C) (Lee *et al.* 2012). This mechanism is largely associated with high solar irradiance, but its contribution to litter decay in the field is largely unknown. Studies of the nitrogen cycle have shown that thermal degradation can result in massive losses of nitrogenous trace gases from soils (McCalley & Sparks 2009) and potentially also from litter (Berryman *et al.* 2013).

Microbial degradation is considered the dominant mechanism of litter decomposition on a global scale, controlled mainly by moisture availability, temperature and litter chemical composition (Aerts 1997, Berg & Laskowski 2005). Because of water limitation, microbial activity is believed to contribute little to decomposition in drylands, especially during dry periods (Rutledge *et al.* 2010; King *et al.* 2012). However, even though rainwater may be absent, other atmospheric sources of water might enable microbial activity. Decades ago, lab experiments showed that high levels of water vapour in the air can facilitate microbial decomposition and induce CO_2 emission from dead plant material (Bartholomew & Norman 1947), with a threshold observed at 13% litter moisture or 75% relative air humidity (RH) (Nagy & Macauley 1982). However, the possibility of microbial degradation of plant litter occurring under high atmospheric humidity, but in the absence of rainwater

has only been reported in a couple of studies in moist environments (salt marsh, Newell *et al.* 1985; wetland, Kuehn *et al.* 2004). Recently, Dirks *et al.* (2010) found a positive relationship between decay rates and the capacity of litter to absorb water vapour in dry shrubland and grassland ecosystems during an extended rainless season. The authors proposed that microbial activity is enabled through the absorption of moisture by plant litter during the frequent nights of high RH. Overall, the actual mechanisms of litter decomposition, and the role of biotic and abiotic degradation in semi-arid ecosystems remains unresolved, particularly during the long dry periods that characterise these biomes.

The objective of the current study was to examine the contribution of microbial, photochemical and thermal degradation to litter CO_2 emission and decomposition in dryland ecosystems of the Mediterranean region. First, the microclimate was experimentally manipulated in Israel to investigate the importance of air humidity and dew as water sources for microbial degradation and of solar radiation for photodegradation of plant litter and concomitant CO_2 emissions. Second, we tested whether these mechanisms could explain litter CO_2 fluxes in three sites across the Mediterranean Basin at the seasonal peak of solar radiation. Our study revealed that microbial degradation enabled by high night-time humidity and dew can be a dominant mechanism of plant-litter decay under dry conditions, and that the biotic and abiotic decay mechanisms interact at daily and seasonal scales.

METHODS

Field sites

Three field sites were selected along an east-to-west transect across the Mediterranean Basin (see Fig. S1 in Supporting Information). All sites had a Mediterranean climate of mild and moist winters and hot and dry summers, with no rain during the summer season in Israel. The sites were located on Carmel Ridge in Israel (Ramat Hanadiv Nature Park, 32°30'N, 34°550'E, 120 m above sea level, asl), the peninsula of Capo Caccia in north-western Sardinia, Italy (Regional Park Porto Conte, 40°37'N, 8°10'E, 300 m asl; a site of the EU INCREASE project), and in the south-west of Madrid, near the village of Chapinería, Spain (40°23'N 4°11'W, 670 m asl; see Appendix SA1 in Supporting Information).

Microclimate manipulation experiment in Israel

Fresh, naturally shed litter was collected from nets placed under the leguminous, summer-deciduous shrub *Calicotome villosa* [(POIR.) LINK.], while vegetative, naturally dehydrated aboveground plant material was sampled from the annuals *Avena sterilis* L. and *Scabiosa prolifera* L. (for extended methods, see Appendix SA1 in Supporting Information, for initial litter quality, see Appendix SA2). Litter was inserted into mesh bags and subjected to one of the following three microclimate treatments: 1) ambient control, with no manipulation (no screens or frames; referred to as "control"); 2) radiation-pass and passive-warming-and-drying treatment composed of a transparent screen (4000TR, Honeywell International, Morristown, NJ, USA) that allows transmittance of most of UV and photosynthetically active radiation (PAR), and reduces heat loss and humidity at night (referred to as "radiation-pass treatment"; Table 1); 3) radiation-block and passive-warming-and-drying treatment where UV and shortwave PAR up to a wavelength of 550 nm is blocked (179 Chrome orange, Lee Filters, Burbank, CA, USA; Brandt *et al.* 2009), and heat loss and humidity are reduced at night as in 2 (referred to as "radiation-block treatment"). The filters

were mounted on a white coloured aluminium double frame (1.22 m x 1.22 m) that was suspended 35 cm above the litterbags at the northern edge and 30 cm at the southern edge. This tilted array of the frames drained any water formed by dew on the screens during the night and prevented direct solar radiation from bypassing the filters from the side during most hours of the day. It needs to be noted that some photochemically active radiation might have reached litter under the radiation-block screen because of incomplete blocking of solar radiation by the screen (Table 1) and penetration of some radiation beneath the filters during early morning and late afternoon. Each treatment was randomly replicated five times in a 1000 m^2 area. Filters were replaced in mid-summer (54 days into the experiment), and were entirely removed at the end of the dry season (end of September 2012). CO_2 fluxes from litter, microbial biomass and litter decomposition were measured between early June 2012 and mid-March 2013 (276 days) four times during the dry season and twice during the wet season.

During a sampling day, litterbags were repeatedly measured for CO_2 fluxes and weighed to determine litter water content in the field. These measurements typically took place at night (0-3 hours before sunrise), morning (2-4 hours after sunrise), midday (2 hours prior and after solar noon) and afternoon (3-4 hours after solar noon). The same litterbags were measured several times during a sampling day, and were immediately returned to their field location between measurements. After the last measurement cycle of the day, litterbags were returned to the lab for analysis of microbial biomass estimated by the substrate induced respiration (SIR) method following Beare *et al.* (1990). SIR did not differ between night and midday (unpublished results). Furthermore, after two of the sampling days, litter quality was determined as C and nitrogen (N) concentrations, $\delta^{13}C$ and $\delta^{15}N$ using a gas isotope-ratio mass spectrometer (DeltaPlus XP IRMS, Thermo Finnigan,

143 Waltham, MA, USA), and as lignin concentration according to the method of Van Soest
144 (1963).

145 We used a closed-path, custom-made respiration system to measure litter CO_2 fluxes in
146 the field. A commercially available container (HPL822, 600 ml, transparent polypropylene,
147 Lock&Lock, Chatswood NSW, Australia) was fitted with a lid transparent to UV and PAR
148 (90% transmittance above 300 nm; SUVT, Spartech Polycast, Stamford, CT, USA) and
149 served as measuring chamber. A small pump (WP1000, 700ml/min flow rate, Welco Co.,
150 Tokyo, Japan) circulated the air between the chamber and the infrared gas analyser
151 (IRGA, LI-7500, LI-COR Inc., Lincoln, NE, USA, with the calibration tube installed; 650 ml
152 overall volume of the system). A thermistor (9975-019#, LI-COR) shielded against direct
153 radiation was placed inside the chamber (for details, contact R. Seligmann). A single
154 litterbag was placed in the chamber for a short time (70-200 seconds, depending on the
155 climate conditions), with the measurement starting at ambient CO_2 concentration. When a
156 litterbag from the radiation-block treatment was measured, a piece of 179 Chrome orange
157 screen was placed on the SUVT lid. Every few samples, we took measurements with an
158 empty chamber as blank. All parts of the system besides the measuring chamber were
159 shielded from radiation to keep measurement temperature similar to litter temperature
160 when placed on the ground.

161 Air temperature and RH (HOBO, Pro v2 U23-001,Onset, Bourne, MA, USA) were recorded
162 at 0.2 m above the ground, duration of dew formation (237-L Leaf Wetness Sensor,
163 Campbell Scientific, Logan, UT) was measured at ground level (one sensor of each type
164 per treatment). Air temperature and RH were also recorded at the soil surface under the
165 litterbags (DS1923, iButtons, Embedded Data Systems, Lawrenceburg, KY, USA) and at
166 the litter surface (DS1922L-F5#). Indication of dew formation was recorded by the leaf-
167 wetness sensors and, for validation in the control treatment only, from the difference

between litter surface temperature and dew-point temperature (dew formation was assumed, if this difference was less than 2°C). During each day-time CO_2 flux measurement, UV radiation and PAR were recorded (MU-200 and MQ-200, Apogee Instruments, Logan, Utah, USA) under the same conditions as the CO_2 measurements (under a SUVT sheet for the control and radiation-pass treatments, under SUVT and 179 Chrome orange screens for the radiation-block treatment).

Mediterranean transect (Israel, Italy, Spain)

Carbon dioxide fluxes and litter water content were measured on fresh litter at field sites across the Mediterranean transect in June 2013, according to the following sequence: In Israel, two sampling campaigns between the night and the subsequent afternoon; in Italy, a midday sampling; in Spain, a midday sampling and a campaign between the night and the subsequent afternoon. In Israel and Spain, desiccated vegetative standing plant material of winter annuals was collected (*A. sterilis* at both sites, *S. prolifera* in Israel and *Sisymbrium officinale* (L.) SCOP. in Spain). In Italy, desiccated standing plant material was collected from the shrubs *Dorycnium pentaphyllum* [subsp. *amani* (ZOHARY) PONERT] and *Helichrysum italicum* (G. DON F.), together with freshly fallen litter from the shrub *Cistus monspeliensis* (L.) (for simplicity, all species will be mentioned by genus name in the remainder of the text). For each measurement cycle during a sampling day, a new set of samples was collected. CO_2 emission measurements were performed as described earlier, with the exceptions that no litterbags were used and that two measurements were performed, one under solar radiation and another one after shading the litter sample.

Calculations

In the manipulation study in Israel, we developed empirical models to assess the relative contribution of biotic and abiotic decay mechanisms to litter CO_2 fluxes over the dry season. First, we estimated night-time litter moisture-content throughout the season by relating measured litter moisture to the continuously recorded microclimatic variables during the sampling campaigns using a stepwise procedure (Table S1 in Appendix ST4). Then, we calculated night-time litter CO_2 fluxes according to the predicted seasonal course of litter moisture using a simple linear relation (see Results section). Day-time CO_2 emissions were computed using a multiple linear regression model that included UV irradiance, time and litter type (Table S2). The contribution of photochemical and thermal degradation to day-time CO_2 fluxes was estimated from the radiation-filter treatments (pass and block), assuming that day-time CO_2 emissions under the radiation-block filter were driven by temperature alone and that the differences in fluxes between the radiation-pass and block treatments were driven by solar radiation. Sums of CO_2 fluxes were scaled up to mean dry-season length (202 days, calculated as the period between 5-mm rain events, 10-yr mean) at the microsite scale using litterfall rates (77 and 67 g C m^{-2} yr^{-1} for *Calicotome* and herbaceous litter; the latter was applied both to *Avena* and *Scabiosa*). Sums of CO_2 fluxes were also compared to mass loss from the litterbags on a carbon concentration basis.

Statistical analysis

To assess the relation between litter moisture content and CO_2 fluxes, and between mass loss and microbial biomass we used linear regression, while between mass loss and nitrogen mass change we used an exponential relation. For comparing categories of interest, the Tukey–Kramer HSD test was used, for using several contrasts at $\alpha = 0.05$, Holm's correction was applied (Rice 1989). We used a two ways full factorial ANOVA for

217 analysing the effect of habitat and radiation treatment on CO_2 flux per unit of litter moisture
218 and for CO_2 flux per unit of UV irradiance. In the Mediterranean transect, we analysed the
219 effect of litter moisture content and UV irradiance on CO_2 emissions by a multiple linear
220 regression model. Additionally, we described the influence of litter moisture content and
221 temperature on CO_2 fluxes measured in the shade using linear regression. When
222 heterogeneity of variance occurred, data were log transformed. All data were analysed
223 using JMP 7.0.1 software (SAS Institute, Cary, NC, USA).

224 **RESULTS**

225 **Decomposition and CO_2 fluxes following microclimate manipulation**

226 Minimum night-time air temperature over the dry season averaged 20°C in the control,
227 which was cooler by 1.3°C than that measured in the radiation pass and block treatments
228 (Table 1, Figs. S2-3). Likewise, maximum RH averaged 95% in the control and was
229 moister by 4-5% than maximum RH in the other two treatments. Following those changes,
230 dew deposition was dramatically reduced by the treatments. In the control, dew formation
231 occurred on 4.8 h per night on average when measured by the leaf-wetness sensor (6.4 h
232 per night according to the temperature-difference calculation, which was available only for
233 the control), whereas sensors mounted under radiation filters (pass and block) measured
234 only 0.5-1 h of dew during the entire season (Table 1, Fig. S4). The levels of maximum RH
235 at the soil-litter interface (soil surface) were relatively low (<65%), but higher by 5-6% in
236 the control than in the radiation pass and block treatments (Table S3). Likewise,
237 temperature measurements showed a 3-4°C cooler soil surface in the control at night.

238 Litter moisture closely matched microclimatic conditions, and was twice as high in control
239 plots as it was in the radiation pass and block treatments (Fig. 1b). Night-time litter-

moisture was closely related to dew hours and the difference between soil-surface and dew-point temperature (R^2 = 0.87, Table S1).

Carbon-dioxide fluxes from litter at night were positively and linearly related to litter moisture across all litter types and treatments (R^2 = 0.75, Fig. 2), and were on average 5 and 9 times higher in the control than in the radiation-pass and the radiation-block treatments, respectively (Fig. 1a, Table S4c). Notably, litter CO_2 flux per percent water content was twice as high in the radiation-pass as in the radiation-block treatment (Table S5, P = 0.001). The highest CO_2 fluxes during the rainless dry season reached 20-40% of those measured during a rain event in the wet season (used as a reference point for maximal values; Table S4c).

At midday, UV irradiance was high in the control and the radiation-pass treatment and low following radiation blocking (Fig. 1), while maximum daily air temperature did not differ much among the three treatments (Table 1). Minimum daily RH (21% on average) and litter moisture (3%) were low at midday, and varied little among treatments (Fig. 1b, Tables 1 and S4a). Litter CO_2 fluxes at midday were considerably higher in both the control and the radiation-pass treatments than in the radiation-block treatment (Fig. 1a, Table S4c). Notably, litter in control plots emitted significantly more CO_2 per unit UV irradiance than litter in the radiation-pass treatment (Table S6), even though the measurements were performed under identical levels of temperature (Fig. 1d). Day-time CO_2 fluxes were positively related to UV irradiance (morning to afternoon; Table S2).

Microbial biomass as evaluated by SIR was 1.5-3 times higher on litter in control plots than on litter under the radiation pass and block screens (Fig. 3a). Microbial biomass tended to increase over the course of the season (Table S4b). By the end of the dry season, SIR reached values that were about half to four times the values measured in the control at the end of the wet season.

Litter-mass loss indicating decomposition over the dry season was about twice as high in the control as mass loss measured under the radiation pass and block screens, with the latter two treatments not differing significantly from each other (Fig. 3b). Decomposition rates showed a strong positive relationship with microbial biomass across all litter types, treatments and sampling times (R^2 = 0.74, Fig. 3c). Mass loss also increased exponentially with an increasing ratio of litter N pool before to N pool after decomposition in the field (R^2 = 0.57, Fig. S5). Dry-to-wet season comparisons for the control showed that litter decay at the end of dry season amounted to 13-30% of total mass loss when viewed across both the dry and wet seasons (Fig. 3b, Table S7).

Decay mechanisms contributing to litter CO_2 fluxes

Empirical models generated to assess the relative contribution of decay mechanisms to litter CO_2 fluxes in the microclimate manipulation study showed that on average 56% of C loss over the dry season occurred during the night (Fig. 4) and was attributed to microbial degradation (see Discussion). Litter CO_2 emissions during the day were attributed to abiotic decay mechanisms, and were further partitioned into photochemical (35%) and thermal degradation (9%). This breakdown into the two types of abiotic degradation was derived from day-time CO_2 fluxes (morning to afternoon) that were 3.3 times higher in the radiation-pass treatment (high solar radiation and temperature) than in the radiation-block treatment (low solar radiation and high temperature; Fig. 1). Litter CO_2 emissions summed to 7-14 g C m^{-2} 202 d^{-1} when scaled up using annual litterfall rates and the interannual mean dry-season length (Fig. 4). Carbon dioxide fluxes could explain well the weighed mass loss from the litterbag experiment of *Avena*, but slightly overestimated mass loss of *Scabiosa* litter (within the upper range of the 95% confidence interval of the observed

mass loss from litterbags) and considerably underestimated that of *Calicotome* (leaving 60% of mass loss unexplained).

Radiation screens were removed at the end of the dry season, which enabled us to show that the legacy of dry season processes was crucial for decay of *Avena* litter in the subsequent wet season. By the end of the wet season, *Avena* litter in control plots lost 70 and 150% more mass than litter that was exposed to radiation-pass and radiation-block treatments in the dry season (Table S7; for further differences in microbial biomass and CO_2 fluxes, see Table S4b-c).

Drivers of litter CO_2 fluxes along the Mediterranean transect

In the rainless month of June 2013, field campaigns were carried out along an E-W Mediterranean transect from Israel to Spain to test relationships between litter CO_2 fluxes and abiotic drivers across sites and species. Maximum RH was higher in Israel during both measuring nights (almost 100% RH, with abundant dew deposition, and 96% RH) than in Spain (71% RH). Litter moisture reflected air humidity conditions, and was high in the first and lower in the second night in Israel and the night in Spain (Fig. 5b). Night-time CO_2 fluxes followed the patterns of litter moisture and peaked at the humid first sampling night in Israel, were lower during the second night in Israel and were lowest in Spain (Fig. 5a). During the day, temperature and UV irradiance were similar and high, and RH and litter moisture were low at all Mediterranean sites (Figs. 5b-d). Consequently, fluxes varied less during the day than at night, and at midday were comparable in magnitude at all sites across the Mediterranean transect. A single statistical model with litter water content and UV irradiance explained well all night- and day-time CO_2 fluxes from litter across the transect (R^2 = 0.75, Table S8). Litter moisture was not significantly correlated with fluxes

measured in the shade during day-time (P = 0.98). Additionally, the fluxes measured while litter was exposed to radiation were 3.2 times higher than those measured in shade (Fig. 5a), similar to our findings of the day-time flux ratio between radiation pass and radiation block treatments in Israel.

DISCUSSION [It allows authors to propose their interpretation of the results, and to suggest what they might mean in a wider context. It should end with a clear statement of the main conclusions of the research, and a clear explanation of their importance and relevance.]

Our study shows that microbial degradation as enabled by non-rainwater sources at night and abiotic degradation during the day were responsible for CO_2 fluxes from litter and contributed significantly to litter decomposition under semi-arid conditions. The results from the trans-Mediterranean study indicate that these litter decay drivers operate similarly across a broad geographic range.

Following our expectations, microbial activity during dry rainless periods was evident by the large microbial biomass on all litter types and by the significant correlation between litter moisture and CO_2 fluxes at night, when abiotic decay could be ruled out. In addition the relationship between mass loss and change in litter N pool possibly indicates activity of microorganisms in absorbing or releasing N during decomposition (Parton *et al.* 2007). In the absence of rain, dew and water vapour from the atmosphere proved to be effective facilitators of microbial activity in a range from heavy dew events in Israel to a relatively dry night in Spain [at about 70% RH and 10% litter moisture, which was below the thresholds for activity established in the laboratory (Nagy & Macauley 1982)]. The significantly lower

RH at the soil-litter interface as compared with RH above the litter rules out the soil as a major contributor of water vapour to plant litter. So far, these non-rainwater sources were shown to drive microbial degradation only in moist ecosystems (salt marsh, wetland) (Newell *et al.* 1985; Kuehn *et al.* 2004). Notably, the high sensitivity of microclimate and decomposition to experimental manipulation may explain partly why the humidity driver was overlooked in decomposition studies that applied radiation filters in drylands. Microbial degradation exerted a large impact on litter decay at the site in Israel during the dry season as indicated by the strong positive relationship between decomposition and microbial biomass, and by the large fraction of the total dry-season CO_2 emissions contributed by microbial activity.

At day-time when litter moisture is normally <10%, strong irradiance and high temperatures drive CO_2 emissions as a result of photochemical and thermal degradation of litter in the hot semi-arid regions (Rutledge *et al.* 2010; Lee *et al.* 2012). Photodegradation was the dominant day-time decay mechanism, outnumbering thermal degradation by a factor of 3.2-3.3. This dominance was indicated by i) the positive relationship between CO_2 fluxes and UV irradiance in the Mediterranean transect, and ii) the similar and strong diminishing effect of radiation-blocking on CO_2 fluxes in the manipulation study in Israel and of shading in the Mediterranean transect. Similar ratios between photodegradation and thermal degradation were also found under lab conditions for temperatures comparable to the ones in our study (Lee *et al.* 2012). However, the contribution of photodegradation was insufficient to create a significant difference in mass loss between the two radiation-filtering treatments (pass and block) in Israel. A similar lack of treatment effect has been observed in many other studies with radiation filters in the field (see King *et al.* 2012 and; Song *et al.* 2013). It needs to be noted that additional decay mechanisms can operate in semi-arid ecosystems under dry conditions. For

example, our CO_2 flux calculation predicted only 40% of the decay of *Calicotome* litter. Presumably, additional processes contributed to litter mass-loss, such as consumption of litter by mesofauna and physical fragmentation and abrasion of the fragile *Calicotome* leaf litter (Throop & Archer 2009).

A key finding of this study is the daily bi-directional interaction between the decay mechanisms. We observed facilitation of abiotic degradation at day by microbial degradation at night ('microbial priming') and facilitation of microbial activity at night by photodegradation at day ('photopriming', Barnes *et al.* 2015). Microbial priming was indicated by the higher CO_2 emissions per unit UV irradiance in the control as compared with emissions in the radiation-pass treatment. This difference in CO_2 fluxes was not caused by the minor and inconsistent temperature differences, or day-time microbial degradation, which must be low or absent. Carbon dioxide fluxes in the shade were not related to the uniformly low litter moisture across the Mediterranean transect. We therefore conclude that high microbial degradation rates at night in the control enhances photodegradation at day, possibly by breaking down litter constituents that masked photodegradable compounds, such as lignin (Austin & Ballaré 2010). Photopriming was observed when exposure to solar radiation in the radiation-pass treatment at day resulted in higher rates of CO_2 emissions per unit of litter moisture at night as compared with emissions measured in the radiation-block treatment. In this case, photodegradation might have broken up recalcitrant material, such as lignin, thus allowing access of labile carbon compounds to microorganisms (Day *et al.* 2007; Henry *et al.* 2008; Gallo *et al.* 2009; Austin & Ballaré 2010). This daily bi-directional interaction between decay mechanisms results in enhanced CO_2 emission as compared with emissions that are not affected by microbial and photochemical priming. In addition to facilitation at the daily scale, we also observed seasonal facilitation, as *Avena* litter exposed to ambient microbial degradation

387 and photodegradation rates during the dry season (control treatment) decomposed faster
388 during the wet season than litter affected by radiation screens in the summer. This implies
389 that on an annual scale the effect of dry-season processes on decomposition in the wet
390 season can be as important as mass loss in the dry season itself (Austin & Ballaré 2010).

391 Litter decay occurring during the dry season reached up to 45% of decay in the wet
392 season, and CO_2 fluxes from all decay mechanisms amounted up to 14 g C m^{-2} season. If
393 scaled to semi-arid ecosystems with relatively high productivity, dry-season processes
394 might be of importance for the global carbon cycle. For example, photodegradation rates
395 alone in a Californian grassland were 16 g C m^{-2} $season^{-1}$ (Rutledge *et al.* 2010),
396 Therefore, adding the microbial contribution and the facilitation processes to
397 photodegradation alone can increase dry-season litter CO_2 fluxes substantially.

398 The decay mechanisms driven by moisture as identified in this study, are likely to be
399 relevant for many regions worldwide that have at least short rainless periods and sufficient
400 atmospheric humidity or solar radiation. Microbially driven litter CO_2 fluxes across our
401 Mediterranean transect were similar to those measured on water-saturated and non-
402 saturated litter in salt marsh and wetland ecosystems (Kuehn *et al.* 2004; and references
403 therein). Therefore, we expect microbial degradation driven by non-rainwater sources to
404 be of importance in a broad range of ecosystems between dry and moist regions.
405 Similarly, photodegradation was shown to operate in all continents (Foereid *et al.* 2011).
406 These mechanisms should operate even during short periods without rainfall, as litter dries
407 quickly after a rainfall event. For example, after 3-4 days without rain, litter moisture
408 reached the typical range achieved by dew and RH in semi-arid and temperate
409 ecosystems (Raison *et al.* 1986; Harpole & Haas 1999; Gliksman and Grünzweig, unpub.
410 res.).

Our results show that microbial degradation of litter at night was driven by dew and air humidity, and that this process, together with abiotic degradation during the day, explained most of the litter CO_2 fluxes and decomposition in semi-arid ecosystems across the Mediterranean region during the dry season. The results further imply that night-time microbial facilitation of litter decomposition resulted in greater day-time photodegradation which in turn fed back to stimulate night-time microbial degradation. The contribution of these mechanisms, and especially of microbial degradation driven by non-rainwater sources has been largely overlooked (Dirks *et al.* 2010), leading to a possible overestimation of rain as a water source for decomposition in semi-arid regions (Austin 2011). This information improves our understanding of litter decomposition in semi-arid ecosystems and enhances the knowledge of organic carbon cycling in dryland biomes for better predictions of global carbon-cycle responses to climate change.

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Table 1. Microclimatic variables as affected by radiation-filtering and passive-warming-and-drying treatments in Israel during the dry season. Mean ± s.e., *n* = 104 days for mean daily values.

Treatment	Irradiance[a]	Air temperature (°C)		Relative humidity (%)		Dew duration (h)
	seasonal mean	daily max.	daily min.	daily max.	daily min.	daily mean
Untreated control	1.0	37.4 ± 0.3	20.4 ± 0.2	95.5 ± 0.4	42.9 ± 0.6	4.8[b] / 6.4[c]
Radiation pass & night-time warming and drying	0.86	38.7 ± 0.2	21.7 ± 0.2	90.2 ± 0.6	39.1 ± 0.4	0.0 / n.a.
Radiation block & night-time warming and drying	0.15	36.9 ± 0.3	21.7 ± 0.2	91.1 ± 0.6	43.3 ± 0.8	0.0 / n.a.

[a] Fraction of ambient radiation; [b] Measured by leaf-wetness sensors (n = 87 days); [c] Calculated according to difference between dew point and litter surface-temperature (see Methods); n.a. = not available.

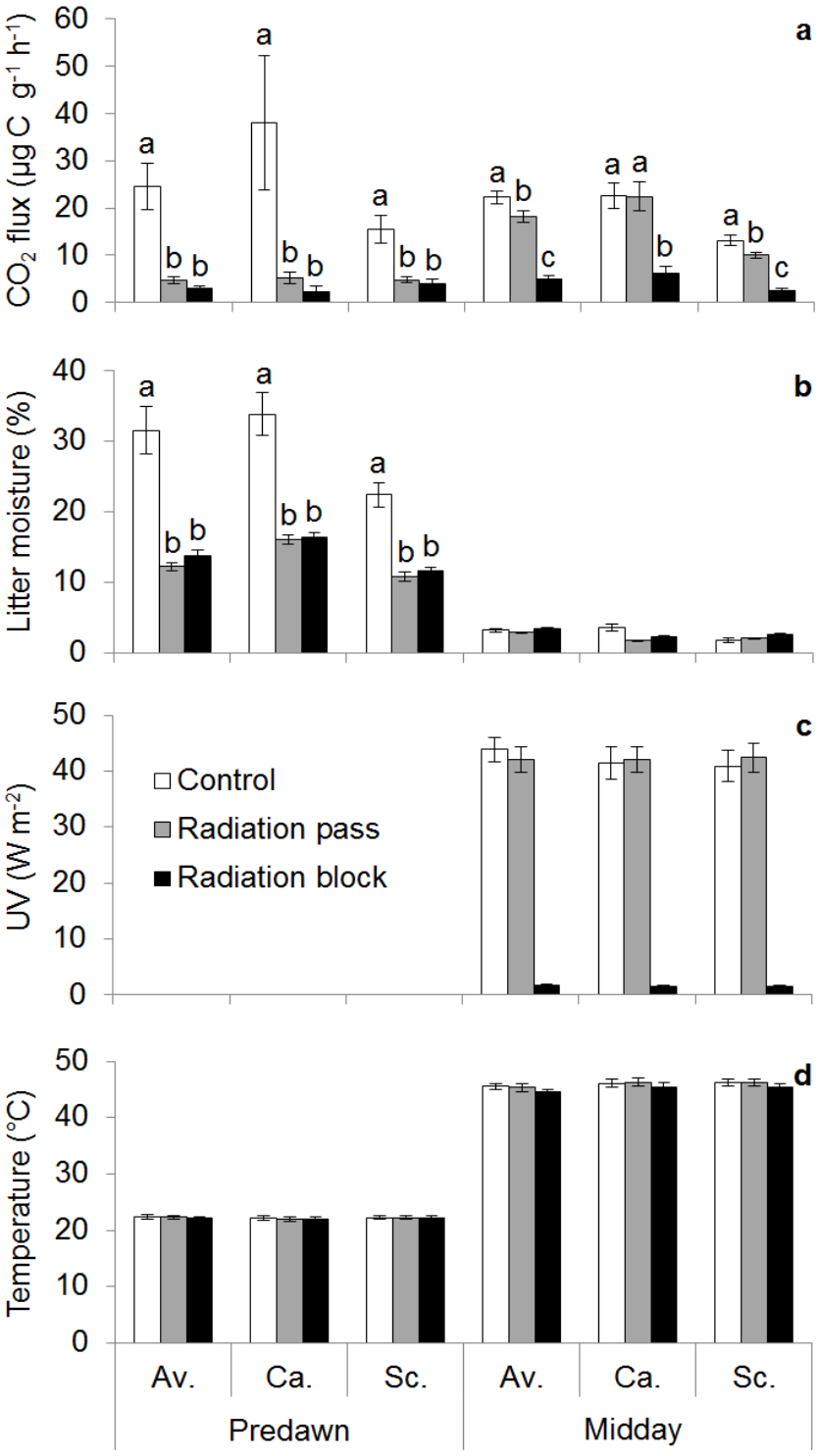

Figure 1. Litter CO_2 flux (a) and water content (dry-mass basis) (b) in three litter types as affected by microclimate manipulation and time of day in Israel. Data were averaged over four sampling days (three for Ca.) in the dry season 2012. Also shown are mean UV irradiance (c) and air temperature (d) as recorded during the flux measurements. Av. – *Avena sterilis*, Ca. – *Calicotome villosa*, Sc. – *Scabiosa prolifera*, Different letters indicate

statistically significant differences within a litter type per time of the day ($P \leq 0.05$, Tukey–Kramer HSD test). Mean ± s.e., n = 11-20 litterbags.

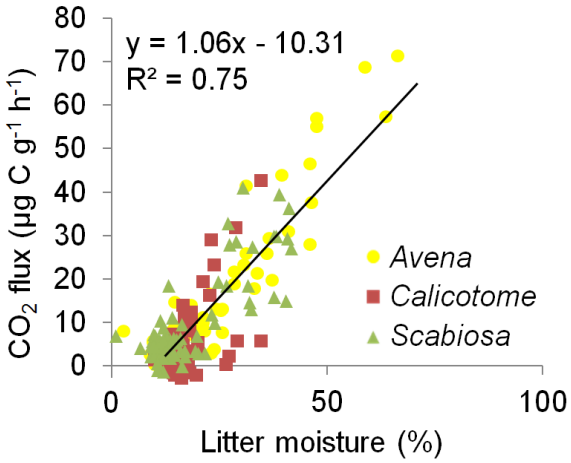

Figure 2. Relationship between night-time litter CO_2 fluxes and litter water content on a dry-mass basis at the study site in Israel. All treatments, litter types and sampling dates (including the early wet-season sampling) were included in the regression analysis, except of the last sampling at the end of the wet season, which occurred during rain. *n* = 184.

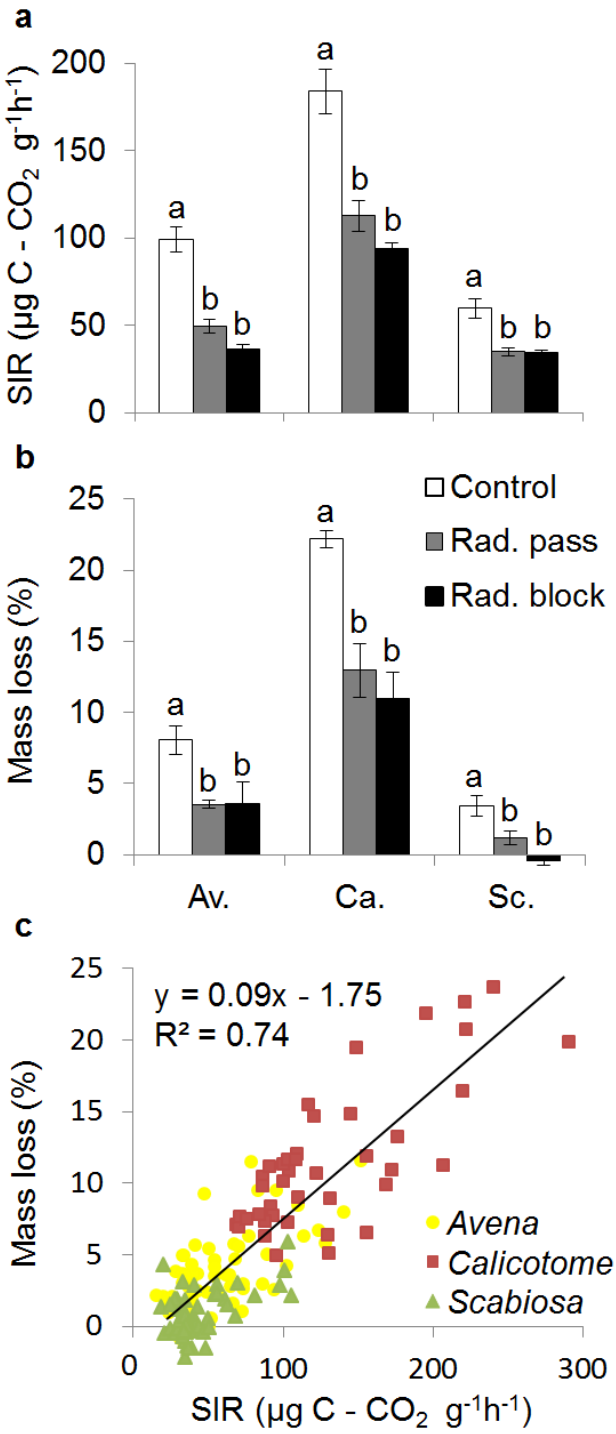

Figure 3. Litter microbial biomass (a), decomposition (b), and their relationship (c) in the microclimate manipulation study in Israel during the dry season. Microbial biomass was expressed as substrate-induced respiration (SIR), averaged over 3-4 sampling dates. Mass loss was recorded at the end of the dry season. Av. – *Avena sterilis*, Ca. – *Calicotome villosa*, Sc. – *Scabiosa prolifera*. Different letters indicate a statistically significant difference between means within a litter type at $P \leq 0.05$ (Tukey–Kramer HSD

test). Mean values ± s.e.; for (a) *n* = 11-20, (b) *n* = 5 replicated plots and (c) *n* = 160 litterbags.

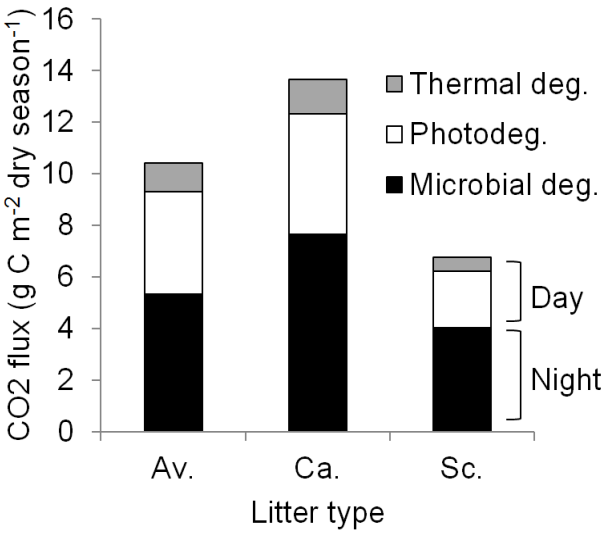

Figure 4. Partitioning of the mechanisms for litter CO_2 fluxes during the entire dry season in Israel under ambient conditions. Night-time CO_2 emissions were calculated from litter moisture and attributed to microbial degradation. Day-time emissions were predicted from a model that included UV irradiance and time, and attributed to abiotic degradation. Day-time CO_2 fluxes were partitioned into photodegradation and thermal degradation according to the ratio of CO_2 fluxes measured under the radiation pass and radiation-block treatments.

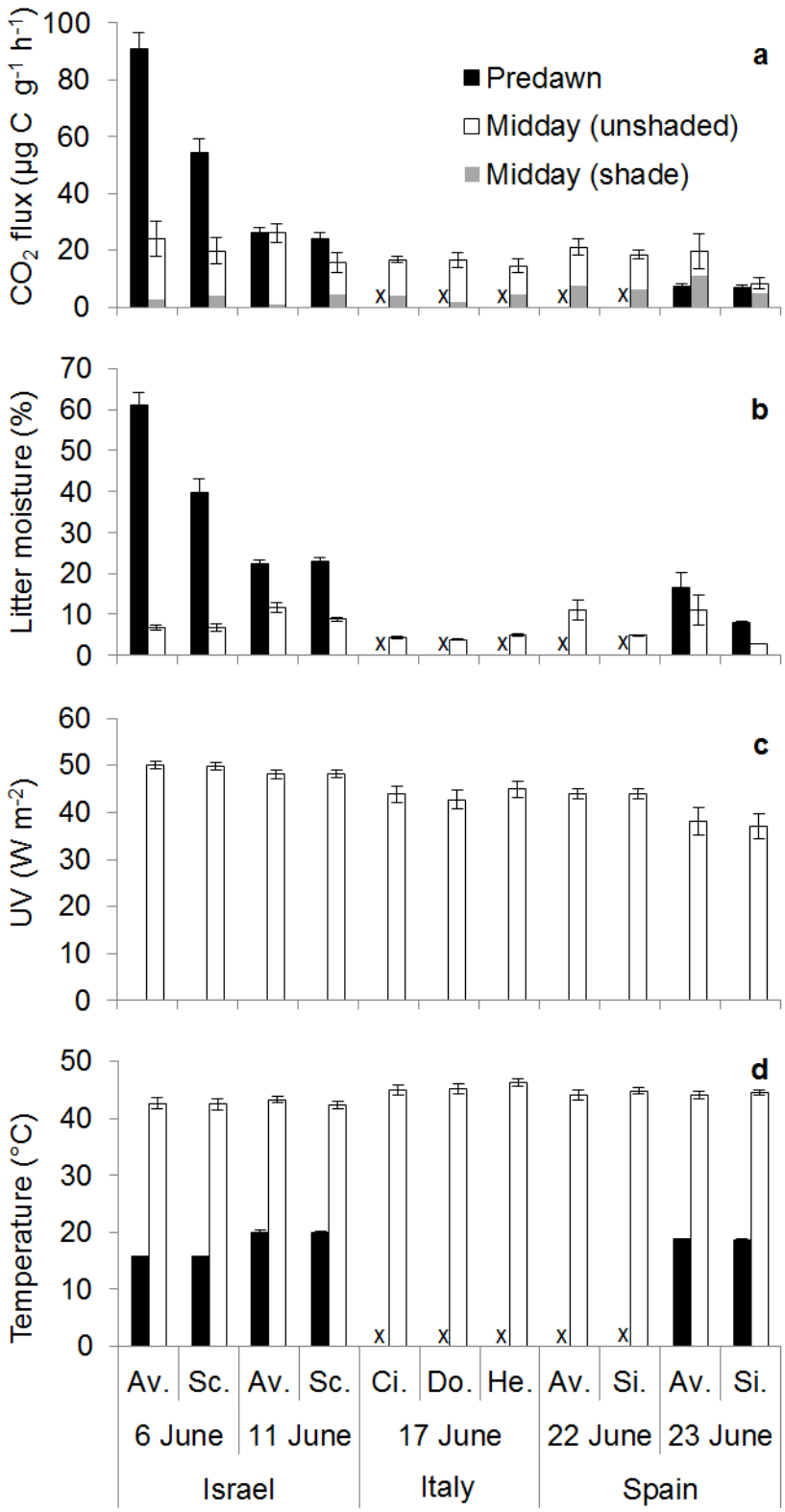

Figure 5. Litter CO_2 flux (a) and water content (dry-mass basis) (b) in various species as affected by time of day along the Mediterranean transect in June 2013. Midday flux

measurements were performed both under full radiation (white bar, starting at zero on the y axis) and when radiation was blocked (“shade”, grey bars). No night-time measurements were performed in Italy (“x”). Also shown are mean UV irradiance (c) and air temperature (d) as recorded during the flux measurements. Temperature measured in the shade was lower by 1°C on average than temperature recorded without shade (ranging +0.1 to -2.8°C; data not shown). Av. – *Avena sterilis*, Sc. – *Scabiosa prolifera*, Ci. – *Cistus monspeliensis*, Do.- *Dorycnium pentaphyllum*, He. – *Helichrysum italicum*, Si. – *Sisymbrium officinale*. Mean ± s.e., *n* = 6-14.